animal sciences

animal sciences

VOLUME 1
A–Crep

Allan B. Cobb, Editor in Chief

MACMILLAN
REFERENCE
USA™

THOMSON
GALE™

New York • Detroit • San Diego • San Francisco • Cleveland • New Haven, Conn. • Waterville, Maine • London • Munich

Macmillan Reference USA
1633 Broadway
New York, NY 10019

The Gale Group
27500 Drake Rd.
Farmington Hills, 48331-3535

Printed in the United States of America
1 2 3 4 5 6 7 8 9 10

Library of Congress Cataloging-in-Publication Data
Animal Sciences / Allan B. Cobb, editor in chief.
p. cm.
Includes bibliographical references and index.
ISBN: 0-02-865556-7 (set) - ISBN 0-02-865557-5 (vol. 1) - ISBN 0-02-865558-3 (vol. 2) - ISBN 0-02-865559-1 (vol. 3) - ISBN 0-02-865560-5 (vol. 4)
1. Animal Culture. 2. Livestock. I. Title.
SF61.C585 2001
590.3-dc21 2001026627
Rev

Preface

Six hundred million years of animal evolution and adaptation have produced a stunning range and variety of life on Earth. From the oldest, single-celled creatures to the most complex mammalian forms, animal diversity defies easy categorization or explanation. The Macmillan *Animal Sciences* encyclopedia provides a clear and comprehensive resource for better understanding this vast domain. By the nature of its interdisciplinary scope, the subject of animal sciences demands an approach that is both specific and general, detailed and thematic. *Animal Sciences* achieves this end in the course of nearly three hundred well-researched, clearly presented entries that explore the wide ranging diversity that exists within the animal kingdom.

Students will learn how animals develop throughout their lives, how they adapt to their changing environments, and how they develop specialized structures over time. Entries in this category explain how animals develop from fertilized eggs to adults. While some forms of development are straightforward—like a puppy maturing to become a dog—other changes are more dramatic—like a caterpillar changing its body forms over the course of its metamorphosis into a butterfly. Other entries study the various forms of animals and how body parts function.

The encyclopedia gives significant attention to animal ecology and behavior. Entries show how animals are part of the world environment while exhibiting unique behaviors within their own particular environments. Animal ecology addresses how animals are a part of ecosystems and how they interact with plants and other animals, both within and beyond their individual species. Given the close relationship of animal behavior and ecology, a number of entries discuss how animals select mates, whether they live alone or as members of groups, or how they share resources within an ecosystem, to give just a few examples.

Finally, *Animal Sciences* surveys the connection between animals and humans. Humans are unique in the animal kingdom because of their ability to alter environments significantly. Agriculture, which includes the domestication of animals and farming, serves as the chief example of such human-inspired environmental change and its impact on animal life worldwide. In addition, humans are the most social of animals and have developed complex social interactions. As human populations grow, habitat once occupied

by other animals is converted to human use. One consequence of such socialization is the pollution generated from an expanding human population and its deleterious effect on animal environments.

Animal Sciences also presents biographies of selected scientists who have made significant contributions to the many related fields, and introduces readers to the myriad career opportunities in the discipline.

The authors who contributed entries to *Animal Sciences* represent diverse backgrounds, and include members of academic and research institutions, as well as practicing scientists. The editorial board sought informative, up-to-date, and engaging articles, most of which include cross references, photographs or illustrations that prove helpful in understanding challenging concepts. A generous collection of sidebars accent related subjects. Every attempt has been made to avoid overly technical terms or scientific jargon, and whenever necessary such terms are highlighted and defined in the margin. Selected bibliographies guide readers to additional up-to-date resources, including those found on the Internet. Each of the four volumes also includes a geologic time scale, with particular emphasis on animals, as well as a phylogenetic tree and an alternative table of contents that groups articles under more general topic headings.

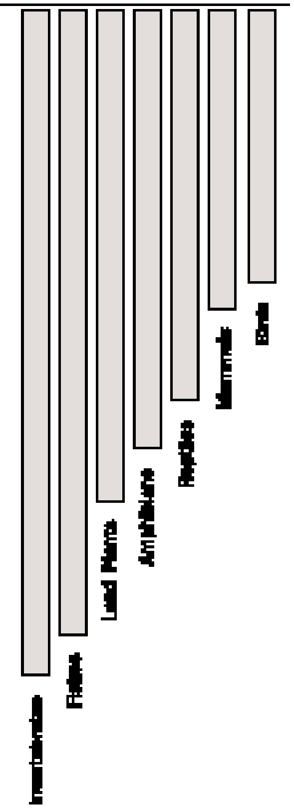
I wish to thank the staff at Macmillan Reference USA and the Gale Group for their hard work and attention to detail. In particular, I would like to thank Hélène Potter, Elly Dickason, Linda Hubbard, and Christa Brelin. I want to offer special thanks to Kate Millson for all her efforts and long hours in helping guide this project to fruition. I wish to thank the editorial board members—Amy Bryan, Andrew Gluesenkamp, and Marvin Elliot Richmond—for their vast knowledge and hard work. Finally, it is my hope that *Animal Sciences* can spark the interest of the next generation of committed scholars, researchers, and laypersons.

Allan B. Cobb
Editor in Chief

Geological Time Scale

Eon	Era	Period	Epoch	Significant Events	Million Years Before Present
Phanerozoic	Cenozoic	Quaternary	Holocene	recorded human history, rise and fall of civilizations, global warming, habitat destruction, pollution mass extinction	0.01
			Pleistocene	Homo sapiens, ice ages	1.6
		Tertiary	Pliocene	global cooling, savannahs, grazing mammals	5.3
			Miocene	global warming, grasslands, Chalicotherium	24
			Oligocene		37
			Eocene	modern mammals flourish, ungulates	58
			Paleocene		66
	Mesozoic	Cretaceous		last of age of dinosaurs, modern mammals appear, flowering plants, insects	144
		Jurassic		large plant-eating dinosaurs, carnivorous dinosaurs, first birds, breakup of Pangea	208
		Triassic		lycophytes, glossopterids, and dicynodonts, and the dinosaurs	245
	Paleozoic	Permian		Permian ends with largest mass extinction in history of Earth, most marine invertebrates extinct	286
		Pennsylvanian		vast coal swamps, evolution of amniote egg allowing exploitation of land	320
		Mississippian		shallow seas cover most of Earth	360
		Devonian		vascular plants, the first tetrapods, wingless insects, arachnids, brachiopods, corals, and ammonite were also common, many new kinds of fish appeared	408
		Silurian		Coral reefs, rapid spread of jawless fish, first freshwater fish, first fish with jaws, first good evidence of life on land, including relatives of spiders and centipedes	438
		Ordovician		most dry land collected into Gondwana, many marine invertebrates, including graptolites, trilobites, brachiopods, and the conodonts (early vertebrates), red and green algae, primitive fish, cephalopods, corals, crinoids, and gastropods, possibly first land plants	505
		Cambrian		most major groups of animals first appear, Cambrian explosion	570
Precambrian	Proterozoic			stable continents first appear, first abundant fossils of living organisms, mostly bacteria and archeobacteria, first eukaryotes, first evidence of oxygen build-up	2500
	Archean			atmosphere of methane, ammonia, rocks and continental plates began to form, oldest fossils consist of bacteria microfossils stromatolites, colonies of photosynthetic bacteria	3800
	Hadean			pre-geologic time, Earth in formation	4600

Time Range of Several Groups of Plants & Animals



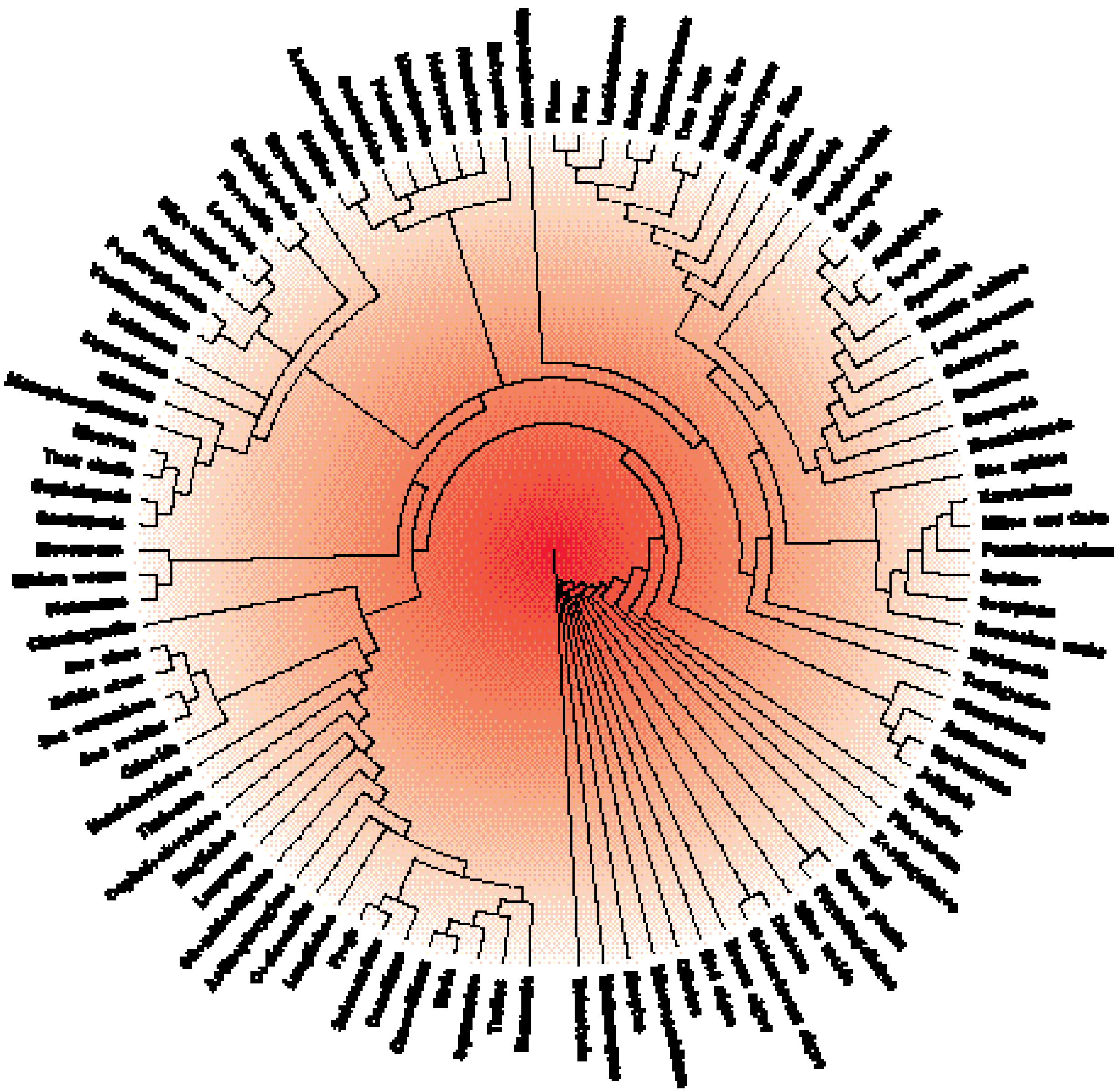
COMPARISON OF THE FIVE-KINGDOM AND SIX-KINGDOM CLASSIFICATION OF ORGANISMS

Five Kingdom	Six Kingdom
Kingdom: Monera Phylum: Bacteria Phylum: Blue-green algae (cyanobacteria)	Kingdom: Archaebacteria Kingdom: Eubacteria

- Kingdom: Protista
  - Phylum: Protozoans
    - Class: Ciliophora
    - Class: Mastigophora
    - Class: Sarcodina
    - Class: Sporozoa
  - Phylum: Euglenas
  - Phylum: Golden algae and diatoms
  - Phylum: Fire or golden brown algae
  - Phylum: Green algae
  - Phylum: Brown algae
  - Phylum: Red algae
  - Phylum: Slime molds
- Kingdom: Fungi
  - Phylum: Zygomycetes
  - Phylum: Ascomycetes
  - Phylum: Basidiomycetes
- Kingdom: Plants
  - Phylum: Mosses and liverworms
  - Phylum: Club mosses
  - Phylum: Horsetails
  - Phylum: Ferns
  - Phylum: Conifers
  - Phylum: Cone-bearing desert plants
  - Phylum: Cycads
  - Phylum: Ginko
  - Phylum: Flowering plants
    - Subphylum: Dicots (two seed leaves)
    - Subphylum: Monocots (single seed leaves)
- Kingdom: Animals
  - Phylum: Porifera
  - Phylum: Cnidaria
  - Phylum: Platyhelminthes
  - Phylum: Nematodes
  - Phylum: Rotifers
  - Phylum: Bryozoa
  - Phylum: Brachiopods
  - Phylum: Phoronida
  - Phylum: Annelids
  - Phylum: Mollusks
    - Class: Chitons
    - Class: Bivalves
    - Class: Scaphopoda
    - Class: Gastropods
    - Class: Cephalopods
  - Phylum: Arthropods
    - Class: Horseshoe crabs
    - Class: Crustaceans
    - Class: Arachnids
    - Class: Insects
    - Class: Millipedes and centipedes
  - Phylum: Echinoderms
  - Phylum: Hemichordata
  - Phylum: Cordates
    - Subphylum: Tunicates
    - Subphylum: Lancelets
    - Subphylum: Vertebrates
      - Class: Agnatha (lampreys)
      - Class: Sharks and rays
      - Class: Bony fishes
      - Class: Amphibians
      - Class: Reptiles
      - Class: Birds
      - Class: Mammals
        - Order: Monotremes
        - Order: Marsupials
        - Subclass: Placentals
          - Order: Insectivores
          - Order: Flying lemurs
          - Order: Bats
          - Order: Primates (including humans)
          - Order: Edentates
          - Order: Pangolins
          - Order: Lagomorphs
          - Order: Rodents
          - Order: Cetaceans
          - Order: Carnivores
          - Order: Seals and walruses
          - Order: Aardvark
          - Order: Elephants
          - Order: Hyraxes
          - Order: Sirenians
          - Order: Odd-toed ungulates
          - Order: Even-toed ungulates

PHYLOGENETIC TREE OF LIFE

This diagram represents the phylogenetic relationship of living organisms, and is sometimes called a "tree of life." Often, these diagrams are drawn as a traditional "tree" with "branches" that represent significant changes in the development of a line of organisms. This phylogenetic tree, however, is arranged in a circle to conserve space. The center of the circle represents the earliest form of life. The fewer the branches between the organism's name and the center of the diagram indicate that it is a "lower" or "simpler" organism. Likewise, an organism with more branches between its name and the center of the diagram indicates a "higher" or "more complex" organism. All of the organism names are written on the outside of the circle to reinforce the idea that all organisms are highly evolved forms of life.



SI BASE AND SUPPLEMENTARY UNIT NAMES AND SYMBOLS

Physical Quality	Name	Symbol
Length	meter	m
Mass	kilogram	kg
Time	second	s
Electric current	ampere	A
Thermodynamic temperature	kelvin	K
Amount of substance	mole	mol
Luminous intensity	candela	cd
Plane angle	radian	rad
Solid angle	steradian	sr

Temperature

Scientists commonly use the Celsius system. Although not recommended for scientific and technical use, earth scientists also use the familiar Fahrenheit temperature scale (°F). 1°F = 1.8°C or K. The triple point of H_2O, where gas, liquid, and solid water coexist, is 32°F.

- To change from Fahrenheit (F) to Celsius (C):
  °C = (°F-32)/(1.8)
- To change from Celsius (C) to Fahrenheit (F):
  °F = (°C x 1.8) + 32
- To change from Celsius (C) to Kelvin (K):
  K = °C + 273.15
- To change from Fahrenheit (F) to Kelvin (K):
  K = (°F-32)/(1.8) + 273.15

UNITS DERIVED FROM SI, WITH SPECIAL NAMES AND SYMBOLS

Derived Quantity	Name of SI Unit	Symbol for SI Unit	Expression in Terms of SI Base Units
Frequency	hertz	Hz	s-1
Force	newton	N	m kg s-2
Pressure, stress	Pascal	Pa	N m-2 =m-1 kg s-2
Energy, work, heat	Joule	J	N m =m2 kg s-2
Power, radiant flux	watt	W	J s-1 =m2 kg s-3
Electric charge	coulomb	C	A s
Electric potential, electromotive force	volt	V	J C-1 =m-2 kg s-3 A-1
Electric resistance	ohm	_	V A-1 =m2 kg s-3 A-2
Celsius temperature	degree Celsius	C	K
Luminous flux	lumen	lm	cd sr
Illuminance	lux	lx	cd sr m-2

UNITS USED WITH SI, WITH NAME, SYMBOL, AND VALUES IN SI UNITS

The following units, not part of the SI, will continue to be used in appropriate contexts (e.g., angtsrom):

Physical Quantity	Name of Unit	Symbol for Unit	Value in SI Units
Time	minute	min	60 s
	hour	h	3,600 s
	day	d	86,400 s
Plane angle	degree	°	(π/180) rad
	minute	'	(π/10,800) rad
	second	"	(π/648,000) rad
Length	angstrom	Å	10^{-10} m
Volume	liter	l, L	1 dm^3 = 10^{-3} m^3
Mass	ton	t	1 mg = 10^3 kg
	unified atomic mass unit	u (=m_a(^{12}C)/12)	≈1.66054 x 10^{-27} kg
Pressure	bar	bar	10^5 Pa = 10^5 N m^{-2}
Energy	electronvolt	eV (= e X V)	≈1.60218 x 10^{-19} J

CONVERSIONS FOR STANDARD, DERIVED, AND CUSTOMARY MEASUREMENTS

Length

1 angstrom (Å)	0.1 nanometer (exactly) 0.000000004 inch
1 centimeter (cm)	0.3937 inches
1 foot (ft)	0.3048 meter (exactly)
1 inch (in)	2.54 centimeters (exactly)
1 kilometer (km)	0.621 mile
1 meter (m)	39.37 inches 1.094 yards
1 mile (mi)	5,280 feet (exactly) 1.609 kilometers
1 astronomical unit (AU)	1.495979 x 10^{13} cm
1 parsec (pc)	206,264.806 AU 3.085678 x 10^{18} cm 3.261633 lightyears
1 light-year	9.460530 x 10^{17} cm

Area

1 acre	43,560 square feet (exactly) 0.405 hectare
1 hectare	2.471 acres
1 square centimeter (cm^2)	0.155 square inch
1 square foot (ft^2)	929.030 square centimeters
1 square inch (in^2)	6.4516 square centimeters (exactly)
1 square kilometer (km^2)	247.104 acres 0.386 square mile
1 square meter (m^2)	1.196 square yards 10.764 square feet
1 square mile (mi^2)	258.999 hectares

MEASUREMENTS AND ABBREVIATIONS

Volume

1 barrel (bbl)*, liquid	31 to 42 gallons
1 cubic centimeter (cm^3)	0.061 cubic inch
1 cubic foot (ft^3)	7.481 gallons 28.316 cubic decimeters
1 cubic inch (in^3)	0.554 fluid ounce
1 dram, fluid (or liquid)	⅛ fluid ounce (exactly) 0.226 cubic inch 3.697 milliliters
1 gallon (gal) (U.S.)	231 cubic inches (exactly) 3.785 liters 128 U.S. fluid ounces (exactly)
1 gallon (gal) (British imperial)	277.42 cubic inches 1.201 U.S. gallons 4.546 liters
1 liter	1 cubic decimeter (exactly) 1.057 liquid quarts 0.908 dry quart 61.025 cubic inches
1 ounce, fluid (or liquid)	1.805 cubic inches 29.573 milliliters
1 ounce, fluid (fl oz) (British)	0.961 U.S. fluid ounce 1.734 cubic inches 28.412 milliliters
1 quart (qt), dry (U.S.)	67.201 cubic inches 1.101 liters
1 quart (qt), liquid (U.S.)	57.75 cubic inches (exactly) 0.946 liter

* There are a variety of "barrels" established by law or usage. For example, U.S. federal taxes on fermented liquors are based on a barrel of 31 gallons (141 liters); many state laws fix the "barrel for liquids" as 31½ gallons (119.2 liters); one state fixes a 36-gallon (160.5 liters) barrel for cistern measurement; federal law recognizes a 40-gallon (178 liters) barrel for "proof spirits"; by custom, 42 gallons (159 liters) comprise a barrel of crude oil or petroleum products for statistical purposes, and this equivalent is recognized "for liquids" by four states.

Units of mass

1 carat (ct)	200 milligrams (exactly) 3.086 grains
1 grain	64.79891 milligrams (exactly)
1 gram (g)	15.432 grains 0.035 ounce
1 kilogram (kg)	2.205 pounds
1 microgram (μg)	0.000001 gram (exactly)
1 milligram (mg)	0.015 grain
1 ounce (oz)	437.5 grains (exactly) 28.350 grams
1 pound (lb)	7,000 grains (exactly) 453.59237 grams (exactly)
1 ton, gross or long	2,240 pounds (exactly) 1.12 net tons (exactly) 1.016 metric tons
1 ton, metric (t)	2,204.623 pounds 0.984 gross ton 1.102 net tons
1 ton, net or short	2,000 pounds (exactly) 0.893 gross ton 0.907 metric ton

Pressure

1 kilogram/square centimeter (kg/cm^2)	0.96784 atmosphere (atm) 14.22334 pounds/square inch (lb/in^2) 0.98067 bar
1 bar	0.98692 atmosphere (atm) 1.02 kilograms/square centimeter (kg/cm^2)

Contributors

Allan B. Cobb
Austin, Texas
Jes Marie Creech
University of Texas, Austin
Emily H. DuVal
University of California, Berkeley
Andrew G. Gluesenkamp
University of Texas, Austin
Ann Guidry
Austin, Texas
Brook Ellen Hall
California State University, Sacramento
Laura A. Higgins
University of Texas, Austin
Ryan I. Hill
University of Texas, Austin
Alisha K. Holloway
University of Texas, Austin
Leslie Hutchinson
Flagstaff, Arizona
Jean Krejca
University of Texas, Austin
Stephanie A. Lanoue
Panama City Beach, Florida
Denise Prendergast
Austin, Texas
Ian Quigley
University of Texas, Austin
Elliot Richmond
Austin Community College
Karen Rogowski
University of Texas, Austin
Gil G. Rosenthal
University of California, San Diego
Todd A. Schlenke
University of Texas, Austin
Danielle Schnur
Austin, Texas
Judy P. Sheen
University of California, Berkeley
Kathrin F. Stanger-Hall
University of Texas, Austin
Rebecca M. Steinberg
University of Texas, Austin
Nancy Weaver
Driftwood, Texas
Brian R. West
University of Texas, Austin
Jennifer Yeh
University of Texas, Austin

Table of Contents

VOLUME TWO:

VOLUME THREE:

Absorption

A

The process by which substances are taken into the tissues of organisms is called absorption. It is essential to functions such as digestion, circulation, and respiration.

During digestion, valuable nutrients are absorbed across the **epithelial lining** of the digestive tract. Absorption occurs largely in the small intestine, which has developed a large surface area for this purpose. The walls of the small intestine contain numerous finger-like projections called villi, which are in turn covered by countless microvilli. Different nutrients are absorbed across the gut epithelium in different ways.

The methods of absorption include **active transport**, **facilitated diffusion**, and **passive diffusion**. Active transport requires energy in the form of **adenosine triphosphate** (**ATP**), as well as special carrier molecules that ferry nutrients, (their substrates), across the gut lining. Active transport is involved in the absorption of proteins, which have usually been processed into amino acids or other small peptides. Most ions are also absorbed through active transport, as are most carbohydrates.

Some carbohydrates, however, are absorbed in a process known as facilitated diffusion. Facilitated diffusion describes a situation in which special carrier molecules are necessary, but energy (ATP) is not. Fructose is an example of a carbohydrate that is absorbed through facilitated diffusion.

Other nutrients, such as **lipids**, are absorbed through passive diffusion. In passive diffusion, neither energy expenditure nor a special carrier molecule is required. Lipids interact with bile salts from the liver, combining with them to form structures known as micelles. Micelles are able to diffuse freely through cell membranes and so can pass directly across the gut lining. Water is another substance that diffuses passively across the gut walls.

The circulatory system transfers nutrients and other products throughout the body. Tissues absorb the products they need from tiny blood vessels called capillaries. Capillaries are characterized by very high surface areas and very low blood-flow rates, both of which facilitate absorption. The walls of capillaries are also very thin, consisting of only one or a few layers of flattened endothelial cells. Capillaries also possess small pores through which transport and absorption can occur.

epithelial lining sheets of tightly packed cells that cover organs and body cavities

active transport a process requiring energy where materials are moved from an area of lower concentration to an area of higher concentration

facilitated diffusion the spontaneous passing of molecules attached to a carrier protein across a membrane

passive diffusion the passing of molecules across a membrane from an area of higher concentration to an area of lower concentration without any energy input

adenosine triphosphate (ATP) an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

lipids fats and oils; organic compounds that are insoluble in water

The absorption of materials from the capillaries occurs in one of several ways. Lipid-soluble substances are able to diffuse directly across the cell membranes of capillary cells into the tissues. Water diffuses directly as well, although it makes use of special pores in the cell membranes of capillary cells. Exchange via diffusion is comparatively rapid.

The absorption of other nutrients from the blood requires transportation through the capillary walls inside special vesicles. This process is called transcytosis. The vesicles are membrane-bound and are believed to be constructed by a cellular organelle known as the Golgi apparatus. Vesicles shuttle products repeatedly between the inner and outer walls of capillary cells. Because capillary beds in the brain are characterized by fewer transport vesicles, many substances cannot be absorbed into brain tissue, and the absorption of those that can be is slowed. This is often referred to as the blood-brain barrier.

integument a natural outer covering

lungs sac-like, spongy organs where gas exchange takes place

gills site of gas exchange between the blood of aquatic animals such as fish and the water

trachea the tube in air-breathing vertebrates that extends from the larynx to the bronchi

erythrocytes red blood cells, containing hemoglobin that carry oxygen through the body

respiratory pigments any of the various proteins that carry oxygen

hemoglobin an iron-containing protein found in red blood cells that binds with oxygen

In the process of respiration, oxygen is absorbed by the **integument**, **lungs**, **gills**, or **trachea** from the air or water. As with the circulatory and digestive systems, large respiratory surface areas allow for efficient absorption.

Oxygen is absorbed from the environment by the red blood cells, or **erythrocytes**. Erythrocytes contain **respiratory pigments**, which bind oxygen and works to transport it to tissues. These specialized oxygen-binding molecules are called pigments because they are often brightly colored when carrying bound oxygen. Respiratory pigments have a high affinity for oxygen and are also able to dramatically increase the oxygen-carrying capacity of blood.

Hemoglobin is the respiratory pigment in vertebrate erythrocytes and is also common throughout the animal kingdom. Hemoglobin is a large molecule consisting of four polypeptide chains, each of which is capable of binding an oxygen molecule. The oxygen-binding part of the chain is called the heme group and includes an iron atom. Hemoglobin binds oxygen cooperatively, meaning that once it has bound a single oxygen molecule, it is more likely to bind additional oxygen molecules. Hemoglobin's oxygen affinity, or the degree to which oxygen binds to it, varies according to such external factors as pH. This plasticity (flexibility) of oxygen affinity allows hemoglobin simultaneously to bind oxygen in the oxygen-rich environment of the lungs and to release it in the oxygen-poor environments of the tissues.

Another respiratory pigment, myoglobin, is present in the muscles and is responsible for pulling oxygen molecules from the blood into the tissues. Myoglobin resembles hemoglobin but consists of only a single polypeptide chain. SEE ALSO DIGESTION; TRANSPORT.

Jennifer Yeh

Bibliography

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Withers, Philip C. *Comparative Animal Physiology*. Fort Worth, TX: Saunders College Publishing, 1992.

Acoustic Signals

Acoustic signals are noises that animals produce in response to a specific stimulus or situation, and that have a specific meaning. These may be vocal communications emitted from the animal's larynx, such as a wolf's howl; sounds produced by appendages, such as a cricket's chirp; or sounds created by an animal's interaction with its environment, such as a rabbit thumping the ground with its hind foot when it sights danger. The **physiological** characteristics of animals, such as throat shape or lung size, create constraints on the type of acoustic signals an animal produces. Similarly, the anatomical properties of the ear, and the processing capabilities of the auditory regions of the brain, can limit the range of sound that a species is capable of detecting. Compared with most mammals, humans have an abnormally complex system of **vocalization** that is supported by the expanded language centers of the brain, a dexterous tongue and throat, and powerful lungs. However, humans are unable to hear in the frequency range of animals that communicate at much higher pitches, such as voles, or animals that vocalize with lower pitches, such as certain species of whale.

physiological the basic activities that occur in the cells and tissues of an animal

vocalization the sounds used for communications

Signal Characteristics

Several features combine to create a meaningful auditory signal. The first of these is the frequency, or pitch, of a sound. Another variable is the amplitude, or loudness. Different combinations of these two features can drastically alter the meaning of a sound. For example, a dog that whines quietly is communicating pain with a high-frequency, low-amplitude sound; a dog that growls loudly is expressing anger with a low-frequency, high-amplitude sound. The repetition rate and duration of a particular sound are likewise important. Male frogs of certain species, such as the plains leopard frog, call during breeding season to attract females; females recognize the calls of their own species by the length of the call and its repetition rate (calls per minute). Other species of frog in the vicinity use the same frequency call but vary its length and repetition rate.

The circumstances that surround acoustic signals can also alter their meaning. These include the time of year, time of day, spatial location, weather conditions, and physiological state of the organism (such as reproductive state). A mating call presented to females outside of the mating season may have no effect—the females are not hormonally prepared to respond.

The Uses of Acoustic Signals

Animals use acoustic signals in several instances: conspecific communication, **sexual selection**, mother-young interactions, interspecies communication, orientation, and language.

sexual selection selection based on secondary sex characteristics that leads to greater sexual dimorphism or differences between the sexes

Conspecific communication. This (intraspecies communication) occurs between animals of the same species. Although sexual selection, mother-young interactions, and language are included in the category of conspecific communication, they will be explained separately because of their ecological importance. Conspecific communication can be very complex. For example, black-tailed prairie dogs live in very structured colonies that can cover tens of acres. When a prairie dog recognizes danger, it gives a warning call to

A common tree frog calling. In some species, the male uses his call to attract females during the breeding season.

the rest of the colony. Their vocal abilities are so elaborate that these animals can communicate the size, shape, and behavior of a predator by varying the features of their call. For example, a prairie dog call signifying a running coyote would be different from one signifying a gliding eagle. Intraspecies communication can relate danger, sexual selection, state-of-being, or features of the environment. A fairly universal form of intraspecies communication is the call made by a sick or dying individual. This kind of acoustic signal refers to the animal's state-of-being.

Sexual selection. This is the process by which species evolve characteristics that improve the chances of successful reproduction. Two facets of sexual selection involve acoustic signaling: locating and recognizing a mate, and defending territory. Acoustic signaling can improve the likelihood that an animal will find a mate of its own species over large distances or in the darkness. Sound, which travels at a rate of 340 meters (372 yards) per second in air and 1,230 meters (1345 yards) per second in water, provides an excellent means for quick signal transmission. An animal's reproductive success—the number and health of its offspring—may be seriously compromised if it cannot locate a mate of the same species. As a result of this selective pressure, many species have come to rely upon intricate calls to locate one another.

Territoriality. Another reproductive strategy is a behavior known as territoriality, in which males guard a particular location from other males of their species. Territorial male songbirds, such as nightingale wrens, each have a unique song. They mark their territory by repeating their trademark song at the boundaries of their territory or at the nest. This warns other males away from the chosen female and the chosen tract of land, thereby increasing mating success for that male and assuring a food supply for the young. This strategy is so successful that it can be seen in such diverse animals as the midshipman fish. Males of this species growl, hum, and grunt to attract females to their nests. However, the importance of acoustic signaling to sexual selection varies widely across species.

Mother-young communication. This exists between many vertebrate mothers and their offspring. In some species, including several groups of primates, the mother is able to recognize the distinct vocalizations of her young. Baby bird vocalizations cannot distinguish one hatchling from another, yet a mother bird responds equally to the call of any hatchling of the same age as her own young. In species where the parents invest time and energy into raising their young, it is of the utmost importance for the mother to be able to recognize the acoustic signals of her young. If she cannot distinguish her young from the young of others, she will waste precious time and resources on other individuals while neglecting her offspring. The cuckoo bird takes advantage of this fact by laying its eggs in the nests of other species. The infant cuckoo bird hatches among the young from the other species, but then it pushes the legitimate chicks or unhatched eggs out of the nest. When the mother bird finds her young have disappeared, the infant cuckoo is given all the nourishment, and the mother bird's energy is wasted on an individual that will not carry on her **genes**. Usually the hypersensitivity of a mother to the call of her young diminishes as her offspring mature.

genes segments of DNA located on chromosomes that direct protein production

Interspecies communication. This occurs when the hallmark acoustic signal of one species is conveyed to another species and induces that species to react in a predictable manner. A common example of interspecies acoustic signaling is when a rattlesnake shakes its rattle-shaped tail tip before striking. In this case, the snake is warning offending animals of its presence and its impending strike. This type of acoustic signal is most often a warning, as in the case of the mother bear growling when an animal approaches her cubs too closely. Conversely, an unintentional form of interspecies communication occurs when a predator can track the acoustic emissions of its prey. Woodpeckers listen for the sounds of insects chewing through wood so that they know where to peck, and owls can hear the squeaking of mice in the darkness.

Orientation. Some animals use auditory signals as their primary means of orientation. These animals emit sounds and then listen for the echoes that rebound off objects in the environment. The arrival time of the echo, its amplitude, and its divergence from the original call all give clues about the animal's environment. The best-known example of this strategy is echolocation in New World bats of the suborder **Microchiroptera**. The echoes from their calls are such good indicators of the environment that bats are able to fly through complicated environments in complete darkness, even when they are blinded. They also use their high-frequency echolocation to forage for fruit or flowers and to capture prey such as insects, fish, and small animals.

Microchiroptera small bats that use echolocation

Language. Humans use auditory signals to communicate with each other through language. No other animal is considered to have a system of communication complex enough to be considered language. Language differs from other kinds of communication in four features: flexibility, form, abstraction, and essentiality. Humans do not learn how to speak by memorization, but rather by **learning** rules for forming meaningful speech. The flexibility of language assures that despite the infinite number of experiences that influence the way people speak, they can be readily understood. Rules of sound, word, and sentence combination comprise the framework for the form of language. People express emotional and philosophical abstractions when they speak, not just the physical necessities of life. Essentiality refers to the reliance of human society on the use of language. Language is not

learning modifications to behavior motivated by experience

just a tool—it shapes thinking and speech patterns and constitutes an integral part of one's sense of identity. Aside from language, humans also communicate with sounds such as laughter, screaming, and applause.

terrestrial living on land

invertebrates animals without a backbone

physiology the study of the normal function of living things or their parts

niche how an organism uses the biotic and abiotic resources of its environment

sonar the bouncing of sound off distant objects as a method of navigation or finding food

The acoustic signals of marine and **terrestrial invertebrates** and vertebrates depend on the **physiology**, social structure, and ecological **niche** of the organism. They are so important that the success of a species may depend entirely on acoustic signals, whether for feeding, mating, or interacting with one another. Humans inhabit every environment on Earth, and it is possible that the noise of modern human civilization is interfering with the acoustic signals of other species. A dramatic example of this is the beaching of seven whales in the Bahamas near the site of a naval **sonar** research site in February 2001. All of the whales showed signs of inner ear damage, and scientists hypothesized that the high amplitude noises used at the research site deafened them, causing pain and confusion. Further research into the acoustic signals used by animals could help prevent such ecological disasters. SEE ALSO Communication; Vocalization.

Rebecca M. Steinberg

Bibliography

Hoogland, John L. *The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal*. Chicago: University of Chicago Press, 1995.

Kalman, Bobbie, and Heather Levigne. *What Is a Bat?* New York: Crabtree, 1999.

Knight, Chris, Michael Studdert-Kennedy, James R. Hurford, and James Raymond. *The Evolutionary Emergence of Language: Social Function and the Origins of Linguistic Form*. Cambridge, U. K.: Cambridge University Press, 2000.

Kroodsma, Dolad E., and Edward H. Miller. *Acoustic Communication in Birds*. New York: Academic Press, 1982.

Snowdon, Charles T., and Martine Hausberger. *Social Influences on Vocal Development*. New York: Cambridge University Press, 1997.

Stebbins, William C. *The Acoustic Sense of Animals*. Cambridge, MA: Harvard University Press, 1983.

Truax, Barry. *Acoustic Communication*. Westport, CT: Ablex, 2001.

Whitlow, W. L., Arthur N. Popper, and Richard R. Fay. *Hearing by Whales and Dolphins*. New York: Springer, 2000.

Active Transport *See Transport.*

morphological the structure and form of an organism at any stage in its life history

physiological relating to the basic activities that occur in the cells and tissues of an animal

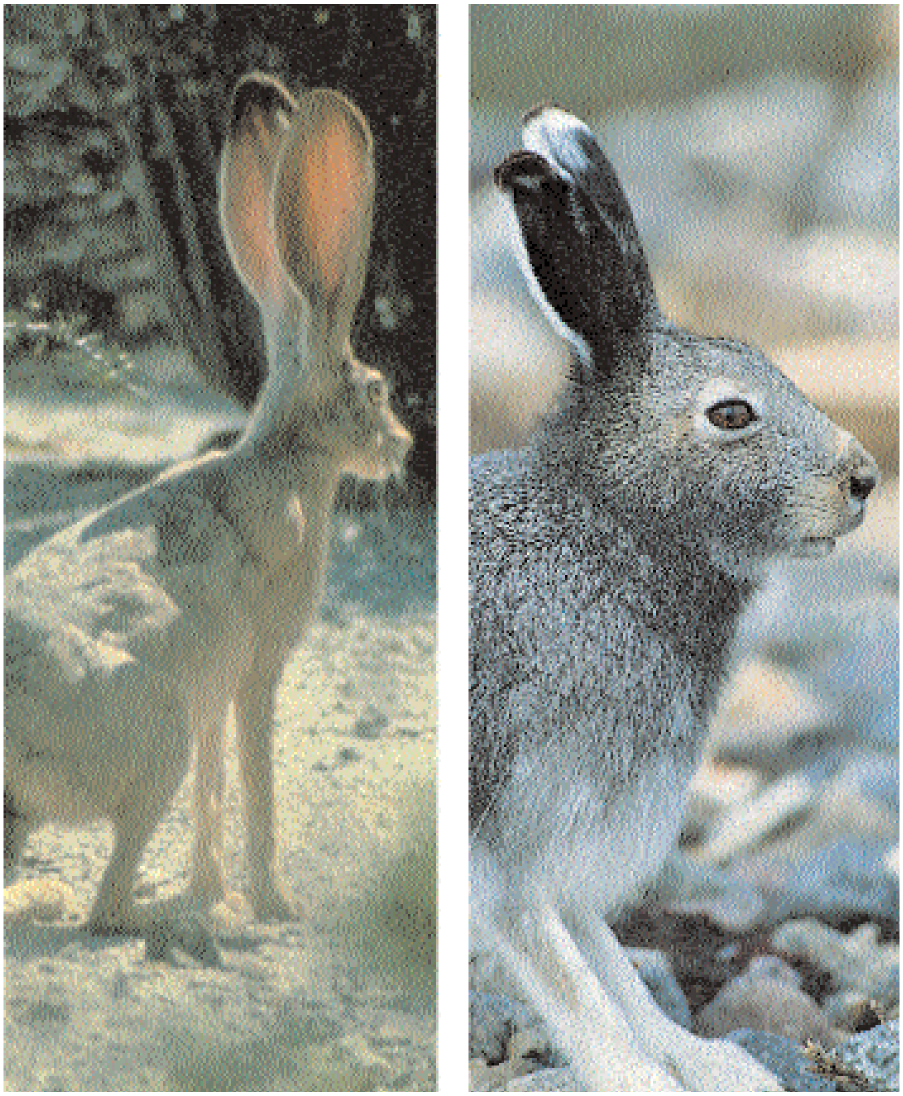
behavioral relating to actions or a series of actions as a response to stimuli

morphological adaptation an adaptation in form and function for specific conditions

Adaptation

Adaptations are the most important features of all organisms. An adaptation is a trait or characteristic that makes an animal survive or reproduce better in its environment. These traits can be **morphological**, **physiological**, or **behavioral**. Adaptations include almost all kinds of traits, such as what makes an organism blend into its surroundings, find food, mate with the correct species, and be able to survive.

An example of a **morphological adaptation** that increases the chance of survival is the coloration of an animal. Most animals that live in the arctic snow are white. Being white helps them blend in with the snow and hide from predators. An example of a physiological adaptation that increases the likelihood of survival is the kangaroo rat's metabolism. Kangaroo rats live



The different fur colors of the rural jackrabbit (left) and the arctic hare (right) allow them to blend into their environments, which helps them to evade predators, therefore increasing their chance of survival.

in the desert of the North American Southwest. It is extremely hot and dry there, and very little water is available. The kangaroo rat never needs to drink water because its metabolism has changed and adapted to conserve water; it gets all the water it needs from seeds it eats. Humans are the opposite; we must drink water daily because our metabolism uses lots of water. An example of a behavioral adaptation that increases reproduction is the croaking and calling of male frogs, which gets female frogs to come to the males for mating. Those frogs that call end up mating with more females and have more offspring than frogs that do not call.

Natural selection is the mechanism that produces adaptations. It is the difference in survival or reproduction between individuals with different traits. If an arctic hare, which lives in the snow, were gray rather than solid white, it would not survive as well as pure white hares. And if it does not live very long before it is killed by a predator such as a fox, then it will not produce as many offspring as a pure white hare, either. Natural selection increases the number of individuals in a **population** that actually has the adaptation; natural selection also maintains adaptations once animals have them.

natural selection the process by which organisms best suited to their environment are most likely to survive and reproduce

population a group of individuals of one species that live in the same geographic area

All traits that are adaptations must have a genetic basis to them. That is to say, the trait must be produced in some way by **genes**, coded for by DNA. Genes enable an animal to pass on to its offspring the survival or reproductive advantage given by the adaptation.

genes segments of DNA located on chromosomes that direct protein production

There is one exception to the rule that adaptations need a genetic basis—traits that are learned within an organism's lifetime. Something that is learned does not have a genetic basis; it was not inherited from the parents. An example of a learned adaptation is that some male songbirds learn the songs of their neighbors. Neighborhoods of birds sing similar songs, and females prefer males that know more songs. A male that has learned more songs will reproduce more; **learning** songs is an adaptation. But learned traits are not completely free from genetics; there is a genetic basis to the ability to learn, even if the actual learning does not have a genetic basis. SEE ALSO Biological Evolution; Morphological Evolution in Whales; Morphology; Natural Selection.

learning modifications to behavior motivated by experience

Laura A. Higgins

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Rose, Michael R., and George V. Lauder, eds. *Adaptation.* San Francisco, CA: Academic Press, 1996.

African Cichlid Fishes

The African cichlid fishes are well-known in the field of evolutionary biology as perhaps the most spectacular example of an **adaptive radiation**. An adaptive radiation describes a group of species that have rapidly diverged, or speciated, from a single ancestor, each of which occupies and is adapted to a distinct ecological niche. Other well-known adaptive radiations include those of two birds, the honeycreepers of Hawaii and Charles Darwin's finches, which occupy several islands in the Galapagos.

adaptive radiation a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

The African cichlids are found in the Great Lakes of the Rift Valley of Africa, including Lakes Victoria, Malawi, Tanganyika, Nabugabo, and others. In these lakes, cichlid fishes have undergone an unparalleled radiation. In all, over 1,500 species have evolved over the course of only ten million years, suggesting a truly remarkable rate of speciation.

Four separate genera and over 200 species occur in Lake Victoria alone. This is particularly impressive given that Lake Victoria is less than one million years old, having made a comparatively recent geological transition from flowing river to lake. When the Lake Victorian cichlids were initially discovered, the remarkably diverse species was initially confusing to biologists because the lake appeared to provide little opportunity for the ecological isolation of **populations**. Isolation is one of the factors generally believed to promote speciation.

populations groups of individuals of one species that live in the same geographic area

The Reasons for Their Success

Why, then, have cichlid fishes been so successful in their African lake **habitats**? One reason is that the lakes provided a novel, underexploited habitat

habitats physical locations where organisms live in an ecosystem with few competing species. However, this cannot be the entire answer because several other species had the same opportunity to diversify in the new habitat soon after it formed. Why, among all the species present, was it the cichlids who underwent a remarkable radiation?

Feeding habits. The diversity of feeding habits is at the heart of the African cichlid radiation. The ancestral cichlid species was likely a generalist and an insect eater. However, extreme specialization now exists among the cichlid species, with each species specializing on a distinct, fairly narrow food niche.

There are, for example, cichlid species that specialize on algae, **plankton**, other fish species, mollusks, and insects, and there are even some species that eat only fish scales, or even fish eyes. This way of dividing up the available resources in a habitat is called trophic specialization ("trophic" refers to feeding). Because increased specialization allows for the coexistence of larger number of species, trophic specialization in cichlids is partly responsible for the great diversity of species.

Morphological specialization. In addition to using different food resources, the various species have also evolved different **morphological** specializations, or specializations of form, that are appropriate to their diet. For example, species exhibit a wide range of tooth shapes and sizes, as well as many different mouth and lip **morphologies**.

But how are individual cichlid species able to exploit such narrow food niches? One hypothesis is that cichlid success is related to their highly unusual anatomic characteristic of having two pairs of jaws. The outer jaws, also called the oral jaws, are **homologous** to the jaws of other vertebrates, and appear externally in the usual position.

The second pair of jaws are invisible externally and lie within the throat area. These are known as the **pharyngeal** jaws. Because the pharyngeal jaws are able to chew and process food, the outer jaws are free to become highly specialized for obtaining food.

Interestingly, trophic specialization is implicated in other instances of adaptive radiation, including those of the Hawaiian honeycreepers and of Darwin's finches. In both these radiations of birds, there is a great diversity in beak morphology, which is in turn related to differences in feeding. Among the Hawaiian honeycreepers, there are species that feed on seeds, insects, and nectar. Among Darwin's finches, as well, different species are specialized on different seed sizes.

Pharyngeal jaws, which characterize cichlids as well as a few other related families of fishes, can be described as the key innovation in the African cichlids that has allowed for the evolutionary success of the group. A key innovation is defined as a novel adaptation that allows a lineage to exploit resources that were previously unavailable. Key innovations are frequently associated with impressive species diversification. Other examples of key innovations include flight in birds, direct development in certain lineages of frogs (which bypasses the **aquatic** larval stage and allows for the occupation of more terrestrial habitats), incisors that grow constantly in rodents, and insect pollination by **angiosperms**.

In addition to the possession of pharyngeal jaws, cichlids appear to be highly adaptable both behaviorally and morphologically. Certain cichlid

The *Aulonocara nyassae* of Lake Nyassa, Africa, is only one species of thousands found throughout the Great Lakes of the Rift Valley. African cichlids are one of nature's best examples of adaptive radiation.

plankton microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

morphological the structure and form of an organism at any stage in its life history

morphologies the forms and structures of an animal

homologous similar but not identical

pharyngeal having to do with the tube that connects the stomach and the esophagus

aquatic living in water

angiosperms a flowering plant that produces seeds within an ovary species are able to alter their tooth and skull morphology depending on available food resources. The ability to change morphologically in response to cues from the environment is known as **phenotypic** plasticity.

phenotypic the physical and physiological traits of an animal

Plasticity allows cichlid species to take advantage of whatever resources become available. One cichlid species found in Lake Victoria, for example, specializes on snails and has the robust skull and teeth necessary to deal with snail shells. However, when introduced into a different habitat, the species switched to an insect-based diet and no longer developed the robust dentition.

Sexual selection. Another factor that may have played a role in the evolution of the African cichlids is sexual selection. **Sexual selection** describes a situation in which different individuals in a population have different reproductive success. Different reproductive success can result from any of several factors. In many animal species, however, including cichlids, sexual selection arises because the reproductive success of males depends on the number of female mates they are able to attract and convince to mate with them. Sexual selection can lead to the rapid evolution of male traits for the attraction of females and of female preferences for these traits.

sexual selection selection based on secondary sex characteristics that leads to greater sexual dimorphorphism or differences between the sexes

Sexual selection has been hypothesized to have played a role in the rapid diversification of many other species-rich lineages, including the songbirds, where both plumage coloration and song are objects of selection; Hawaiian fruitflies of the genus *Drosophila;* ducks; and hummingbirds. All these groups are characterized by elaborate courtship displays. Cichlid fishes are also characterized by a complex courtship behavior in which males build elaborate nests, known as bowers, and females inspect them in order to decide which males to mate with. SEE ALSO HABITAT.

Jennifer Yeh

Bibliography

Futuyma, Douglas J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, 1998.

Ridley, Mark. *Evolution.* Boston: Blackwell Scientific, 1993.

Internet Resources

Oliver, M. K. *The Cichlid Fishes of Lake Malawi, Africa*. <http://www.connix.com/~mko/mwfishes.htm>.

Aggression

Because members of a population have a common niche, there is a strong potential for conflict. Agonistic behavior is displayed when there is a contest that will determine which competitor gains access to a particular resource—for example, food or a mate. The encounter involves both threatening and submissive behavior, and may also involve tests of strength. More often, the contestants engage in threat displays that make them look large or fierce, usually through exaggerated posturing and vocalizations. Eventually one animal will stop threatening and end with a display of submission or appeasement, in effect calling an end to the fight.

Much agonistic behavior includes ritual activity so that serious harm does not occur to either combatant. In many circumstances, escalated vio-

This badger's snarling is known as a "threat display." This badger uses this signal to defend its burrow.

lence over ownership of a mate or commodity is less an adaptive behavior than it is an exchange of signals, whether threatening or submissive. The agonistic signals provide information about the likely intentions and levels of commitment of the senders, as well as the relative fighting ability if escalation occurs. Any future interactions between the same two animals is usually settled much more quickly and in favor of the original victor.

Aggression can be used in a number of different interactions, such as those concerning territorial defense, potential mates, parent-offspring communication, social integration, and food. Conflict resolution usually occurs at short sender-receiver distances. The senders perform actions with tactical and signal functions, and the receivers make decisions based on all the information pooled from the cues and all secondary sources.

Intra– and Interspecific Competition

Conflicts usually arise between two more or less equal individuals who need the same resources to secure or increase their fitness. Both would like to obtain the resource with minimal fighting, so both want the other individual to back down. However, the two opponents are rarely of equal fighting ability or resource-holding potential. Each combatant wants to convey that it is the superior fighter and so uses displays of aggression. However, each one must also assess the other's fighting ability relative to its own. Thus both individuals are senders and receivers simultaneously. The number of signals and tactical acts, and the truthfulness in the information being conveyed, must have something to do with the resolution of the conflict.

Types of Conflict

Intraspecific competition. When the conflict is **intraspecific**, between members of the same species, **dominance hierarchies** come into consideration. For example, placing several hens together that are unfamiliar with each other results in pecking and skirmishing. Eventually, a **pecking order** is established in which the most dominant hen, the **alpha** hen, controls the behavior of all the other hens, mostly through threat rather than actual pecking. The beta (second-ranked) hen does the same and so on to the lowest hen, the omega. The advantage of the top hens is that they are

intraspecific involving members of the same species

dominance hierarchies the structure of the pecking order of a group of individuals where the multiple levels of dominance and submission occur

pecking order the position of individuals of a group wherein multiple levels of dominance and submission occur

alpha the dominant member of a group

assured access to food resources. There is an advantage for the lower-ranked hens as well, because the system ensures that they will not waste energy or risk injury in futile combat.

Interspecific competition. In the event that two or more species in a community rely on similar resources, they may be subject to interspecific competition. Actual fighting between members of two different species is termed interference competition, whereas the use or consumption of the "shared" resources is called exploitative competition. As population densities increase and resources such as food or nesting sites decrease, there is bound to be an increase in competition between the species. The same tactics of agonistic signaling apply here despite the variation in numbers and types of signals among the different species.

Strategies for Victory

Individuals in conflict can employ a number of strategies when assessing their opponent and the minimal level of aggression necessary to be the victor.

Hawk vs. Dove. One theory, termed "hawk versus dove," helps explain why two animals do not always fight over the commodity that is sure to increase the fitness of the winner. Assuming the contestants are equal, there are two clear choices regarding the sought-after commodity: fight (as an aggressive hawk would do) or exhibit peaceable displays (as a dove would be more apt to do). When two hawks meet, they immediately fight over the commodity, with the loser suffering fight injuries as well as the cost of having lost the resource. Because the contest is assumed to be symmetric, each hawk wins half of its battles with other hawks. When a hawk meets a dove, the hawk becomes aggressive and the dove flees. Two doves will both use some costless exchange of displays to decide who gets the commodity and who leaves peacefully.

The take game. Another contest that has been observed is a take game, which again involves two strategies: to be passive or to cheat. The passive animal minds its own business. The cheat, however, increases its own fitness at the expense of the fitness of others. The fishing activity of gulls and terns offers a good example. Some (passive) birds will concentrate solely on catching their own fish. Others (the cheats) will give up some of their own fishing time to monitor the success of other birds. When another bird catches a fish, the cheat will chase after the bird until the fish is dropped and then steal the fish. There is an advantage to cheating only if the bird can steal more fish than it would catch on its own.

The significance of this game is that once any cheats appear, the population will become most stable once all the organisms cheat. Evolution will have therefore lowered the average fitness of the population, a nonintuitive outcome given the assumption that evolution generally improves the average fitness of populations. It is only where evolution models a more passive approach to the acquisition of resources that populations enjoy improvements in their average fitness. However, many evolutionary models lead to lower average fitness, and this simply reflects the costs of competition.

The war of attrition. Certain games employ strategies drawn from a continuous range of possibilities. A classic example is the war of attrition, in which two opponents compete by selecting an amount of strategic investment to be played during the particular confrontation. Neither opponent knows before

the confrontation what level of investment the other has chosen. During the confrontation, the opponent that chose a larger investment wins. The investment might be the amount of time each is prepared to display to the other, or it might be how much energy the players put into the display.

It is unlikely that many animals meet the conditions for a symmetric war of attrition, where all players suffer the same cost of display and would obtain the same benefit in winning. Usually the rate at which costs accumulate will not be the same for any two players. Also, the commodity over which they are fighting is likely to have different fitness values for each player. The critical issue thus becomes which player stands to gain the most from the commodity and lose the least while trying to win it. If the two animals knew at the outset which one was on superior footing, then there would be no confrontation and the animal that stood to lose the most would leave immediately.

However, such complete and accurate information is rarely available as two opponents face each other. The "game" that is then played is called an asymmetric war of attrition. A player that suspects it has the winner role will likely select a higher investment, while a player that suspects it has the inferior role will likely select a lower investment. Of course, it is possible that both players will decide they occupy the same role. These considerations emphasize the uncertainty inherent in this game. Depending on the presumptions of both animals, the confrontation may brief—or it may prove to be a long and vigorous fight. SEE ALSO Behavior; Behavioral Ecology; Dominance Hierarchy; Social Animals.

Danielle Schnur

Bibliography

Bradbury, Jack W., and Sandra L. Vehrencamp. *Principles of Animal Communication.* Sunderland, MA: Sinauer, 1998.

Campbell, Neil A. *Biology*, 3rd ed. San Francisco, CA: Benjamin/Cummings Publishing Company, 1993.

Maynard Smith, J. *Evolution and the Theory of Games.* Cambridge, U.K.: Cambridge University Press, 1982.

Agnatha

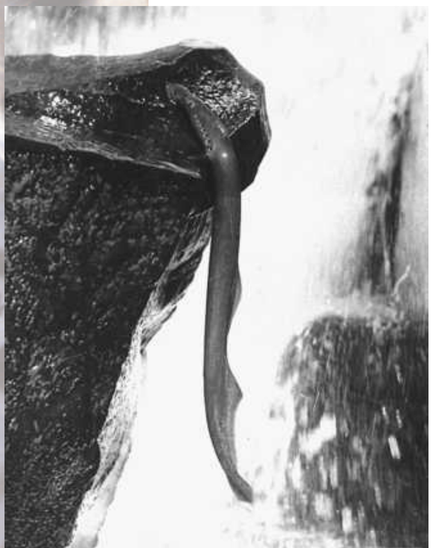
The group Agnatha consists of the jawless fishes, the most primitive group of **extant** vertebrates. While most agnathan species are now extinct, fossil evidence indicates that the group was once highly successful and extremely varied. Two lineages of agnathans have survived to the present, the lampreys and the hagfish.

extant still living

Characteristics of Agnathans

As the most primitive members of the vertebrates, agnathans differ from all others in several important respects. First, they lack hinged upper and lower jaws and instead have unhinged circular mouths. They also lack the paired appendages (fins or limbs) that are found in other vertebrates. In addition, the internal skeleton of agnathans is not bony but **cartilaginous**. However, many extinct agnathans had extensively developed bony plates

cartilaginous made of cartilage



Lampreys have suckerlike mouths which they use to attach to substrates, including the fish they parasitize.

directly under the skin. These were most often found in the region of the skull and served as a protective armor. Bony plates are not present in extant agnathan species.

Major Groups of Living Agnathans

There are two major groups of living agnathans, the lampreys and the hagfish. Both appear fishlike or eel-like.

Lampreys are parasitic species that use their suckerlike mouths to attach to a fish host. They use the many teeth in their mouths and on their tongues to rub at the flesh of their prey. Adult lampreys inhabit a saltwater marine environment but swim up rivers to reach freshwater breeding grounds. Lampreys breed only once in their lifetime, in a single tremendous reproductive bout, and die soon after. Lampreys pass through an immature larval stage before **metamorphosing** into adults. The larval lamprey is always in freshwater. It grows and matures for several years before undergoing metamorphosis and migrating to saltwater **habitats**. Before it was known that the larva was a larval lamprey, it was thought to be a separate species. The larva is of particular interest to biologists who study vertebrate evolution because it shares many features with the cephalochordate *Branchiostoma* (formerly called *Amphioxus*), which is the group believed to be most closely related to the vertebrates. The resemblance between *Branchiostoma* and the larval form of a very primitive vertebrate is striking, and supports the closeness of the relationship between the two groups.

metamorphosing changing drastically from a larva to an adult

habitats physical locations where organisms live in an ecosystem

fossil record a collection of all known fossils

The second group of living agnathans is the hagfish. Hagfish are scavenger species that feed off dead and wounded organisms in the ocean. They are also well-known for their defense mechanism; when threatened, hagfish ooze out great amounts of foul slime.

Evidence from the **fossil record** suggests that agnathans reached their peak of diversity between about 500 million and 340 million years ago. During this period, they were plentiful both in the seas and in freshwater habitats. More than 200 fossil species are known. The majority of these species were fairly small, perhaps a few inches long. The species that have survived to the present are but the remains of a group that was once considerably more diverse. SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

Bibliography

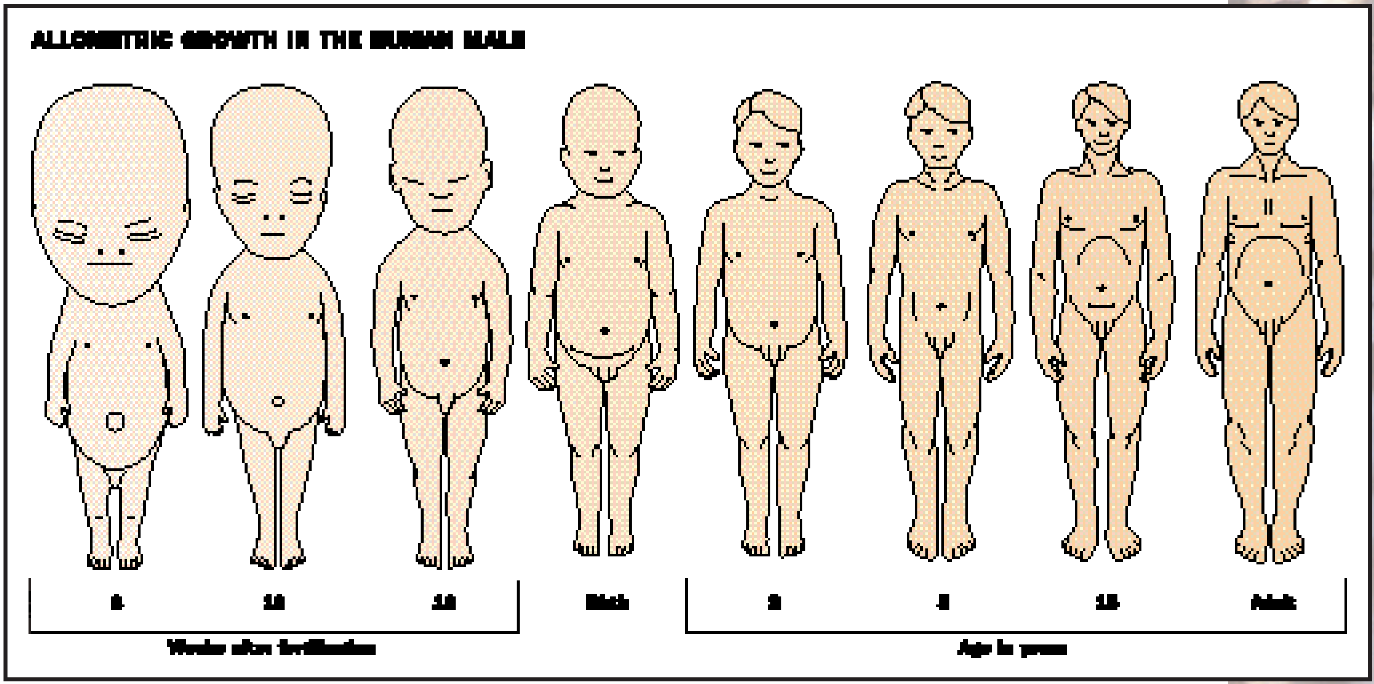
Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton and Co., 1996.

Hickman, Cleveland P., Larry S. Roberts, and Allan Larson. *Animal Diversity.* Dubuque, IA: Wm. C. Brown, 1994.

Hildebrand, Milton. *Analysis of Vertebrate Structure.* New York: John Wiley, 1994.

Allometry

The relationship of the growth of one part of an organism to the growth of another part or the growth of the whole organism is called allometry. The term also applies to the measure and study of such growth relationships. Allometry comes from the Greek word *allos*, which means "other," so allo-

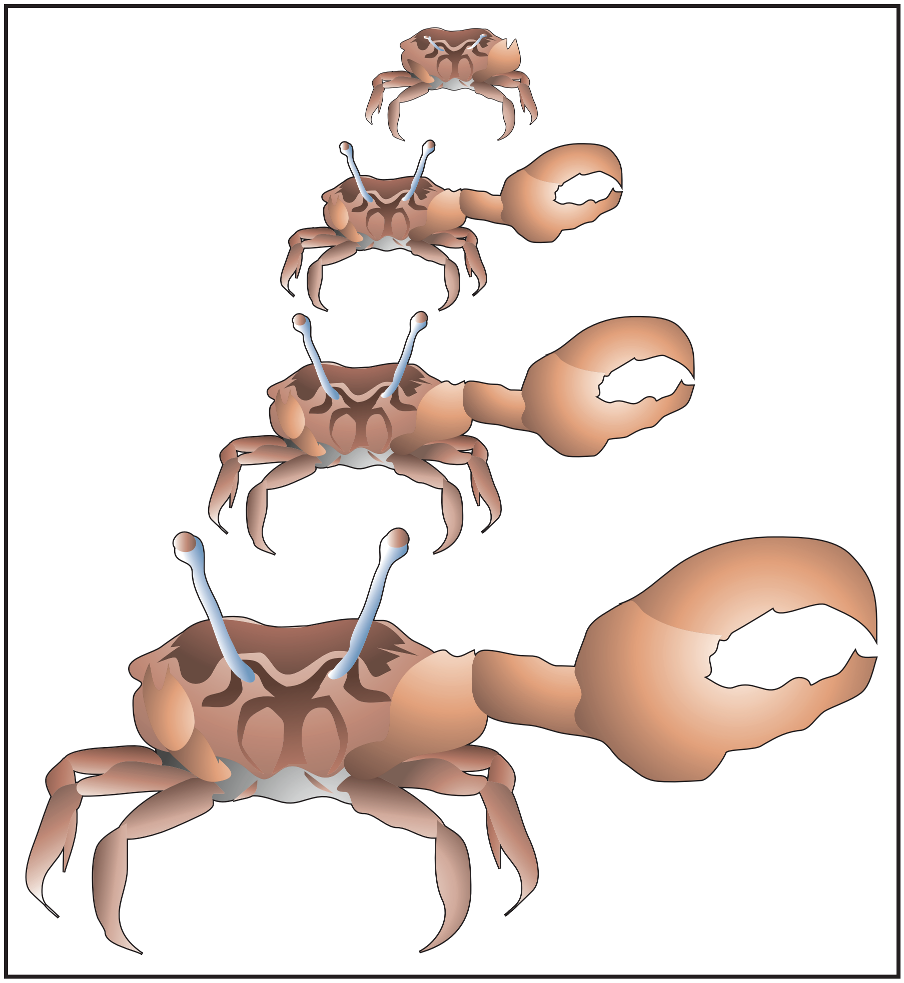


Allometric growth in the human male. Redrawn from Scott Gilbert, 1998.

metric means "other than metric." Isometric growth, where the various parts of an organism grow in one-to-one proportion, is rare in living organisms. If organisms grew isometrically, young would look just like adults, only smaller. In contrast, most organisms grow non-isometrically; the various parts and organisms do not increase in size in a one-to-one ratio. One of the best known examples of non-isometric growth is human growth. The relative proportions of a human body change dramatically as the human grows. Medieval and earlier painters sometimes did not realize this and drew children as tiny adults. But the bodies of tiny adults do not look like those of children. Children have proportionately larger heads and shorter legs than adults. The difference is even more dramatic when human embryos are compared to adults. The figure above shows the relative proportions of a human male at various stages of growth, scaled to the same total height.

A general equation expressing the fundamental relationship of allometric growth is $y = ax^k$ in which y is the size of one organ; x is the size of another; a is a constant; and k is known as the growth ratio. Mathematical tools developed by allometrists have allowed a thorough description of the differential growth of the different parts of an organism. Biologists expect that allometry will eventually improve our understanding of the biological processes that regulate the growth rate.

A change in form with increasing size is a response to increasing instability. For example, body weight increases with the cube of total height. But the strength of muscles and bone depends on cross-sectional area. Area is proportional to the square of a dimension, so the strength increases with the square of total body height. If muscle mass and bone mass did not increase more rapidly than the mass of the body as a whole, the human body would become unstable and unable to support its own weight. On the other hand, metabolic rates (and the heat produced by metabolism) increase less rapidly than total body height, since the larger volume-to-surface-area ratio means



Fiddler crabs (*Uca pugnax*) display allometric growth in their claws. Redrawn from Scott Gilbert, 1998.

that less heat is lost through the skin. In humans, a 100 percent increase in height produces a 73 percent increase in metabolic heat production.

Another example of allometric growth is seen in male fiddler crabs, *Uca pugnax*. These crabs are so named because of their one large claw and "pugnacious" attitude (*pugnare* means "to fight" in Latin). In small males, the two claws are of equal weight, each containing about one-twelfth of the total weight of the crab. However, the size of the large claw increases disproportionately to the growth of the rest of the animal, producing in larger males a claw that may contain two-fifths of the total weight of the crab.

Allometric growth is usually detected by graphing the growth data on a log-log plot. That is, the horizontal and vertical axes of the graph are both logarithmic scales. The general allometric growth equation has the form $y = ax^k$. Taking the logarithm of both sides produces the following equation: $\log(y) = k\log(x) + \log(a)$.

This equation has the basic form of a linear equation in slope-intercept form, $y = mx + b$. If the body mass of *Uca pugnax* is plotted on the x-axis and the claw mass is plotted on the y-axis of a log-log plot, then the result will be a straight line whose slope is the relative growth rate of claw mass to body mass. In the male *Uca pugnax*, the ratio is 6:1. This means that the mass of the big claw increases six times faster than the mass of the rest of the body. In females, the claw grows isometrically and remains about 8 percent of the body weight throughout growth. Allometric growth occurs only in males.

Allometric growth is also seen in nonhuman primates. For example, the jaw and other facial structures of baboons have a growth rate about four and one-quarter times that of the skull. As the baboon matures, the jaw protrudes further and further until it dominates the facial features. SEE ALSO FUNCTIONAL MORPHOLOGY.

Elliot Richmond

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Huxley, J. S. *Problems of Relative Growth.* New York: Dial Press, 1932.

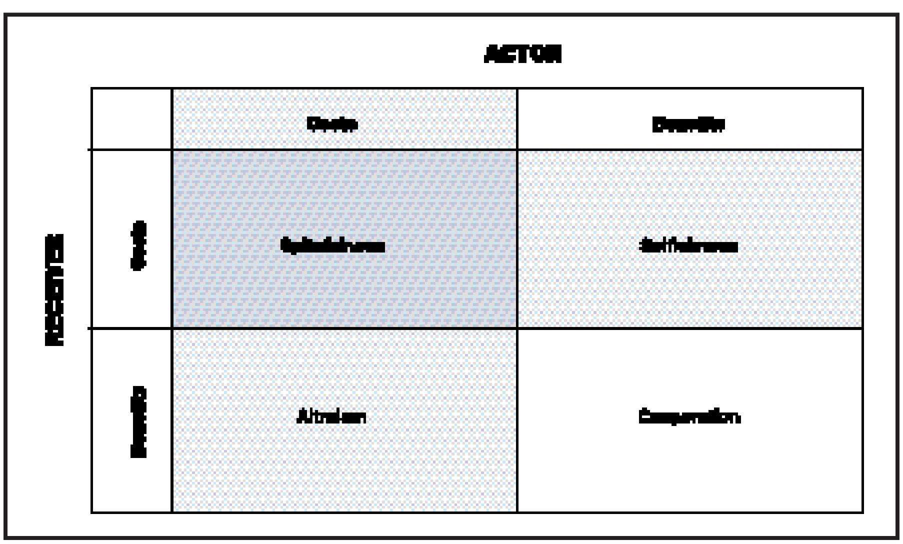
Thompson, D. W. *On Growth and Form.* Cambridge, U.K.: Cambridge University Press, 1942.

Altruism

Altruism, defined as an action that benefits the receiver but comes at some cost to the performer, is one of the four types of social interactions that can occur between animals of the same species. Figure 1 summarizes these four interactions. Cooperation, where both actor and receiver benefit, and selfishness, where the action benefits the actor at the expense of the receiver, are by far the most common of the four interactions in nature. Spite, where both actor and receiver are harmed, and altruism are very rare.

The prevalence of cooperation and selfishness over altruism and spite is explained by the rules of **natural selection**. The currency of natural selection is offspring. Any anatomical, physiological, or behavioral trait that enhances an individual's ability to produce more offspring will be favored, and the trait will be selected regardless of the effects on others. For example, seagulls sometimes steal food from nesting neighbors to feed themselves and their chicks. This behavior clearly increases the fitness of the actor while

natural selection the process by which organisms best suited to their environment are most likely to survive and reproduce



Social Interactions that can occur between animals of the same species.

Within the social structure of the meerkats' community, there is always a sentry "on duty" keeping watch for any predators.

decreasing the fitness of the receiver; it is selfish. Imagine an altruistic seagull that willingly provided food for its neighbors. This trait would not last very long in the population because the helpful gull would not be able to feed many of its own offspring.

Reciprocal Altruism and Kin Selection

Despite the odds against altruism evolving, it does exist in nature. Some biologists, however, consider these instances to be examples of pseudoaltruism, and insist that true altruism has yet to be found. Pseudoaltruistic acts appear to be altruistic, but "in the long run" are actually beneficial to the actor. There are two types of pseudoaltruism—reciprocal altruism and kin selection.

Reciprocal altruism. This occurs when the actor acts altruistically in expectation of having the same done in return at a later time. Many animals that live in groups will post sentinels to watch for predators while the rest forage for food. The sentinel changes several times daily, so the animal "on duty" is assured of being protected later when it is his turn to forage. Vampire bats provide another example. If, when the group returns from hunting, one individual has not found food, a neighbor will regurgitate a portion of its meal for the hungry one. The next evening, the helpful bat may be the hungry one and need the favor returned.

Hamilton's Rule individuals show less aggression to closely related kin than to a more distantly related kin

Kin selection. This other type of pseudoaltruism, kin selection, was proposed by British scientist W. D. Hamilton in 1964. He realized that an individual could not only increase his fitness by having its own offspring, but it could also help a close relative raise its offspring, since they share genes. The combination of individual fitness and fitness through kin selection is inclusive fitness. Hamilton argued that if the benefits the actor receives by helping its relatives outweighs the cost of the action, then altruism can evolve. This concept can be expressed mathematically through **Hamilton's Rule**: $br > c$, where b is the benefit to the actor, r is the relatedness of the actor to the receiver, and c is the cost to the actor. Relatedness is measured by the proportion of genes that are identical between two individuals. Because of Mendelian inheritance, half of a diploid individual's genes are shared with each of its parents, siblings, and children. Diploid grandparents share one-quarter of their genes with their grandchildren, and cousins share one-eighth of their genes with each other. An individual who helps two of its siblings, four of its grandchildren, or eight of its cousins is just as fit as the individual who helps only itself.

Kenyan bee-eaters of the bird genus *Merops*, have evolved behaviors by kin selection. Male bee-eaters will typically forgo reproducing when they are young, instead opting to help more mature birds raise their young. These young males help relatives more often than nonrelatives, thus raising their inclusive fitness. Young males that attempt to have their own offspring actually fare worse than helpers because their territories are too poor to raise more than one chick.

eusocial animals that show a true social organization

haplodiploidy the sharing of half the chromosomes between a parent and an offspring

Conclusion

The classic example of altruism occurs in the **eusocial** bees. Honeybee workers rarely reproduce, letting the queen provide all the offspring. An unusual chromosome condition, called **haplodiploidy**, produces unusual relatedness among the bees in a hive. Workers are actually more related to their sisters (eggs laid by the queen) than their own offspring! Although honeybees are considered the classic example of altruism, they really practice a form of kin selection. True altruism has not yet been found in nature, and some scientists believe that true altruism can be found only in human populations. SEE ALSO Social Animals.

Jes Marie Creech

Bibliography

Alcock, John. *Animal Behavior*, 6th ed. Sunderland, MA: Sinauer Associates, 1997.

Pfennig, David W., and Paul W. Sherman. "Kin Recognition." *Scientific American* 272, no. 6 (1995): 98–103.

Sherman, Paul W., and John Alcock. *Exploring Animal Behavior: Readings from American Scientist*, 2nd ed. Sunderland, MA: Sinauer Associates, 1998.

Wilson, Edward O. *Sociobiology: The New Synthesis*. Cambridge, MA: Harvard University Press, 1975.

Amphibia

Amphibia is one of the five major classes of vertebrates. There are three orders in the amphibia group, two of which are widely familiar, frogs (Anura) and **salamanders** (Caudata), and one of which is less well-known, the tropical caecilians (Gymnophiona). The name "amphibian" refers to the use of both aquatic and terrestrial habitats, and the life history patterns of species in the group.

salamander a four-legged amphibian with an elongated body

Amphibian Characteristics and Life History

The earliest tetrapods (four-legged, terrestrial vertebrates) were amphibians, and living amphibian species retain some of the primitive characteristics of the first terrestrial vertebrates, which invaded land habitats during the geologic period known as the Devonian, which was approximately 408 million years ago. For example, unlike other terrestrial vertebrates, amphibians lack scales and claws, and are instead characterized by a moist, glandular skin composed of living cells. The skin is involved in respiration to some degree in most amphibians. Certain lungless salamanders rely largely on the skin for gas exchange. In many species, skin glands secrete noxious, or sometimes highly poisonous, substances that serve as deterrents to predators. This is sometimes associated with a warning coloration that advertises toxicity, and some species have even evolved specific defensive postures to show off effectively their warning coloration. One example of this is the "unken reflex," in which the animal throws back its forelimbs to display the bright warning colors on its belly. The possession of skin with living cells limits many amphibian species to fairly moist habitats, although certain species have drier skins and are able to tolerate drier habitats. Amphibian eggs also require moist environments. These lack the water-conserving eggshells found in other terrestrial vertebrate groups and are instead covered with a gelatinous capsule.

Many amphibian species make use of both aquatic and terrestrial habitats, either simultaneously or sequentially during different life stages. A typical amphibian life cycle involves semiterrestrial adults that breed and lay eggs in water. Eggs then develop into aquatic larvae. After a period of

This tree frog belongs to the Anura order of the amphibian group.

growth, the larvae undergo metamorphosis, or transformation, and become semiterrestrial adults. Metamorphosis is triggered by changes in concentrations of circulating **hormones**. Numerous anatomical changes occur during metamorphosis. These include the loss of gills; the development of lungs; the development of eyelids; the loss of aquatic sensory systems such as the **lateral line,** which is responsible for underwater "hearing"; tongue development; maturation of the kidneys and **gonads**; and changes in the skin, which becomes thicker and develops dermal glands. Of the three amphibian **clades**, or orders, metamorphosis is most extreme among frogs, where there is a striking difference between the larva (the tadpole) and the adult. Particularly striking is the rapid development of fore- and hindlimbs and the loss of the tail. In addition, there are anatomical changes associated with the transition from an **herbivorous** tadpole to a **carnivorous** adult. These include reshapings of the jaws and mouthparts, as well as a shortening of the digestive tract. The rapid and extreme nature of metamorphosis in frogs results in unusually high mortality levels during this period. Locomotion is difficult both in the water and on land because of the simultaneous presence of limbs and a tail.

hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

lateral line a row of pressure sensitive sensory cells in a line on both sides of a fish

gonads the male and female sex organs that produce sex cells

clades a branching diagram that shows evolutionary relationships of organisms

Although aquatic larvae, metamorphosis, and semiterrestrial adults make up a typical amphibian life history, it is important to remember that there are numerous exceptions to this pattern. These include egg laying in drier habitats, including trees, rather than in aquatic habitats; bypassing the larval stage via direct development of eggs into miniature versions of adults; and even live-bearing in select species. In fact, the diversity of reproductive modes is greater among amphibians than other vertebrate groups.

herbivorous describes animals that eat plants

carnivorous describes animals that eat other animals

All amphibians are carnivorous, with the exception of larval frogs (tadpoles), which are primarily herbivorous. Most amphibians are generalists, and will eat anything they can capture and ingest. Frogs and salamanders capture prey with their tongues, which are highly developed. Certain salamander species have specialized projectile tongues that they fire with impressive accuracy to capture prey.

Major Amphibian Groups

The three orders of amphibians are salamanders, frogs, and caecilians.

Salamanders. There are approximately 400 species of salamanders worldwide. Salamanders retain a fairly primitive vertebrate **body plan**, with slender bodies, four limbs, and tails. Some species have undergone limb reduction, and a few species lack hindlimbs, possessing only two front limbs. Although a few species of salamanders are characterized by external **fertilization** of eggs, the majority use internal fertilization via spermatophore. After an often extensive courtship, in which mating pairs swim or walk together, the male releases a spermatophore that consists of a gelatinous pedestal capped with a ball of sperm. The female walks over the spermatophore and picks it up with the lips of her cloaca, the common chamber into which digestive, urinary, and reproductive tracts discharge. Sperm are then stored internally in the spemathecae, where they are used to fertilize eggs that are laid later. A large number of salamander species are actually direct developing, with eggs hatching directly into miniature adults. In this way, the aquatic larval stage is bypassed. Other species are perrenibranchiate, and never **metamorphose**. These species retain the larval morphology their entire lives. Among amphibians, only salamanders include perrenibranchiate species. The axolotl, a well-studied organism, is perrenibranchiate. There are also a small number of live-bearing salamanders, with development taking place in the oviduct of the female.

body plan the overall organization of an animal's body

fertilization the fusion of male and female gametes

metamorphose to change from a larva to an adult

Frogs. There are over 4000 species of frogs, making it the most diverse of the amphibian orders. Frogs have made striking modifications in the ancestral amphibian body plan, many of these associated with their saltatory (jumping) mode of locomotion. These include the loss of the tail, a shortened vertebral column, and the fusion of many bones of the forelimbs and hindlimbs. Frogs are ecologically diverse, and have adapted to a wide variety of habitats. Some species are highly aquatic, with adults never making use of terrestrial habitats. Highly aquatic species are characterized by streamlined bodies and extensively webbed hindfeet. They swim by kicking their hindlimbs simultaneously, which essentially represents the use of saltatory motions in the water. Several separate lineages of frogs have adapted to **arboreal** habitats. These species are characterized by adaptations such as expanded toe pads and opposable thumbs. They also tend to locomote by

arboreal living in trees

walking hand over hand rather than jumping. A few arboreal species are even able to parachute from tree to tree. These "flying frogs" have extensive webbing between their fingers and toes, which they extend as they parachute. Finally, some frogs are fossorial and live underground. These species often possess digging specializations such as muscular forearms or hard, keratinized spade-shaped digging tools on the hindfeet. Certain fossorial frogs are even able to survive in desert environments. Individuals remain **torpid** in burrows much of the time, but come out once a year during heavy rains to reproduce.

torpid a hibernation strategy where the body temperature drops in relation to the external temperature

Frogs are unique among amphibians in that courtship in most species involves vocal calling by males. Calls are species specific, and considerable research has been done on sexual selection in certain species. Mating typically involves amplexus, in which the male clasps the female either at the shoulders or at the hindlegs. Fertilization is most commonly external, although certain species use internal fertilization.

Caecilians. The third group of amphibians is the caecilians, which are found only in tropical regions. There are approximately 200 species. Caecilians are wormlike amphibians that lack limbs. They have rings on the outside of the body that cause them to appear segmented. Many species lack a tail, and the cloaca is at the end of the body. They vary in size, with the largest species attaining lengths of up to three feet. Caecilians are fossorial or aquatic, and eyes are smaller than in the other two groups. In certain species the eyes are buried beneath the skin or even beneath skull bones. Caecilians also possess a unique sense organ called the tentacle, which is found between the nostril and the eye. It functions as a chemical sensor (detector). Caecilians feed primarily on earthworms and other invertebrates. Unlike frogs and salamanders, caecilians do not use tongue projection to capture prey. Rather, they catch a worm with their jaws, spin it lengthwise in order to remove and ingest a piece, and then try to catch the worm again.

Also in contrast to frogs and salamanders, more than half of caecilian species are **viviparous**, or live bearing. Fertilization is internal, via a male organ called the phalloideum. Free-swimming larvae hatch within the maternal oviduct, where they live and feed until birth. Caecilian larvae are characterized by special larval teeth that they use to scrape the walls of the oviduct. This stimulates maternal glands to secrete a fatty milk on which the larvae feed. The adult teeth develop prior to birth. Larvae in viviparous species also possess large gills that they flatten against the wall of the oviduct to obtain oxygen.

viviparous producing living young (instead of eggs) that were nourished by a placenta between the mother and offspring

Recent Amphibian Declines

In the last few decades of the twentieth century, scientists began observing a rapid and alarming global decline in numerous species of amphibians. This is particularly disturbing in that certain previously abundant species have apparently gone extinct in relatively undisturbed pristine habitats. Many causes have been suggested as possibly being involved in the declines, including increased levels of ultraviolet radiation due to destruction of the ozone layer through human activities; declining pH levels from **acid rain**; parasites; disease; and **habitat loss**. It is quite possible that a combination

acid rain rain that is more acidic than non-polluted rain

habitat loss the destruction of habitats through natural or artificial means of these factors is responsible. SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

Bibliography

Behler, John H., and F. Wayne King. *National Audubon Society Field Guide to North American Reptiles and Amphibians.* New York: Alfred A. Knopf, 1995.

Conant, Roger, and Joseph T. Collins. *Reptiles and Amphibians: Eastern/Central North America.* New York: Houghton Mifflin Company, 1991.

Duellman, William Edward, and Linda Trueb. *Biology of Amphibians.* New York: McGraw Hill, 1986.

Pough, F. Harvey et al. *Herpetology.* Upper Saddle River, NJ: Prentice Hall, 1998.

Stebbins, Robert C. *Western Reptiles and Amphibians.* New York: Houghton Mifflin Company, 1985.

Zug, George R. *Herpetology: Introducing the Biology of Amphibians and Reptiles.* San Diego, CA: Academic Press, 1993.

Animal

Animals are multicellular, **heterotrophic eukaryotes**. Because animals are unable to make their own food, they must have some means of ingesting food. They do this by consuming plants, other animals, or decomposing organic matter, or by absorbing nutrients directly from a host. Animals typically store food reserves in their body as glycogen. Animals have nerve tissues to gain information about the environment and muscle tissue to allow them to move. They have membrane-bound cells that lack rigid walls. Most animals reproduce sexually and spend most of their life cycle as diploid organisms. These are the characteristics that generally separate animals from other groups.

heterotrophic eukaryotes organisms containing a membrane-bound nucleus and membrane-bound organelles that do not make their own food

PLANTS	ANIMALS
Multicellular	Multicellular
Cell wall and cell membrane	Cell membrane
Autotrophs—make their own food	Heterotrophs—must ingest food
Store excess food as starch	Store excess food as glycogen
No form of locomotion	Most animals have a form of locomotion

Comparison of basic characteristics of plants and animals.

By this definition the first animals appeared on Earth in the Precambrian oceans over 500 million years ago. Since that time animals have evolved into many diverse forms. Some of those forms have become extinct while others continue to thrive. At the start of the twenty-first century, more than one million species of animals are known on Earth, with more being discovered all the time. Animals are grouped into about thirty-five **phyla**. Over 95 percent of the animal species lack a vertebral column and are called invertebrates.

phyla broad, principal divisions of a kingdom

Animals are found in nearly all environments on Earth. The oceans are home to the largest number of animal phyla. Freshwater environments are home to a large number of phyla, but those environments are not as

terrestrial living on land

diverse as the oceans. **Terrestrial** environments have the smallest number of animal phyla.

Allan B. Cobb

Bibliography

Barnes-Svarney, Patricia, ed. *The New York Public Library Desk Reference.* New York: Macmillan USA, 1995.

Animal Rights

The opinions regarding animals and their rights greatly vary. To some, animals have no rights and are merely a form of property that exists only to fulfill human needs. To others, they are creatures that can be used or owned by people, but which also have feelings and are not to be subjected to needless suffering or pain. (Some would say that people with this belief are animal welfare, as opposed to animal rights, advocates.) Finally, there are those who believe that at least certain animals, such as those with sophisticated levels of intelligence and emotions (including nonhuman primates such as monkeys and chimpanzees), are not property at all nor meant to be utilized by man in any way. Such people believe that these animals are entitled to fundamental moral and legal rights that are currently accorded only to humans.

The animal rights movement includes many different organizations. In the United States alone, more than 100 groups are interested in the welfare of animals, and the focus of their activities and their tactics vary widely. For example, the Humane Society uses public education to promote responsible pet ownership, eliminate pain and cruelty in hunting and animal research, and advance similar causes. In contrast, the Animal Liberation Front commits illegal acts such as break-ins, the destruction of property, and the releasing of animals in its efforts to end all forms of what it considers to be animal exploitation.

Opponents to the animal rights movement also vary. Some see it as a group of do-gooders who are interfering with their right to treat or use their property as they wish. Others believe that the movement (or at least a part of it) consists of extremists who threaten the economic, political, and religious institutions in our country. Virtually every other country has one or more anticruelty statutes that prohibits the mistreatment of animals, but the provisions and effectiveness of those laws vary greatly. Many nations also have organizations that are interested in protecting the welfare of animals. Aside from the United States, the animal rights movement is most active in Canada, Western Europe, Australia, and New Zealand.

Historical Groundwork

Humans have long used animals for a variety of purposes. For hundreds of thousands of years, people have hunted for food and clothing. Between 10,000 and 18,000 years ago, humans began to domesticate animals such as dogs, goats, sheep, and chickens as beasts of burden and as food. For at least 2,500 years, animals have been used in circuses and other forms of entertainment. In the second century C.E., the Greek scientist Galen conducted some of the first medical experiments on living animals.

Animal rights activists gathered on the steps of the statehouse in Boston, Massachusetts (1999), with their greyhound dogs to protest the treatment of animals still used in dog racing.

Antiquity. The ancient Greeks believed that nonhuman creatures were created by the gods to be used however people wished. According to the Bible, God gave man dominion "over the fish of the sea, over the birds of the air, and over the cattle, over all the Earth and over every creeping things that creeps on the Earth" (Gen. 9.1–3). This statement reflects the understanding of the ancient Israelites of how the world began, of why humankind hunted and domesticated the animals for food and clothing, and of how God provided for the human race which He made in His image. These same principles were in the laws of the ancient Greeks and Romans, which then evolved into or influenced the laws of the various western European countries (including England's common law) and those nations in the New World that were settled by western Europeans. For hundreds of years, no act committed upon an animal was prohibited, no matter how cruel or unnecessary.

physiology the study of the normal function of living things or their parts

New ideas. The concept that animals have rights is relatively new. The first animal-protection law in western civilization was adopted in 1641 by the Massachusetts Bay Colony. This law made it illegal to "exercise any Tirranny or Crueltie towards any bruite Creature which are usuallie kept for man's use." However, the rest of the western world continued as before. Indeed, during most of the seventeenth and eighteenth centuries, many experiments were conducted using living animals. This was largely because of the new idea that scientific conclusions had to be based on observable facts and because the dissection of human bodies and the use of living people in medical experiments were illegal. This meant that scientists had to experiment with animals to learn more about **physiology** and anatomy. There were no controls on how these experiments were conducted, but there were few qualms because most believed that animals had no souls and, thus, felt no pain.

> Since the days of ancient Greece, the common belief for centuries was that animals were nothing more than living machines that had no consciousness. Without consciousness, the animals could not reason or think nor could they suffer or feel pain. Later, with the establishment of Christianity, this consciousness, which the animals supposedly did not have, became known as a "soul."

Ironically, these very experiments proved that animals do experience pain. By the end of the eighteenth century, many argued that animal abuse

contributed to a person's cruelty. Others said that the mistreatment of animals was a misuse of a gift from God. In 1789, the English philosopher Jeremy Bentham became the first to say that animals have rights. According to Bentham, animals suffer pain just as humans and thus deserve the same freedom from pain.

Modern Movements

Slowly, most people came to accept Bentham's idea. Maine adopted the first modern anticruelty law in the United States in 1821, and every other state eventually enacted similar legislation. To encourage the police to enforce these laws, private organizations such as the American Society for the Prevention of Cruelty to Animals (ASPCA) were created throughout the last third of the nineteenth century. In addition, since World War II, a number of federal animal-rights laws have been adopted. These laws regulate animal experimentation and the treatment of animals by medical research facilities, slaughterhouses, and circuses, as well as people such as animal dealers who use animals as a source of livelihood.

Protection of animals. Many groups concerned with the treatment and welfare of animals still believe in the superiority of humans and the right to use other living creatures to meet human needs. However, in 1975, the Australian philosopher Peter Singer argued that animals are entitled to live free from the infliction of pain and suffering, whether from animal experimentation, the raising of animals for food, or other causes.

Eight years later, the American philosopher Thomas Regan argued that every individual animal has an inherent value and thus has moral rights that should not be violated even if to do so benefits society. The ideas of both Singer and Regan provide the basis for those who argue that animals have rights that must be observed and protected as opposed to those who believe that it is all right to use animals so long as it is done without cruelty.

State and Federal Statutes

The provisions of anticruelty statutes vary state to state. In addition, the effectiveness of these laws depends to a large degree on whether one believes animals are property and whether there should be limits on how to use animals to meet human needs. Many of these laws were written about 100 years ago and have rarely been amended. Some are only a few paragraphs long. Most statutes contain broad exemptions that usually include agricultural practices (e.g., dehorning, castration, docking, and limiting feed) as well as hunting and scientific experiments.

Even when an anticruelty law does not have exemptions, the courts have often created them by ruling that the statutes do not prohibit the infliction of pain, suffering, or death so long as it is not outside the traditionally accepted use of animals. In addition, while some laws define "animals" as all living creatures other than man, some laws apply only to warm-blooded vertebrate animals. Others list specific animals or types of animals that the provisions do or do not protect.

In a few states, persons are guilty of violating the anticruelty statutes if they are criminally or unreasonably negligent in their treatment of an animal. Most states, however, require that the defendant have some form of

POLIO

Polio was once one of the world's most dreaded diseases. Between 1948 and 1952 alone, 11,000 people in the United States died of polio and another 200,000 became partially or completely paralyzed.

In 1953, Dr. Jonas Salk announced the development of a vaccine. Salk and his colleagues developed the vaccine by growing three strains of the polio virus in monkey tissue and then killing the viruses with formaldehyde. This vaccine is between 80 percent and 90 percent effective and has saved millions of lives.

intent before a conviction can be obtained. For instance, if a jurisdiction requires willful intent, then the prosecutor must prove not only that the defendant acted intentionally and voluntarily, but also that the defendant acted without just cause or reason. In one case in North Carolina, two dog trainers were found not guilty of violating the local anticruelty law when they beat a dog and submersed its head under water because they did it to teach the animal not to dig holes.

In most states, violations of anticruelty laws are considered as summary offenses, which only involve a fine, or as misdemeanors with penalties that do not exceed a year in jail and a fine. Some states have recently made the violation of these laws a felony, but it is not yet known if this will make any substantial difference in the obedience to, or the enforcement of, the statutes. Most police and prosecutors are not very concerned about crimes against animals and are reluctant to spend the time or the money to make arrests or to take the cases to court. As a result, the enforcement of the anticruelty laws is frequently left to such organizations as the Humane Society and the ASPCA.

Animals and science. Since World War II, the number of scientific experiments involving animals has increased dramatically. Although the number of animals used in these experiments is just a small percentage of the millions killed every year for the benefit of humans for food and other reasons (such as clothing and the use of animal fats, oils, bones, and other by-products in the manufacture of commercial goods), much of the recent focus of the animal rights movement has been on attempts to prohibit experimentation on live animals.

In addition to the state anticruelty statutes, animal experimentation is governed by the federal Animal Welfare Act which was enacted in 1966 and substantially amended in 1985. This law and its accompanying administrative regulations prohibit the use of animals in a scientific experiment if a nonanimal alternative is readily available. Scientists are also required to keep an animal's pain to a minimum, and to consider alternatives to any procedure that causes pain or distress. However, the law does not apply to rats or mice, the animals used most often in experiments, nor does it limit the type of experiments that may be conducted.

In the last decade of the 20th century, groups such as the Animal Liberation Front have used illegal means to fight what they believe is animal exploitation. In response, many states have adopted laws that specifically target these activities. The federal government has also enacted the Animal Enterprise Protection Act (1992). This law makes it a crime to cross a state border with the intent to physically disrupt zoos, aquariums, or similar public attractions, as well as to physically disrupt commercial or academic facilities that use animals for food production, research, or testing. SEE ALSO Animal Testing; Bioethics.

Mark A. Thorburn

Bibliography

Bloyd, Sunni. *Animal Rights.* San Diego, CA: Lucent Books, Inc., 1990.

Day, Nancy. *Animal Experimentation: Cruelty or Science?* Springfield, NJ: Enslow Publishers, Inc., 1994.

Francione, Gary L. *Introduction to Animal Rights: Your Child or the Dog?* Philadelphia: Temple University Press, 2000.

Marquardt, Kathleen. *Animal Scam: The Beastly Abuse of Human Rights.* Washington, D.C.: Regnery Gateway, 1993.

Regan, Thomas. *The Case for Animal Rights.* Berkeley: University of California Press, 1983.

Roleff, Tamara L., and Jennifer A. Hurley. *The Rights of Animals.* San Diego, CA: Greenhaven Press, Inc., 1999.

Sherry, Clifford J. *Animal Rights: A Reference Handbook.* Santa Barbara, CA: ABC-CLIO, Inc., 1994.

Singer, Peter. *Animal Liberation: A New Ethics for Our Treatment of Animals*, 2nd ed. New York: Random House, 1990.

Animal Testing

In order to more completely understand biology, researchers sometimes conduct experiments on animals. Animal experimentation has a lengthy and productive history in biological research, especially in biomedicine. For example, the organ transplant pioneer Thomas E. Starzl conducted his early surgical transplantation experiments on dogs in the 1960s before successfully attempting them on humans. Psychiatrist John Cade made the discovery that lithium aids manic-depressive patients by experimenting with guinea pigs in the 1940s. Today, many animals are used for a variety of purposes in experimental science. While some studies use primates or other animals, over 90 percent of studies involve mice and rats, for experiments from immunological projects to cancer research. While animal research is enormously important to the advancement of biomedical science, some activists feel that animals should not be used as experimental subjects.

The Animal Welfare Act (1966)

To ease undue suffering inflicted on these experimental subjects, scientists William Russell and Rex Burch published *The Principles of Humane Experimental Technique* in 1959, wherein they described the three Rs: Reduce animal experiments, Refine them to make the experiments less unpleasant, and Replacement of animals by different techniques. Their concern over the "distress" suffered by animals, along with more general feelings of humaneness, led to the creation of the Animal Welfare Act by the federal government in 1966. The act was designed to protect animals that might be test subjects by requiring proper care of them, and it sets forth a list of guidelines researchers must comply with. For example, it stipulated that the animals must receive adequate veterinary care. In 1970, the act expanded from protecting dogs, cats, primates, guinea pigs, rabbits, and hamsters to "all warm-blooded animals." Significantly, the act exempts mice, rats, and birds from the protection it confers on other species. The act originally applied largely to pet dealers but with subsequent amendments grew to include, and even focus on, scientific research animals.

As the act forced scientists to care more properly for their test subjects (and with consistently healthy animals, enjoy more predictable and complete experimental results), a movement began in the 1970s to stop the use of animals in experimental science altogether. In 1975, philosopher Peter

Singer published *Animal Liberation*, in which he argued that all animals capable of perceiving pain were moral equals to human beings. In subsequent years, some animal rights activists (who, willing to cede moral rights to animals, must be differentiated from animal welfare activists, who only wish to see animals treated humanely) have taken increasingly severe stances on the subject of animal research. In 1986, the then-director of People for the Ethical Treatment of Animals, Ingrid Newkirk, asserted to the *Washingtonian* that "animal liberationists do not separate out the human animal, so there is no rational basis for saying that a human being has special rights. A rat is a pig is a dog is a boy. They're all mammals." She also likened the deaths of broilerhouse chickens to those of Jews during the Holocaust. Extreme animal rights activists have targeted scientists with terrorist or destructive acts in an effort to stop research. In particular, behavioral scientists and addiction researchers receive a lot of attention from activists because of the use of live primates in these fields.

Electrodes, used to detect neurological activity, protrude from the brain of a Japanese macaque who is immobilized in a laboratory cage.

Ethics vs. Research Imperatives: Finding a Compromise

Many activists protest cosmetics research rather than biomedicine, as some consider makeup to be less crucial to human existence than, say, cancer research. Additionally, not all animal rights activists are terrorists or extremists. For example, the Johns Hopkins Center for Alternatives to Animal Testing promotes the 3 Rs wherever it can. While many alternative suggestions for scientists may not be feasible, no scientist is so cruel as to want animals to suffer unnecessarily. However, for certain experiments, there are many advantages to using animals over other methods. The creation and maintenance of tissue and/or organ cultures in a test tube to simulate biological systems is extremely difficult, and using a live animal instead makes studying such systems possible. For addiction research, it is impossible to gain behavioral data without working with some sort of living animal. Many drug studies require the observation of treated animals, as do experiments on blood vessels (such as angioplasty research) and immune system tolerance (for investigations of transplantation biology). While many activists call for the use of computer simulations as an alternative to animal research, such simulations rarely work or reflect reality.

This is not to say that animals are required for every study. There are plenty of in vitro (test-tube) tests for the toxicity of certain compounds. Using human cells grown in culture has proved to be particularly accurate in this regard. For educational purposes, computer simulations can be as effective as real-life dissections. Only 70 percent of agents that cause cancer in mice will cause it in rats, suggesting that comparisons across species are not always valid: conclusions reached by studying animals may not be true for humans. In 1990, David Wiebers and colleagues from the Mayo Clinic reported that of twenty-five drugs found to reduce damage following strokes in animals, none proved effective in human trials. There are many instances in which animal studies may not work, simply because animal organ systems and cellular structure differ from humans.

Knowledge can be gleaned from epidemiological studies, or studies that follow the spread of disease, as an alternative. Clinical study, or the investigation of disease and how it manifests itself in a human population, can also offer insights to biological questions that cannot be answered with the use of animals. Some diseases, like HIV, rely heavily on these tactics because the animal simulations are too different or unwieldy. While studies of the transmission of Simian Immunodeficiency Virus (SIV), a close relative of HIV, in nonhuman primates can be useful, SIV is still a different disease.

It is worth noting that the animal rights movement has gained momentum at a time when there are far fewer Americans living on farms. A familiarity of animals as house pets, and not dinner, may have contributed to the movement. Animals may prove invaluable to certain studies. Moral considerations aside, the practical constraints of a given study might dictate that the use of animal subjects will not answer the question. Explorations of alternatives can be a good idea, because they may produce experiments that more closely mimic the human response to a treatment. And, after all, a more perfect model system is good news for everybody. SEE ALSO Animal Rights; Bioethics.

Ian Quigley

Bibliography

Barnard, Neal D., and Stephen R. Kaufman. "Animal Research Is Wasteful and Misleading." *Scientific American* 276 (February 1997):80–82.

Botting, Jack H., and Adrian R. Morrison. "Animal Research Is Vital to Medicine." *Scientific American* 276 (February 1997):83–85.

Annelida

The phylum Annelida includes three main groups: the earthworms, the leeches, and the bristleworms. Annelids are found worldwide, and inhabit terrestrial, freshwater, and marine **ecosystems**. There are over 15,000 described species.

Characteristics of Annelids

All annelids are segmented. Segments, also called metameres, are structures that occur repeatedly along the body of the animal. Each annelid segment contains units of the circulatory, nervous, and excretory systems. In the earthworms and bristleworms, but not the leeches, segmentation extends to the interior of the body, and includes the **coelom**, which is partially divided into units by structures called septa.

The annelid body is covered by a moist outer cuticle that is secreted by the **epidermis**. Both earthworms and bristleworms also possess hairlike setae, composed of **chitin**, the hard material that also forms the **exoskeletons** of insects. These are absent in leeches.

Annelids have a true coelom, that is, one that is lined with cells originating from the embryonic **mesoderm**. The coelom is fluid-filled, which creates hydrostatic (water) pressure and acts as a **hydrostatic skeleton**. Annelids have a well-developed, closed circulatory system (one in which blood is limited to vessels) that is segmentally arranged. They also have a complete, one-way digestive tract with a mouth and anus. The digestive tract is not segmented.

ecosystems self-sustaining collections of organisms and their environments

coelom a body cavity

epidermis the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

chitin a complex carbohydrate found in the exoskeleton of some animals

exoskeletons hard outer protective coverings common in invertebrates such as insects

mesoderm the middle layer of cells in embryonic cells

hydrostatic skeleton a pressurized, fluid-filled skeleton

Respiration in annelids occurs primarily through their moist skin, although certain species have evolved specialized gills or use paired projections called parapodia in gas exchange. The annelid excretory system consists of paired nephridia found in each segment which function in excreting nitrogenous waste. In terms of nervous system structure, annelids possess a pair of ganglia (masses of nerve tissue) at the front end of the body; this serves as their brain. A double nerve cord runs along the **ventral** (belly) side of the body, and sends branches into each segment. Annelids have many types of sensory receptors, including **tactile** (touch) receptors, **chemoreceptors** (smell or taste), and **photoreceptors** for light. Some have well-developed eyes.

Annelids possess both circular and lengthwise muscle fibers. These, combined with their segmentation and hydrostatic skeleton, allow for great flexibility in movement. One part of the body is able to contract, or change its diameter and length, without affecting the rest of the body. It is believed that the need for elaborate mechanisms to control motion led to the development of the comparatively complex nervous system of annelids.

Some annelids are **hermaphroditic** while others are **dioecious**, that is, the sexes are separate. Some species have direct development, in which eggs develop directly into miniature versions of the adult. In other species, there is a larval stage. The annelid larval form is called the trochophore larva. Some annelid species can also reproduce asexually by **budding**.

ventral the belly surface of an animal with bilateral symmetry

tactile the sense of touch

chemoreceptors a receptor that responds to a specific type of chemical molecule

photoreceptors specialized cells that detect the presence or absence of light

hermaphroditic having both male and female sex organs

dioecious having members of the species that are either male or female

budding a type of asexual reproduction where the offspring grow off the parent

filter feeders animals that strain small food particles out of water

gametes reproductive cells that have only one set of chromosomes

Classes of Annelids

Annelids have been divided into three classes. The Polychaeta is exclusively composed of the bristleworms, the Oligochaeta the earthworms, and the Hirudinea include the leeches.

Polychaeta. The Polychaeta, or bristleworms, are a large and diverse group that includes polychaete worms, lugworms, ragworms, and sandworms, among other groups. It is the largest annelid class, with over 10,000 species, most of which are marine. Bristleworms are found in a wide variety of habitats and employ various feeding strategies. There are active burrowers whose habitat is at the bottom of the water, that which live within tubes they secrete, and pelagic (open ocean-dwelling) forms. Some are sedentary **filter feeders** that extract small food particles from the water while others process sediment. Also, some species are active predators; these generally prey on small invertebrates.

Bristleworms are characterized by paired paddle-like appendages called parapodia, used for gas exchange. These are covered with setae ("polychaete" means "many hairs"). Bristleworms have a well-developed head region, often with tentacles, and well-developed sense organs, including paired eyes, antennae, and sensory palps (projections). They are unusual among annelids because their reproductive organs are developed only during the breeding season; afterward, they wither away. The sexes are separate. **Gametes** (eggs and sperm) are shed into the water, and fertilization is external. Development is indirect, via a trochophore larval stage.

The polychaetes are believed to be the most primitive of the annelid classes. Some species, however, are highly specialized.

Various species of earthworms typically feed on organic debris and are capable of passing large quantities of soil through their guts.

Oligochaeta. The class Oligochaeta includes the familiar terrestrial earthworms, found just about everywhere, as well as some freshwater annelid species. Approximately 3,000 oligochaete species have been described.

"Oligochaete" means "few hairs," and oligochaete species generally have fewer setae than bristleworms. Oligochaetes lack parapodia, eyes, and tentacles. Many aquatic oligochaete species have gills to aid in gas exchange. Species typically feed on debris and algae. Earthworms are critical components of land-based ecosystems. By passing large quantities of soil through their guts, they speed the rate of nutrient turnover. Their burrowing activity also supplies the soil with air.

Most oligochaete species are hermaphroditic, with each individual producing both eggs and sperm. Earthworms, however, generally do not self-fertilize. During mating, two worms line up next to each other, with swollen regions called clitella placed next to each other. Sperm is released through grooves in the skin by both individuals, and these are passed to sperm receptacles in the other worm. The clitellum of each then secretes a ring of mucus that carries eggs from the oviduct (a tube for transporting eggs) and collects sperm from the sperm receptacles. This ring slides over the head of the worm, drops into the soil, and closes off, forming a cocoon. Fertilization takes place within the cocoon and a few eggs hatch two weeks later. Development in earthworms, as well as in the other oligochaetes, is direct, without a larval stage.

Hirudinea. The Class Hirudinea consists of the leeches. Leeches differ from other annelids in that most have a fixed number of segments. Leeches lack the hairlike setae of the other annelids and their bodies are somewhat dorsoventrally flattened (i.e., in such a way that the back and belly are close together). As with the oligochaetes, leeches are primarily hermaphroditic and exhibit direct development. There are about 500 described species.

ectoparasites organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

endoparasites organisms that live inside other organisms and derive their nutrients directly from those organisms

Most leeches are aquatic, and of these, nearly all are found in freshwater environments. A few species are terrestrial, but are found only in fairly warm, moist habitats. Leeches are almost all **ectoparasites**, which attach to the external surface of the host (as opposed to **endoparasites**, which live within their hosts). Segments at the front end of the animal are specialized to form suckers, while back-end segments are specialized for attaching to the host. The mouth contains teeth that are used to make an incision in the host. Leeches secrete an anticoagulant that keeps the blood of their host from coagulating, or clotting. They have been put to medical uses for thousands of years. In fact, bloodletting was extremely common as a standard prescription for a wide variety of ailments. The anticoagulants produced by leeches are still of great interest to medical scientists. SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

Bibliography

Brusca, Richard C., and Gary J. Brusca. *Invertebrates.* Sunderland, MA: Sinauer Associates, 1990.

Gould, James L., and William T. Keeton. *Biological Science,* 6th ed. New York: W. W. Norton and Co., 1996.

Hickman, Cleveland P., Larry S. Roberts, and Allan Larson. *Animal Diversity.* Dubuque, IA: Wm. C. Brown, 1994.

Antibody

Antibodies are protein molecules that function in the body's immune response. They are present throughout the circulatory and lymph systems, and are therefore exposed to all tissues in the body. An antibody is able to recognize and bind to a particular offending **antigen**. Antigens stimulate immune responses because they are recognized to be foreign, or "non-self." Invaders such as bacteria, viruses, fungi, toxins, and other foreign substances generally carry a variety of antigens on their surfaces.

antigen foreign substances that stimulate the production of antibodies in the blood

The antibody for a particular antigen functions by binding to that antigen. This results in one of two possibilities. The antibody may deactivate the antigen by either blocking its active site or otherwise changing it so that it can no longer harm host cells. Alternatively, an antibody may label the antigen-carrying object for destruction. In this case, one part of the antibody binds to the antigen while another part binds to immune system cells that are specialized to destroy antigens, cells such as **macrophages** or neutrophils.

macrophages a type of white blood cells that attacks anything foreign such as microbes

Foreign organisms such as bacteria or viruses typically possess numerous antigens on their surfaces. In addition, any particular antigen can usually be recognized by numerous antibodies, each of which binds to a slightly different site on the antigen. Each part of an antigen that can be bound by an antibody is called an **epitope**. With multiple epitopes on each antigen, and multiple antigens for any foreign invader, numerous antibodies can potentially be involved in an immune response.

epitope a localized region on a antigen that is recognized chemically by antibodies

Antibodies are made by immune system cells known as **B-lymphocytes**. B-lymphocytes are produced in the red marrow of bones. After they mature, the cells move to lymph nodes and begin to secrete antibodies into the lymph and blood. Each B-lymphocyte cell produces a unique antibody that targets a specific antigen.

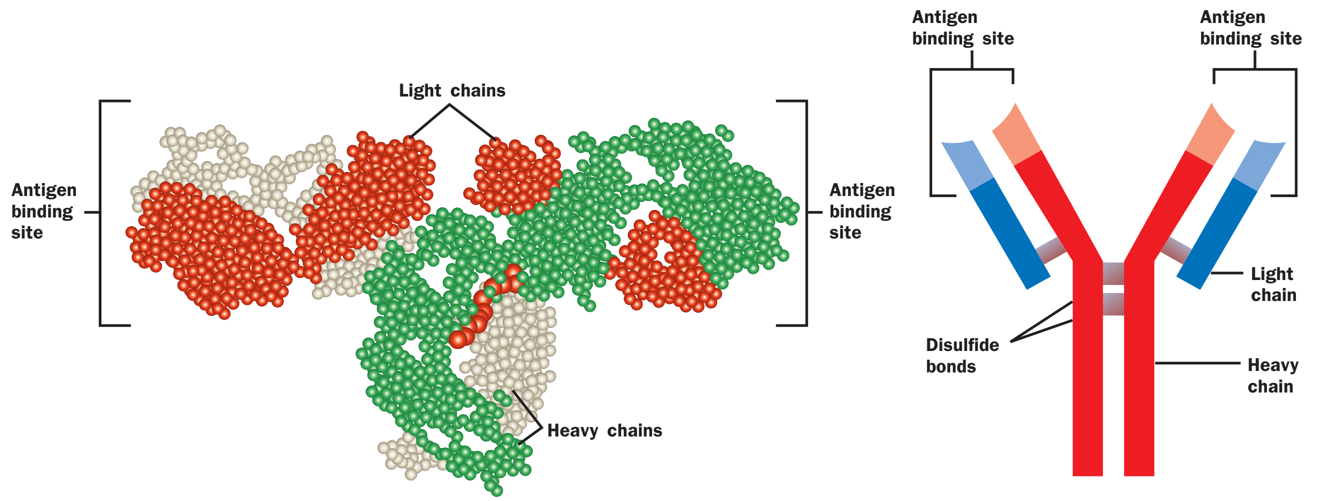
B-lymphocytes specialized cells produced from stem cells in the bone marrow that secrete antibodies that bind with antigens to form a pathogen fighting complex

Antibodies are Y-shaped proteins with binding sites at the tips of the branches of the Y. The antibody binds to an antigen in a way similar to how a key fits into a lock. The site on the antibody that binds to the antigen is known as the Fab region.

The antibody protein bundle contains two pairs of chains of proteins held together by disulfide bonds. The two identical longer chains, called heavy chains, form the base of the Y and one-half of each branch of the Y. The two identical shorter chains, called light chains, form the other halves of the branches of the Y. The ends of the branches of the Y contain a variable region on both the heavy and light chains. These are the Fab regions.

There is great diversity in Fab regions, which is essential to the body's ability to respond to a wide range of antigens. High diversity is possible because each heavy and light chain consists initially of numerous different segments, which can be spliced and combined in a variety of different ways. Consequently, there are thousands of possible heavy chains and light chains, with each giving rise to a slightly different binding site.

Antibodies are divided into five different classes. IgA antibodies function at mucous-producing surfaces such as the bronchioles, nasal passages, vagina, and intestine. They are also present in saliva, tears, and breast milk.



Antibodies are made by immune system cells known as B-lymphocytes. Redrawn from Hans and Cassady.

The function of antibodies of the IgD group is unclear. Most of these antibodies are not secreted into the bloodstream but, rather, are associated with B-lymphocytes.

IgE antibodies are found at mucous-producing surfaces, as well as in blood and tissues. They are responsible for many hypersensitive, or allergic, responses, in which the immune reaction to a relatively unharmful antigen is disproportionately intense. IgG antibodies are abundant in the bloodstream. They are able to cross the **placenta** and therefore provide the only protection for babies until their own immune systems mature. IgG antibodies are a very active antibody group that also plays a role in neutralizing toxins. IgM antibodies are largely found on B-lymphocytes.

placenta the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

Medical Uses of Antibodies

Vaccinations against various diseases are often made using antigens isolated from bacteria or viruses. Removed from their carriers, these antigens are in and of themselves harmless. However, they still trigger an immune response, after which antibodies specific for those antigens continue to circulate in the bloodstream. This allows those antibodies to be produced quickly and in great quantity in case of a future invasion by the entire pathogen.

Antibody-binding activity can also be used to diagnose disease. That is how HIV infections are identified.

In addition, attempts have also been made to produce antibody-related therapies for cancer. These aim to take advantage of the great specificity of antibodies to fight tumors. Some scientists are optimistic about the use of monoclonal antibodies in cancer therapy. These are antibodies that are specifically designed to recognize molecules present in tumor cells but not in healthy cells.

These antibodies can then be used to target antigens that are present only in small quantities, as is the case with many cancer cells. Monoclonal antibodies can function on their own by tagging cancerous cells for destruction, or can be attached to toxins or radioisotopes that help to destroy cancer cells.

Cancer cells do not typically induce an immune response in the host because they are not foreign. However, they can be transplanted to another organism, such as a mouse, where an immune response can be induced. After antibodies are harvested from the reaction, monoclonal antibodies can be isolated and cloned.

Jennifer Yeh

Bibliography

Curtis, Helena. *Biology*. New York: Worth Publishers, 1989.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Kuby, Janis. *Immunology*, 3rd ed. New York: W. H. Freeman, 1997.

Antlers and Horns

Antlers and horns are two kinds of ornamentation present on the front of the heads of mammals. Antlers consist of pure **bone tissue** and are shed and regrown annually, whereas horns consist of a bony knob and an exterior horn sheath and typically grow throughout life. Both structures were first seen in fossils from about 25 million years ago. Most even-toed **ungulates** (Artiodactyla) have head ornaments, such as deer, reindeer (antlers), antelopes, oxen, cows, and giraffes (horns). Some odd-toed ungulates (Perissodactyla), such as rhinoceroses, have horns. In most species, only males have antlers, but both females and males can have horns.

The number of branches, or "points" on a set of antlers can be used to indicate an individual's age and/or social status.

bone tissue dense, hardened cells that make up bones

ungulates animals with hooves

cartilage a flexible connective tissue

matrix the nonliving component of connective tissue

Antlers stem from the upper part of the frontal bone processes, called burrs. They grow by the accumulation of a **cartilage**-like bone **matrix**. The development of antlers begins in the spring with small nubs covered with "velvet," a layer of skin with oil and scent glands and nerves, as well as the sparse coating of hair that gives the velvet its name. Nutrients are supplied from the diet to the underlying bone through the velvet, and the antlers grow quickly throughout the summer. Not uncommonly in urban areas where the animal is malnourished or overpopulated the antlers are deformed, twisted and assymetrical because of inadequate nutrients. Toward the end of the velvet stage, growth slows and mineralization begins to increase. The velvet begins in spring and ends in the fall. During this period the interior of the bone becomes more dense, increasing the final weight from the beginning of mineralization process by about 70 percent. The velvet dies in the fall, and the animal rubs its antlers against tree trunks and branches to get the dead velvet off. Mating occurs later in the fall and in early winter when the antlers are at their peak size and weight, afterward the antlers are shed. Over a lifetime, the antlers usually grow more branches, or "points," so that an individual's approximate age can be estimated based on the number of points its antlers have.

Horns arise from an independent horn bone (the *os cornu*) that forms in the mesoderm (deep skin layers) of the forehead during fetal development, and the frontal bone fuses with the horn bones after birth. As the animal matures, the horn bones grow longer and wider, and the skin around the bone (the ectoderm) forms a horny outer covering, with the growth originating from the base. As it grows, the horn accumulates layers, and the horns of many species have grooves around them, the rings of which can be counted to determine the age of the animal. Although the structure of a horn is a single shaft, there are variations such as spirals and hooks or horn parts that are greatly broadened like those of the African buffalo, whose horn bases meet at the center of the head, and are broad and flat to form a giant shield over the top of the skull before curving up and outward.

Antlers and horns can be used as a defense against predators, but scientists believe that their primary function is to establish an individual's ranking within its species. Many animals point the ends of their horns or antlers away from their target during an advance, and adaptations such as branches, rings, and grooves facilitate direct, nonlethal combat with similarly adorned individuals. Antlers and horns are also used in ritual fights among individuals of the same species. Their size and scent indicate to other members of the same species an individual's rank and maturity, and this information often avoids the need to fight to establish the same ranking.

Jean K. Krejca

Bibliography

Nowak, Ronald M. *Walker's Mammals of the World*, vol. 5. Baltimore: Johns Hopkins University Press, 1991.

Parker, Sybil, ed. *Grzimek's Encyclopedia of Mammals*, vols. 4–5. New York: McGraw-Hill, 1990.

Apiculture

Apiculture is the science of beekeeping. Humans have collected honey from wild bee hives for more than 8,000 years, as shown in Mesolithic rock paintings dating from 6000 B.C.E. By 2500 B.C.E., Egyptians were keeping bees in artificial hives. Hives exploit the honeybees' natural tendency to build nests in cavities, and allow apiculturalists to easily move (via boat, wagon, truck) and manipulate bee colonies. This mobility has allowed beekeepers to introduce honeybees around the world: The first hives were brought to the New World in the 1620s by European settlers.

Primitive hives were made of hollow logs, holes built in mud walls, or cones of mud, earthenware, or thatch. A modern apiary hive is a series of stacked boxes. The bottom box serves as the brood chamber where larvae develop; the upper boxes provide a space to store honey. Each box contains eight to twelve frames, which are set so they approximate the distance between combs in a natural hive. Bees then build their comb on the frames, which can be removed individually. Beekeepers remove the wax caps that cover each cell of the comb and let the cells' contents drip out by gravity, or use a specialized machine to spin the frames and draw the comb contents out by centrifugal force. The honey is then filtered and stored. Honey quality is determined by its flavor, clarity, and color.

The Products of Apiculture

The most widely cultivated and economically important bee species is the European honeybee (*Apis mellifera*), but beekeepers also keep a range of other species from the subfamilies Apidae (honeybees) and Meliponinae (stingless bees). Honeybees gather large amounts of flower nectar and pollen.

This beekeeper is holding one of the eight to twelve frames that the apiary box would contain.

They transform nectar into honey by evaporating water through fanning the nectar with their wings, and by adding **enzymes** produced by specialized glands on their bodies. Finally, the bees usually seal the finished honey in the hexagonal cells of their comb. Pollen is a source of protein, fats, and vitamins for the bees; carbohydrates from honey provide vital energy. While gathering pollen and nectar, bees cross-pollinate flowers and allow or improve the production of seeds and fruit. Economically, honeybees are more valuable as pollinators than as honey producers. Farmers rent more than one million colonies each year to pollinate crops valued at more than $10 billion. Unlike other pollinating insects, bees can be easily moved to agricultural fields where crops need to be pollinated.

enzymes proteins that act as catalysts to start biochemical reactions

Most beekeepers maintain hives for honey, but bees also produce other useful products. Beeswax from cell caps and old combs is used for high-quality candles, pharmaceuticals, lotions, and friction-reducing waxes for skis and surfboards. As well as honey, several other bee products are sources of food for humans. Bee brood (young bees that are housed in the brood comb of a hive) is consumed as a form of meat in many non-European countries. Food additives for humans and domestic animals are made from bee-collected pollen and from royal jelly, which bees produce as food for their larvae. Several bee products are also used as medicines. Since the 1930s, researchers have been refining extraction techniques to collect bee venom, because bee stings can relieve the symptoms of arthritis, rheumatism, and other diseases. Propolis, a gluelike plant resin that bees use to maintain the comb, is used in cosmetics and healing creams and may have antibiotic or anesthetic properties. Propolis was formerly an ingredient in some varnish, including the varnish on Stradivarius violins.

Threats to Apiculture

Cultivated bee colonies are susceptible to a number of diseases, parasites, and insect predators. Honeybee populations declined dramatically across the United States during the 1990s, when tracheal and *Varroa* mites destroyed up to 90 percent of hive populations in some areas. Another recent and widely publicized threat to apiculture comes from Africanized bees, *Apis mellifera suctellata*. This subspecies of the European honeybee commonly takes over the hives of its more docile European relatives. Africanized bees were imported from Africa to Brazil in 1957 with the hopes that their hardiness in tropical conditions would improve the Brazilian apiculture business. Unfortunately, some colonies escaped captivity and founded populations in the wild or took over other cultivated hives. The bees steadily spread northward into the United States, reaching Texas in 1990 and continuing to move up both coasts. The presence of Africanized bees in a hive makes beekeeping difficult because they are aggressive toward handlers, tend to swarm and leave the hive, and produce less honey than European honeybees. These bees are famous for their easily provoked mass stinging, which can be lethal to humans and other animals and has caused the deaths of several people. Public concern over Africanized bees has led to increased insurance liability for beekeepers, since they have had to pay more insurance because of the risk of keeping hives that may be taken over by Africanized bees, hence posing a threat to humans and animals in the area. Beekeepers in regions of Venezuela where people have been killed by Africanized bees have had their hives burned and been physically attacked by other citizens, regardless of whether their hives housed the Africanized bees that caused the problem. Many beekeepers also voluntarily destroyed their hives because they were unable to handle the more aggressive bees. SEE ALSO FARMING.

Emily H. DuVal

Bibliography

Crane, Eva. *Bees and Beekeeping: Science, Practice, and World Resources.* Ithaca, NY: Comstock Publishing Associates, 1990.

———. *The World History of Beekeeping and Honey Hunting.* New York: Routledge, 1999.

Eckert, John E., and Frank R. Shaw. *Beekeeping.* New York: The Macmillan Company, 1960.

Flakus, Greg. *Living with Killer Bees: The Story of the Africanized Bee Invasion.* Oakland, CA: Quick Trading Company, 1993.

Gojmerac, Walter L. *Bees, Beekeeping, Honey, and Pollination.* Westport, CT: AVI Publishing Company, Inc., 1980.

Aposematism

The term "aposematism" is commonly used as a synonym for warning coloration (i.e., something that is aposematic is warningly colored). The word literally means "away signal." Aposematism is the combination of a conspicuous signal and an unprofitable trait in a prey species.

Conspicuous signals are most often bright colors presented in banded or contrasting patterns. The banding pattern of coral snakes or the contrasting colors of Heliconius butterflies are obvious examples. These signals are easily seen over large distances. Auditory signals are also used. For example, some arctiid moths **emit** ultrasonic clicks upon approach of a bat predator. Rattlesnakes, with their caudal rattle, warn of their venomous bite.

emit to send out or give off

The rattle of the rattlesnake is an aposematic signal that warns its predators of its venom.

An additional possibility is the use of offensive or unpleasant odors to signal unprofitable traits.

Unprofitable traits include anything that harms the predator or reduces its efficiency. Some examples are the distastefulness (unpalatability) of butterflies and other insects, the stings of wasps, the bites of snakes, the skin toxins of some tropical tree frogs and **salamanders**, or perhaps even an exhaustive chase between a bird and butterfly that ends with wasted energy for the bird.

salamanders four-legged amphibians with elongated bodies

Aposematism works by advertising to potential predators, rather than by hiding or escaping from them. Advertising to predators seems dangerous, but the obvious signals allow predators to quickly learn which prey are unprofitable. Predators encountering aposematic animals will have an unpleasant experience. This interaction may be so unpleasant that the predator immediately associates the visual or auditory characteristics of the prey with the experience. When the predator subsequently encounters the same signal, it will be more cautious and may avoid the prey. Not all unprofitable traits are so unpleasant. Some are only mildly deterrent and require frequent resampling by predators in order to reinforce the avoidance response.

Benefits and Costs of Aposematism

Aposematism has benefits for predator and prey. Efficient interactions between predator and prey in this context allow each to pursue other activities such as mating, care for offspring, and feeding. The prey benefit by avoiding death or injury because trained predators will not attack them as frequently as naive predators. Predators benefit by not expending energy on suboptimal prey.

There can also be costs for prey that have unprofitable traits. For example, unprofitable traits such as unpalatability require special chemicals to be manufactured or sequestered from host plants and these chemicals may be expensive to produce or detoxify.

Batesian mimicry a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

Established aposematic signals may give rise to further interactions among species. Unprotected prey species could benefit by appearing the same as an aposematic species if they share the same predators. Predators might mistakenly avoid an unprotected prey if it closely resembles a well-established signal. This type of interaction is known as **Batesian mimicry**. Müllerian mimicry can also arise between two similar signals. In that case, two aposematic species converge on a common signal. In effect, each species contributes to the work of training the predators. In times of prey scarcity, predators may be forced to consume relatively unprofitable prey. This may lead to predator specialization on such unprofitable prey. For example, in Mexico, black-headed grosbeaks and black-backed orioles both consume large numbers of distasteful monarch butterflies when the butterflies are overwintering.

Adopting an aposematic lifestyle may alter prey behavior and lead to changes in other aspects of prey biology. This is because aposematic prey no longer require other defenses such as escape behaviors. For example, Heliconius butterflies have evolved differences from their palatable relatives that allow them to live longer, fly in more microhabitats, invest more energy in reproduction, and be more selective about where they lay their eggs.

Aposematism and Evolution

Evolutionary biologists have pointed out that it is paradoxical that an association between conspicuous signals and unprofitability could evolve. It would be difficult for a conspicuous signal to evolve in prey with unprofitable traits because predators will quickly sample the prey and kill it. Thus, any genes for the conspicuous signal are eliminated from the population. An alternative scenario is for unprofitability to evolve in prey with conspicuous coloration. However, this is not likely because being conspicuous without a defense offers no protection and simply makes the prey more visible to predators. Of course, evolution need not follow such mutually exclusive pathways, and unprofitability and conspicuous signals could evolve together.

A debate has developed over whether individual selection is sufficient for aposematism to evolve. Individual selection works by aposematic individuals training their own predators and passing on more genes than non-aposematic individuals. Evolutionary biologists have questioned whether aposematic individuals are able to survive the predator's attacks. Some experimental evidence suggests that aposematic animals, especially insects, are durable and can survive sampling by the predator. This means that one unprofitable individual with a newly evolved conspicuous signal could train predators in the area to avoid its own color pattern. Assuming this individual does not suffer damage and can reproduce normally, it will pass on genes for the conspicuous signal. However, if the individual dies or has fewer offspring than nonaposematic individuals because of predator sampling, then individual selection might not be sufficient by itself to cause aposematism to evolve. In this case, sharing genes for the aposematic traits with other individuals could aid in the evolution of aposematism.

Research on aposematism is ongoing and resolving the debate over how aposematism evolves will require experiments and observations of predation on aposematic species in the wild. SEE ALSO MIMICRY; PEPPERED MOTH.

Ryan I. Hill

Bibliography

Chai, Peng, and Robert B. Srygley. "Predation and the Flight, Morphology, and Temperature of Neotropical Rain-Forest Butterflies." *American Naturalist* 135, no. 6 (1990):748–765.

Endler, John. "Interactions between Predators and Prey." In *Behavioral Ecology: An Evolutionary Approach*, 3rd ed., eds. John R. Krebs and Nicholas B. Davies. Oxford, U.K.: Blackwell Scientific Publications, 1991.

Fink, Linda S., and Lincoln P. Brower. "Birds Can Overcome the Cardenolide Defence of Monarch Butterflies in Mexico." *Nature* 291 (1981):67–70.

Gilbert, Lawrence E. "Biodiversity of a Central American Heliconius Community: Pattern, Process, and Problems." In *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, eds. Peter W. Price, T. M. Lewinsohn, G. Wilson Fernandes, and W. W. Benson. New York: Wiley and Sons, Inc., 1991.

Guilford, Tim. "The Evolution of Conspicuous Coloration." *American Naturalist* 131 (1988):S7–S21.

Järvi, T., B. Sillen-Tullberg, and C. Wicklund. "The Cost of Being Aposematic: An Experimental Study of Predation on Larvae of *Papilio machaon* by the Great Tit *Parus major*." *Oikos* 36 (1981):267–272.

Mallet, James, and Mathieu Joron. "Evolution of Diversity in Warning Color and Mimicry: Polymorphisms, Shifting Balance, and Speciation." *Annual Review of Ecology and Systematics* 30 (1999):201–233.

Aquaculture

Aquaculture is the rough equivalent of agriculture on land. Aquaculture is the raising of fish, shellfish, or aquatic plants to supplement the natural supply. Although aquaculture includes the growing of aquatic plants, most people use the term to mean fish and shellfish farming. Fish and shellfish are raised as food under controlled conditions all over the world. The goal of fish and shellfish culture is to increase the yield of useful products, including increased food production.

While most aquacultural production is in food items such as fish, **mollusks**, and **crustaceans**, some marine algae, kelp, and other aquatic plants are raised commercially. Cultured pearls are created by placing small bits of material in the shells of young oysters. Various types of floating algae and phytoplankton are also grown, primarily as food for animals.

mollusks large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

Aquatic animal husbandry includes all of the activities terrestrial farmers and ranchers have used, such as selective breeding, care of the young, feeding, sanitation, environmental modifications, and harvesting. Species having characteristics that make them suitable and practical for culturing are selected for extensive cultivation. This includes considerations of con-

Aquaculture worker sorts salmon as they come down a water-filled chute in Anacortes, Washington.

sumer choice. Aquaculture is relatively expensive, so most aquacultural products are luxury items such as trout, oysters, and shrimp. Some less expensive fish species, such as carp and tilapia, are successfully cultured in China, India, and southeast Asian countries.

History of Aquaculture

Aquaculture has been practiced for thousands of years. Chinese in the fifth century C.E. practiced aquaculture, and temple friezes (ornamented bands on a building) dating from the Middle Kingdom of Egypt (2052–1786 B.C.E.) depict what appear to have been intensive fish farming. The ancient Romans are known to have cultivated oysters.

Commercial Importance

As suitable arable land diminishes and the world's population increases, aquaculture is expected to become increasingly important. Aquaculture is an environmentally friendly source of high-quality animal protein. Many countries with limited arable land, such as Japan, are actively developing an aquaculture industry.

Problems of Aquaculture

Aquacultural practices are not as efficient as they could be. Lack of capitalization in developing countries, inefficient and outdated techniques, and poor marketing all contribute to the lack of commercial success in aquaculture. Another factor limiting production is the lack of suitable domesticated species. Only a few aquatic animals are used, and much of the life cycle of these animals is not controlled. Research into new species, development of commercially viable **hybrids**, and new techniques of breeding should improve the efficiency of commercial aquaculture. Continued research and the dissemination of new skills and techniques holds promise for substantially increased aquacultural production, perhaps exceeding 30 million metric tons (33 million short tons) per year.

hybrids offspring resulting from the cross of two different species

Selection of Suitable Species

In order to be aquaculturally useful, species must be able to reproduce in captivity, have robust eggs and larvae, feed on inexpensive food, and grow quickly to harvestable size. For example, trout and carp have large, hardy eggs; mullet fry are easily collected; and young oysters are easily collected and grown. So these were the species of choice for aquaculture. The feeding habits of species also limit suitability. Wide-ranging plankton feeders, such as herring, are not suitable. **Sessile** animals, such as oysters and mussels, which filter the water for their food, can be cultured extensively but still must be supplied with a rich food supply if they are to grow rapidly.

sessile immobile, attached

Selective Breeding

Aquaculturists, like their terrestrial counterparts, selectively breed for desirable traits in captive organisms. Since the traits that enhance success in a wild population are often inconsistent with a successful captive population, these traits must be eliminated through breeding. Desirable characteristics include fast growth and a body shape that provides more edible tissue. Since captive populations are usually held at a higher density than wild populations, disease is a problem. So resistance to disease is desirable. Since aquatic animals usually produce many offspring per generation, selective breeding is somewhat easier than with terrestrial animals.

One desirable characteristic of captive populations is an accelerated onset of sexual maturity. This event is triggered in the wild by a combination of factors, including water temperature, length of daylight hours, and salinity. These factors in turn act on the animal's pituitary gland, which controls the output of sexual hormones. Attempts to control environmental factors to accelerate spawning have been largely unsuccessful, except in the cases of oysters and shrimp. A more generally successful method involves the injection of pituitary hormones. This is expensive and labor intensive so alternatives are being sought.

Evolving Technologies

Large-scale fish culture projects, if properly managed, have the potential to produce thousands of tons of fish. Community ponds and reservoirs created by the damming of tropical rivers are often designed to include large-scale fish farming. When a new reservoir is created, nutrients from the soil trigger the growth of abundant algae and aquatic plants. So herbivorous fish must be included in the plans. These fish can provide the first harvested "crops."

Fish "ranching" is also widely practiced. For example, salmon are raised in hatcheries then released into wild streams. This allows the establishment of new salmon runs, the reintroduction of salmon into previously used streams, and the replenishment of depleted stocks. This form of aquaculture also helps alleviate losses due to human-induced environmental degradation.

Hybridization is another technique coming into use in aquaculture. Crossing one trout with another trout having seagoing tendencies enables breeders to send fish to new oceanic pastures and then to harvest them when they return to freshwater to spawn. Promising crossbreeding experiments with tilapia have also resulted in species exhibiting hybrid vigor.

Both coal-fired and nuclear power plants use water for cooling. This water is generally discharged into a reservoir of evenly warmed water. This water has significant potential to be used in aquacultural programs. Many aquatic animals grow more rapidly in somewhat warmer water. Other species, such as carp and catfish, prefer warmer water. Many of the farm-raised catfish available in supermarkets are grown in ponds warmed by water from power plants.

Pelagic (open ocean) fish have not been raised in captivity with any great success. They are desirable species because they grow fast. But they require huge quantities of food fish or other pelagic organisms, which are also hard to raise in captivity. As research continues, it is likely that new aquacultural techniques will be developed that will permit the farming of many new species such as spiny lobsters, crayfish, octopus, and others not presently husbanded. Improved techniques will increase the yield of existing aquacultural species. As demand continues to increase for world food supplies, aquaculture promises to grow into a thriving and productive industry. SEE ALSO FARMING.

Elliot Richmond

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Lovell, Tom. *Nutrition and Feeding of Fish.* New York: Van Nostrand Reinhold, 1988.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth, 1990.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer, 1987.

Aristotle

Philosopher
384 B.C.E.–322 B.C.E.

Aristotle, Greek philosopher and scientist, was born in 384 B.C.E. in Stagira, northern Greece. He died in 322 B.C.E. He is considered one of the most influential thinkers in history.

Aristotle's father was the physician to the king of Macedonia. Being a doctor's son most likely influenced his strong interest in science. Upon the death of his father in 367 B.C.E., Aristotle was sent to the Academy of Plato in Athens. He remained there for twenty years, first as a student, then as a teacher. He studied a wide variety of subjects, earning the nickname "the reader." After Plato's death, Aristotle left Athens and traveled about for twelve years. For a number of years during this time, he tutored Alexander the Great, the son of Phillip II of Macedonia. Aristotle married once or twice and had two children. At the age of fifty, he returned to Athens and founded his own school, the Lyceum. There, for twelve years, Aristotle studied a wide range of subjects, especially nature. When Alexander the Great died in 323 B.C.E., Aristotle feared political persecution, so he left Athens. He moved to Chalcis in central Greece, where he lived for a year until his death.

Aristotle, philosopher and biologist.

Aristotle made many important contributions to biology. He was the first to classify animals. He grouped animals as having blood or not in his most basic classification. His observations led to the knowledge that mammals are warm-blooded, have lungs, breathe air, and suckle their young. In classifying animals, Aristotle realized that they should not be grouped based only on their external parts. Instead, he understood that even animals that appeared very different could be related. Aristotle identified four means of reproduction: the **abiogenetic** origin of life from nonliving mud; **budding** (**asexual reproduction**); **sexual reproduction** without **copulation**; and sexual reproduction with copulation. Aristotle did not believe in natural selection, or survival of the fittest. Instead, he believed in teleology, that plants and animals have natural goals. Their form could be fully understood only when those goals were known. Aristotle believed that all organisms are perfectly adapted to their surroundings. His observations led to the principle that general structures appear before specialized ones, and that tissue forms before organs.

budding a type of asexual reproduction where the offspring grow off the parent

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

abiogenetic pertaining to a nonliving organism

sexual reproduction a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

copulation the act of sexual reproduction

mutations abrupt changes in the genes of an organism

Aristotle's theory is in opposition to Charles Darwin's "theory of evolution by natural selection." Darwin argued that random genetic **mutations** produced slightly different characteristics in members of a species. Those individuals with advantageous traits would reproduce more successfully than those without them, resulting in a constantly evolving population. Darwin's ideas of constant change, chance, and chaos are in contrast with Aristotle's explanation of biology through order and purpose.

Although it is known that Aristotle wrote a huge amount of material, most of it has been lost. The few documents that remain appear to be notes he used for teaching. Also, it is not certain whether some of the books attributed to him were actually written by him or by others who were summarizing his writings and teachings.

Aristotle made lasting contributions in fields other than the natural sciences. These were philosophy, logic, ethics, and psychology.

Denise Prendergast

Bibliography

Muir, Hazel, ed. *Larousse Dictionary of Scientists.* New York: Larousse Kingfisher Chambers Inc., 1994.

The New Encyclopedia Britannica, 15th ed. Chicago: Encyclopedia Britannica, Inc., 1993.

Internet Resources

University of California, Berkeley, Museum of Paleontology. <http://www.ucmp.berkeley.edu/history/aristotle.html>.

Arthropoda

trilobites an extinct class of arthropods

The phylum Arthropoda is the largest and most varied in the animal kingdom. It includes well over one million described species. This represents approximately three-quarters of all known biological organisms, living or extinct. Countless arthropods remain undescribed (not yet named and studied), and the actual number of living species could be as high as ten million or more. Some of the more well-known arthropods include insects, crustaceans, and spiders, as well as the fossil **trilobites**. Arthropods are found in virtually every known marine (ocean-based), freshwater, and terrestrial (land-based) ecosystem, and vary tremendously in their habitats, life histories, and dietary preferences.

Characteristics of Arthropods

exoskeleton a hard outer protective covering common in invertebrates such as insects

chitin a complex carbohydrate found in the exoskeleton of some animals

molted the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

Despite the remarkable variety of arthropod species, all share aspects of a single basic body plan. All arthropods possess a stiff **exoskeleton** (external skeleton) composed primarily of **chitin**. In some species, lipids, proteins, and calcium carbonate may also contribute to the exoskeleton. The external skeleton offers organisms protection as well as support for the body. Its walls provide anchors for the attachment of muscles. The exoskeleton is incapable of growth, and is **molted** (shed) repeatedly during the growth of the animal. This process is called ecdysis. Molting allows for rapid growth until the newly secreted exoskeleton hardens.

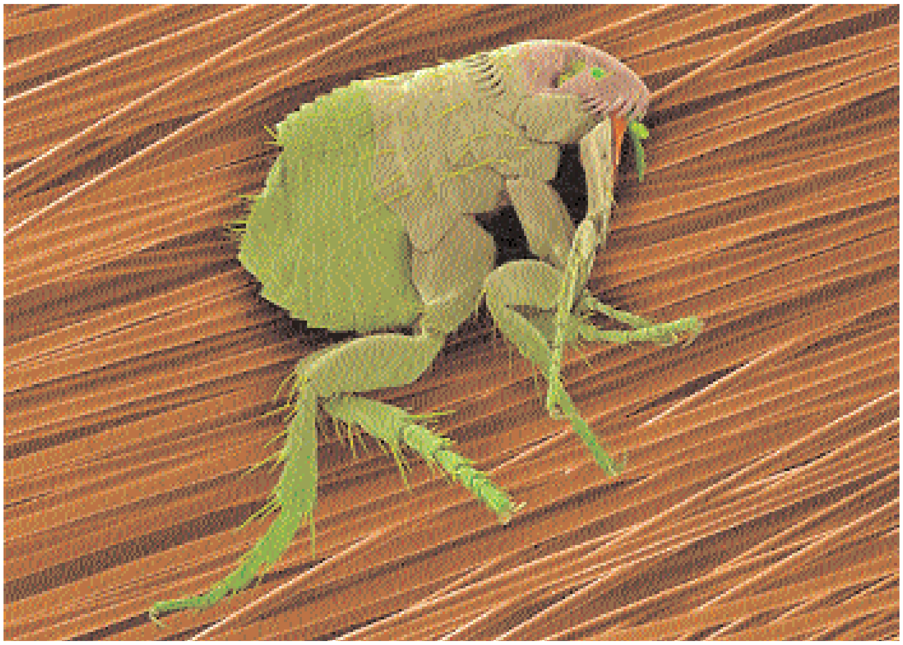
Arthropod bodies are divided into segments. However, a number of segments are sometimes fused to form integrated body parts known as tagmata. This process of fusion is called tagmosis. The head, thorax, and abdomen are examples of tagmata. Arthropods also have appendages with joints (the word "arthropod" means "jointed feet"). In early, primitive anthropods, each body segment was associated with a single pair of appendages (attachments). However, in most species some appendages have been modified to form other structures, such as mouthparts, antennae, or reproductive organs. Arthropod appendages may be either biramous (branched) or uniramous (unbranched).

compound eyes multifaceted eyes that are made up of thousands of simple eyes

hemocoel cavity between organs in arthropods and mollusks through which blood circulates

Some arthropods have highly developed sense organs. Most species have paired **compound eyes**, and many also have a number of simpler eyes called ocelli. Arthropods have an open circulatory system (without blood vessels) that consists of a tube that is the heart and an open **hemocoel**, the coelom of the animal, in which blood pools. Arthropods also have a complete gut with two openings, the mouth and the anus.

Gas exchange in the phylum occurs in various ways. Some species have gills, while others employ tracheae, or book lungs. The tracheal respiratory system consists of external openings called spiracles that are linked to a system of branched tubules which allow respiratory gases to reach internal tissues. Arthropods are characterized by a brain as well as a nerve ring around the area of the pharynx, in the oral cavity. A double nerve cord extends back-



This scanning electron micrograph of a dog flea reveals the structure of its rigid exoskeleton, a characteristic of arthropoda, in detail.

wards along the **ventral** surface of the body, and each body segment is associated with its own ganglion, or mass of nerve cells. In most arthropod species, the sexes are separate. Fertilization usually occurs internally, and most species are egg laying. While some species exhibit direct development, in which eggs hatch as miniature versions of adults, other species pass through an immature larval stage and undergo a dramatic metamorphosis before reaching adult form.

ventral the belly surface of an animal with bilateral symmetry

Major Groups of Arthropods

Arthropods are divided into four subphyla. These are the Chelicerata, the Crustacea, the Uniramia, and the Trilobita. The last consists exclusively of extinct forms.

Subphylum Chelicerata. The chelicerates include the **horseshoe crabs**, scorpions, spiders, ticks, mites, sea spiders, and other related species. They are characterized by the presence of two tagmata (fused segments), a cephalothorax (fused head and thorax), and an abdomen. They possess six pairs of unbranched appendages. These include a pair of **chelicerae**, a pair of pedipals, and four pairs of legs.

horseshoe crab a "living fossil" in the class of arthropods

chelicerae the biting appendages of arachnids

The class Arachnida includes scorpions, spiders, ticks, and mites. There are over 100,000 described species in this class. The majority are land-based and most are found in fairly warm, dry habitats. Like other chelicerates, arachnids have six pairs of appendages. The first pair, the chelicerae, is typically adapted for killing and consuming prey. The second pair, pedipals, have a sensory function, and may include both receptors sensitive to touch and receptors sensitive to chemical changes. The final four pairs of appendages are walking legs. Arachnids have fairly simple eyes that register only changes in light levels. Of the arachnids, spiders (which make up the Order Araneae) are the most diverse. All spiders are able to spin webs using modified appendages called spinnerets. These are located in the rear abdomen. Webs are used for a variety of purposes in different species. In many, they are used to catch prey and to build nests. Spiderwebs can even be used for movement, as in those species that create parachutes to catch the air, enabling them to descend safely. Many spiders have toxic poisons to immobilize prey or to use in self-defense; perhaps the most famous of these is the black widow. Spiders prey primarily on insects, and are often ecologically important for this reason. Scorpions (order Scorpiones) are arachnids characterized by a pair of claws and a long, jointed tail with a poisonous sting at the end. Ticks and mites (order Acari) are ectoparasites. They embed themselves in the skin of vertebrate animals and feed on blood. Certain tick species carry diseases such as Lyme disease and Rocky Mountain spotted fever.

The class Merostomata includes the horseshoe crabs. Horseshoe crabs are an extremely ancient marine lineage. Only five species have survived to the present. They are characterized by a long appendage called a telson that projects from the rear end of the body, which is used in flipping the animal over when it is lying on its carapace. They use book gills to breathe and generally feed on small invertebrates.

The class Pycnogonida consists of the sea spiders. There are 2,000 described species, all of which are marine. Most species are fairly small. Like spiders, they have small bodies with long legs. They use an extensible proboscis to suck nutrients from the bodies of soft invertebrates.

Subphylum Crustacea. The subphylum Crustacea includes lobsters, crabs, shrimp, barnacles, and other related organisms. There are approximately 40,000 described species. The majority are marine, but there are freshwater and land-based representatives as well. Unlike other arthropods, the crustacean exoskeleton often includes calcium carbonate, which offers added rigidity. Crustaceans generally have three tagmata: a head, a thorax, and an abdomen. There are two pairs of antennae, complicated mouthparts consisting of two pairs of maxillae (upper jaws) and one pair of mandibles (lower jaws) used in food processing, and a series of branched appendages. These appendages are associated with the thorax. Some function as walking legs while others may be specialized for capturing prey. The abdomen is sometimes equipped with swimmerets (small swimming legs that are also used for other purposes, including as copulatory organs in males and for egg carrying in females) and a tail that is composed of modified appendages in addition to a telson. Some crustacean species have well-developed sensory systems, including highly sensitive compound eyes on stalks, ears, chemoreceptors for taste and/or smell, telson and hairs or bristles that function as touch receptors. Crustaceans have a wide variety of ways to capture food. Some are **filter feeders**, while others are **scavengers** or predators. In most species, the sexes are separate. Some species pass through what is called a nauplius larval stage prior to metamorphosing into adults, while others have direct development and bypass the larval stage. Crustaceans use gills to inhale and exhale air.

filter feeders animals that strain small food particles out of water

scavengers animals that feed on the remains of animals that they did not kill

The class Branchiopoda include the brine shrimp, water fleas, and other related groups. Species in this class are generally small and tend to live in freshwater habitats or in salty lakes. Most species have a large number of segments with minimal fusing of segments, or tagmiosis. The majority are filter feeders.

The class Maxillopoda includes the barnacles and related groups. Maxillopods have a head, thorax, and abdomen along with a telson projecting from the back end of their bodies. Most species are small and feed using their maxillae. Barnacles, however, are sessile (immobile) filter feeders. They are often seen in large numbers, anchored to structures such as ship bottoms or piers.

The class Malacostraca has over 20,000 species and is the largest group within the Crustacea. Most species are marine, but others are freshwater or terrestrial. The largest order, Decapoda, includes shrimp, crabs, crayfish, and lobsters. Other well-known malacostracans include **krill** as well as a terrestrial group, the sowbugs. The malacostracans exhibit a variety of feeding strategies. The more primitive species tend to be filter feeders. Others are scavengers. Crabs and lobsters are active predators. They have a pair of chelipeds, also known as claws or pincers, which are used to capture and carry prey. Pincers have evolved to serve other functions as well, however, and in various species are used for digging, defense from predators, or in courtship rituals. Some malacostracan species are parasites. Many malacostracans, including many of the larval forms, are critical components of oceanic plankton, a critical component of oceanic food webs.

krill an order of crustaceans that serves as a food source for many fish, whales, and birds

Subphylum Uniramia. Uniramia is the largest subphylum within the arthropods. It includes the centipedes, the millipedes, and the insects, as well as a few smaller related groups. The name Uniramia comes from the unbranched appendages that characterize members of the group. Species generally have two or three tagmata. There are one pair of antennae and two pairs of maxillae. Respiration occurs via tracheae. Uniramians generally have separate sexes.

The class Chilopoda includes the centipedes, a diverse group of over 5,000 species. These terrestrial organisms are characterized by a very large number of segments, often well over 100. The largest centipedes reach lengths of up to 25 centimeters (10 inches). Each centipede body segment, aside from a few at the head and tail of the organism, is associated with a single pair of legs. All centipedes are carnivorous, and the appendages that are frontmost have been modified to form large poisonous fangs that are used to immobilize prey. Centipedes feed primarily on earthworms and insects. Species of centipedes are generally egg laying, and in some, the female remains to guard the eggs. Development is direct—there is no larval stage. In some species, juveniles hatch with the same number of segments as an adult, while in others, individuals add segments with each molt.

The class Diplopoda consists of the millipedes, a group that includes over 8,000 described species. Like centipedes, millipedes have a large number of segments. However, they differ from centipedes in that each segment has two pairs of legs rather than just one. Millipedes do not have fangs, and in fact, most species are either herbivorous or scavengers. Many millipedes do, however, exude (ooze) poisonous or noxious substances as a defense against potential predators. Millipedes are often found in decaying organic matter or in moist soils. They are effective burrowers. Like some species of centipedes, they lay eggs in nests that are attended by the female. Millipedes add body segments as they grow and molt.

This chewing louse belongs to the order Mallophaga. Its head is wider than its thorax in order to accommodate its complex mouthparts. Most lice are host-specific, and feed on their hosts' hair, feather, and skin scales.

pheromones small, volatile chemicals that act as signals between animals and influence physiology or behavior

The class Insecta is the largest class in the animal kingdom. There are nearly one million described species, and no doubt countless others that have yet to be named. Insects are found in a wide variety of terrestrial and freshwater habitats, and there are even a few marine forms.

Insects have three tagmata, or fused segments: a head, a thorax, and an abdomen. They have a pair of antennae; a series of complex, highly variable mouthparts, which vary greatly from species to species; and three pairs of legs. Both the antennae and mouthparts are evolved from modified appendages (walking legs, most likely). Most insect species also have two pairs of wings, although these are absent in a few very primitive species and have been reduced in others, becoming nonfunctional or adapted for a different purpose. Insect legs and wings are associated with the thorax, not the abdomen, which does not usually carry appendages except for appendages that are evolved into reproductive organs. A theory of the origin of insect flight maintains that wings evolved from external gills that were present in certain primitive groups. Aside from their breathing function, these gills served as flaps that assisted insects in leaping and jumping, and were advantageous because they made escape from predators more likely. Gradual increases in wing size allowed for gliding movement, and ultimately for flapping flight.

Insects have highly elaborated sense organs. For example, they may possess a pair of compound eyes as well as several cranial ocelli, or simple eyes. The compound eye is made up of hundreds of individual facets, or parts. Each facet points in a different direction. An individual facet provides information regarding the color and intensity of light but does not provide a complete image. Together, however, the numerous facets create a combined, mosaic image of the world. Compound eyes are particularly effective for seeing nearby objects; distance vision is not as good. The greatest advantage of compound eyes is that they are able to register changes in the visual field much more quickly than eyes with lenses. This is particularly important for detecting motion, as well as for the rapid maneuvering required during flight. Many insects also have well-developed ears. Some species also have an extraordinary ability to detect chemicals. This is especially true in species that use chemical signals called **pheromones** for detection of a sexual partner. The pheromones are emitted by receptive females and picked up by males, which use them to locate potential mates.

Insects breathe through the tracheal system, described earlier. Because of limits on the spread of gas in the trachea, insects are restricted to a comparatively small size. The excretory system of insects consists of structures known as Malpighian tubules. The sexes are separate in insects, and fertilization occurs internally in most species.

The variety in patterns of insect development is exceptionally high. Most insects pass through several stages before reaching the final adult form. Insects may be described as either hemimetabolous or holometabolous. In hemimetabolous forms, the hatched young resemble adults reasonably closely, although they may be sexually immature and may lack wings. In holometabolous insects, on the other hand, there is a distinct larval stage that is dramatically different from the adult stage in almost all ways: morphology (form and structure), diet, and habitat. In holometabolous insects, there are usually several different larval stages separated by molts. After a period in which the larva grows, it then enters a sessile pupal phase during

which a dramatic metamorphosis occurs, and the insect emerges from the pupa with its adult form.

Certain insect groups are highly social. Termites and many species of Hymenoptera (ants, wasps, and bees) are **eusocial**, meaning that their colonies include a caste (a segment of the population) that reproduces as well as a large number of individuals that do not. The evolution of nonreproductive species seems to pose a problem because it appears to defy natural selection, which emphasizes the production of offspring. However, direct reproduction is not the only way for an individual to pass on its genes. For example, because an individual's siblings share some of its genes, contribution to the production of a large number of siblings will also result in an individual's genes being represented in the population. This is what occurs in the eusocial insects. In addition, unusual behaviors in termites (repeated cycles of inbreeding) and unusual genetic systems in hymenopterans (haplodiploidy, in which males of the species are haploid while females are diploid) increase the proportion of genes shared by siblings.

eusocial animals that show a true social organization

Insects play many vital roles in maintaining ecological systems. Many insects act as pollinators to higher plants. Others are important in decomposition. Many species are agricultural pests or parasites, and have a dramatic impact on humans. The fruit fly *Drosophila melanogaster* is one of the most well-studied biological organisms and serves as a model species for studies of **genetics**, development, and evolution.

genetics the branch of biology that studies heredity

Some well-known insect groups include the Thysanura (silverfish), Ephemeroptera (mayflies), Odonata (dragonflies), Orthoptera (grasshoppers, crickets, katydids), Blattaria (cockroaches), Isoptera (termites), Heteroptera (true bugs), Homoptera (cicadas and aphids), Coleoptera (beetles), Siphonaptera (fleas), Diptera (flies), Lepidoptera (butterflies and moths), and Hymenoptera (ants, bees, and wasps).

Subphylum Trilobita. The subphylum Trilobita includes only extinct species found in fossil form. The trilobites were a primitive group of marine species that was particularly abundant during the Cambrian (570 million years ago) and Ordovician (505 million years ago) periods. The group became extinct at the end of the Permian (286 million years ago). Trilobites had flattened, oval-shaped bodies. Most were a few inches long, although one species is known to have attained a length of 0.6 meters (2 feet). SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

Bibliography

Blaney, Walter M. *How Insects Live.* London: Elsevier-Phaidon, 1976.

Brusca, Richard C., and Gary J. Brusca. *Invertebrates.* Sunderland, MA: Sinauer Associates, 1990.

Chapman, Reginald Frederick. *The Insects: Structure and Function.* New York: Cambridge University Press, 1998.

Corti, Walter Robert. *Butterflies and Moths.* New York: Odyssey Press, 1964.

Dunca, Winifred. *Webs in the Wind: The Habits of Web-Weaving Spiders.* New York: Ronald Press Company, 1949.

Evans, Arthur V. *An Inordinate Fondness for Beetles.* New York: Henry Holt and Company, 1996.

Foelix, Rainer F. *Biology of Spiders.* Cambridge, MA: Harvard University Press, 1982.

Fortey, Richard A. *Trilobite!: An Eyewitness of Evolution.* New York: Alfred Knopf, 2000.

Friedlander, Cecil Paul. *The Biology of Insects.* New York: Pica Press, 1977.

Gauld, Ian David, and Barry Bolton, eds. *The Hymenoptera.* New York: Oxford University Press, 1988.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton and Co., 1996.

Hickman, Cleveland P., Larry S. Roberts, and Allan Larson. *Animal Diversity.* Dubuque, IA: Wm. C. Brown, 1994.

Holldobler, Bert, and Edward O. Wilson. *The Ants.* Cambridge, MA: Harvard University Press, 1990.

Wade, Nicholas, ed. *The Science Times Book of Insects.* New York: Lyons Press, 1998.

Aves

Eggs and poultry make up a significant part of peoples' diets. Similarly, products made from feathers such as pillows, comforters, or down-lined coats are widely used. There is an increasing awareness and heightened passion for our feathered friends sweeping the nation. The popularity of feeding wild birds has actually changed the ranges of several common songbirds. Additionally, because of the low fat content of turkey and chicken meat and America's fascination with losing weight, the poultry industry is booming. And what other animal has a day dedicated to it like the tradition of roast turkey at Thanksgiving? Clearly, birds are a relevant and special part of our lives.

But what makes them so unique? How are they different from animals in the other major classes of organisms? And most importantly, how are they different from us?

Position in the Animal Kingdom

Birds make up the class Aves of the subphylum Vertebrata, phylum Chordata. Class Aves contains 28 orders, 163 families, 1,975 genera, and nearly 10,000 species. Their distribution is worldwide, including open oceans. While the majority of the world's bird species are known to science, a handful of new birds are still discovered each year. Most of these rare birds are found in remote regions of the world.

It is widely believed that birds descended from two-footed, lizard-like reptiles that lived in the Jurassic period some 208 million years ago. Birds still have many resemblances to reptiles, such as their habit of laying eggs, the possession of scales on their beaks and legs, and the arrangement of many internal structures.

The three highest classes of vertebrates—reptiles, birds, and mammals—have adapted their reproduction to terrestrial life, largely through the evolution of an egg whose embryo is enveloped in a protective membrane called the **amnion**. Hence these three classes are grouped under the term "amniota," or "**amniotes**." Among all animals, only birds and mammals have evolved the high, constant temperature or **homeothermism** that makes energetic activity possible in all habitats and at all seasons. This,

amnion the membrane that forms a sac around an embryo

amniotes vertebrates which have a fluid-filled sac that surrounds the embryo

homeothermism maintainenance of body temperature

The yellow warbler's bright feathers provide warmth, protection, and the ability to fly.

more than any other advance, is what makes these two classes the dominant vertebrates.

Birds have numerous characteristics that make them distinct from all other classes of organisms. While not all birds fly, a large number of these characteristics complement their amazing adaptation for flight.

Feathers

All birds have feathers, which no other animals living or extinct are known to have had. The number of feathers is relatively constant within a species, although birds tend to have more feathers in the winter than in the summer. Smaller birds tend to have more feathers per square surface inch than larger birds, although fewer total feathers. For example, a ruby-throated hummingbird, with a relatively small surface area, has approximately 940 feathers, while a Canada goose, with a much larger surface area, has 33,000.

Feathers serve many purposes, including warmth, protection, flight, attractive adornment for courtship, and sex recognition. The heat-insulating value of feathers is so extraordinarily effective that it permits birds to live in parts of the Antarctic too cold for any other animal.

For their weight, it is estimated that feathers are as strong as the best human-made materials used in the aerospace industry today. Their flexibility allows the broad-trailing edge of each large wing feather to bend upward with each downstroke of the wing. This produces the equivalent of pitch in a propeller blade, so that each wingbeat provides both lift and forward propulsion.

There are well-documented stories of birds deliberately swallowing their feathers. Grebes, for example, consume feathers by the hundreds. Fifty percent of the stomach contents of horned or pied-billed grebes may be feathers. This odd behavior seems to have a purpose. Scientists believe the action

gizzard the muscular part of the stomach of some animals where food is ground

of the **gizzard** in these primarily fish-eating birds is insufficient to crush the bones that are swallowed. The feathers are thought to protect the stomach by padding the sharp fish bones and slowing down the process of digestion so that the bones dissolve rather than pass into the intestine. This belief is supported by the observation that the least grebe, which, of all the grebes consumes the fewest fish, also accumulates the smallest amount of feathers in its stomach. Additional studies are needed to test this hypothesis.

Fusion and Reduction of Bones

pectoral of, in, or on the chest

fusion coming together

Bird bones are extensively fused and thus reduced in number. Birds have no teeth or heavy jaws. Unlike mammals, which have a single bone, the lower jaw of birds is made up of five small fused bones. Additionally, the bones in the **pectoral**, pelvic girdle, and spinal column are fused, which serves as a rigid framework for flight muscles, limbs, and major flight feathers of the wing and tail. Birds have no tail vertebrae. The upper limbs show extensive **fusion** in the carpal and metacarpal bones. The finger bones are reduced in both size and number; two of them are completely missing and two of the other three are fused together. The ankle and foot bones in birds have also been fused and reduced in number.

Hollow, Thin Bones

The major bones of most birds' bodies are thin and hollow, while most other animals possess denser, more solid bones. The skeleton of the pigeon, for example, accounts for a mere 4 percent of its total body weight, while the skeleton of a mammal of comparable size, such as a rat, amounts to almost 6 percent of its total body weight.

Although the bird skeleton is thin and lightweight, it is also very strong and elastic. This is very helpful, since most birds' skeletons are subject to great and sudden stresses of aerial acrobatics. Interestingly, the wing, leg, and skull bones in some large, soaring birds have internal, trusslike reinforcements much like the struts inside airplane wings.

buoyancy the tendency of a body to float when submerged in a liquid

Not all birds have such hollow bones. To decrease their **buoyancy** and make diving easier, some diving birds, such as loons and auklets, have relatively solid bones.

Air Sacs

In addition to lungs, birds possess an accessory system of air sacs connected with the lungs. These air sacs often branch throughout their bodies, frequently entering the larger bones of the body to occupy their hollow interiors. While this system of air sacs certainly contributes to weight reduction, it is believed that they have a more important contribution. The air sac system appears to supplement the lungs as a supercharger, increasing the utilization of oxygen.

thoracic the chest area

In addition, air sacs provide buoyancy for aquatic birds. Swimming species have particularly large abdominal and **thoracic** air sacs whose volume can be controlled for swimming or diving.

Air sacs also serve as a cooling system for the bird's speedy, hot metabolism. It has been estimated, for example, that a flying pigeon uses one-fourth of its air intake for breathing and three-fourths for cooling.

Nervous System and Sense Organs

Birds have a very high metabolism. They may consume thirty times the amount of energy as reptiles of similar size. Several factors contribute to their metabolism level. Of all the million or so animals on Earth, birds have evolved the highest operating temperatures. Their average body temperatures range between 104°F and 110°F (42°–43.5°C). Birds live intense lives and their metabolic "engine" is always warm and ready for action.

Behind the high temperature in birds lie some interesting anatomical and physiological refinements. Besides eating an energy-rich diet, birds possess digestive equipment that processes their food rapidly, efficiently, and in large amounts. Fruit fed to young cedar waxwings passes through their digestive tracts in as little as sixteen minutes. Other perching birds may take from one-half to two hours to pass food through their bodies.

The excretory system of birds is also extremely efficient and fast. Their kidneys are roughly twice as large as those of comparable mammals. Except in ostriches, there is no urinary bladder. Its absence further assists flight by reducing weight, since there is no stored urine. Birds do not have a **urethra** to discharge urine.

urethra a tube that releases urine from the body

Avian cardiovascular systems are extremely efficient, enabling birds to withstand **cardiopulmonary** stresses far beyond what mammals can tolerate. Like mammals, birds have a four-chambered heart. Relative to their size, however, it is large, powerful, and very rapid in beat. The world altitude record for birds is held by a Rüppell's griffin, which was pulled into the jet engine of an airliner at nearly 11,000 meters (36,000 feet). Although the vulture was undoubtedly soaring passively, no mammal of equivalent size could breathe enough air even to remain conscious at that altitude.

cardiopulmonary of or relating to the heart and lungs

Birds also have blood sugar concentrations averaging about twice that found in mammals. This elevated blood sugar supports a greater amount of activity.

The respiratory system of birds is a complex network of lungs and specialized air sacs. This unique system acts as a supercharger for their fast metabolism by supplying large amounts of oxygen. While the lungs of humans constitute about 5 percent of body volume, the respiratory system of a duck makes up about 20 percent of its body volume (2% lungs and 18% air sacs).

Birds have no sweat glands and lose heat through their respiratory system and exposed skin. To cool off, most birds pant, which is an important form of heat loss. Additionally, many if not all birds flutter the throat area during heat exposure, resulting in heat loss from the mucous membranes of the throat. This throat flutter may account for 35 percent of heat loss in chickens, for example.

Finally, birds have a highly developed central nervous system and rapid nerve impulses. Birds are highly visual animals; they must be in order to fly. The importance of birds' eyes is implied by their size; of all animals, theirs are the largest relative to the body. Some hawks and owls have eyes as large as human eyes. In some owls, the eyes comprise up to one-third of the total weight of the head. In starlings the eyes comprise 15 percent of the head weight; in humans it is only one percent. In most aspects, the avian eye structure resembles that of mammals. The eyes of birds are able to adjust to light about two times as well as those of a twenty-year-old person.

There has been a lot of debate regarding the acuteness of avian vision. Generally, it appears that it is better than human vision, but there are exceptions. A vulture sees about as sharply as humans, whereas a chicken appears to see only about one twenty-fifth as well as humans. Hawks and songbirds see about two and one-half times as sharply. Birds also appear to see in dim light better than humans because of the density of receptor cells in the **retina**. Barn owls can see an object at two meters with an illumination of 0.00000073 foot candles. This is the equivalent to a person seeing an object by the light of a match a mile away.

retina a layer of rods and cones that line the inner surface of the eye

The brain of a small perching bird weighs about ten times that of a lizard of the same body weight. The cerebral hemispheres in birds are large and well developed, as in mammals, but the location of the complex behavior in the cerebrum is different in the two. The brain of a mammal is dominated by the top layer of the cerebral hemispheres, which have a high capacity for learning. The bird brain is dominated by the middle of the cerebral hemisphere, which lacks learning capacity. So mammals, in general, learn behavior, while bird behavior tends to be instinctive and stereotyped. This is probably the basis for the well-known phrase "bird brain."

Laying of Eggs

All birds lay shelled eggs and incubate them outside of their body. Eggs range in size from 25 centimeters (10 inches) long for ostriches to only 8.5 millimeters (0.3 inch) long for hummingbirds. Smaller birds lay eggs that weigh more in proportion to body weight than do the eggs of larger birds. Hummingbirds lay eggs that are 15 percent of their body weight, while ostriches lay eggs that are only 2 percent of their body weight. Flightless kiwis lay only one huge egg that can be 25 percent of their body weight. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Stephanie A. Lanoue

Bibliography

Ehrlich, Paul R., David S. Dobkin, and Darryl Wheye. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds.* New York: Simon and Schuster, 1988.

Faaborg, Janus. *Ornithology: An Ecological Approach.* Upper Saddle River, NJ: Prentice Hall, 1988.

Forshaw, Joseph, ed.*The Encyclopedia of Birds*, 2nd ed. New York: Facts on File, Inc., 1998.

Gill, Franklin B. *Ornithology*, 2nd ed. New York: W. H. Freeman and Company, 1995.

Kaufman, Ken. *Lives of North American Birds.* New York: Houghton Mifflin, 1996.

Koeppel, Dan. "Eureka! An Antpitta!" *Audubon* 100 (1998): 96–101.

Natural History of North American Birds. New York: Simon and Schuster, 1998.

Proctor, Noble S., and Patrick J. Lynch. *Manual of Ornithology.* New Haven, CT: Yale University Press, 1993.

Van Tyne, Josselyn, and Andrew J. Berger. *Fundamentals of Ornithology.* New York: John Wiley and Sons, 1976.

Welty, Joel Carl, and Louis Baptista. *The Life of Birds*, 4th ed. Orlando, FL: Harcourt Brace Jovanovich, 1988.

Bailey, Florence Augusta Merriam

American Ornithologist
1863–1948

Florence Augusta Merriam Bailey was born in Locust Grove, New York. Bailey was an important ornithologist, who spent nearly fifty years observing, protecting, and writing about birds.

The natural setting of her home in the country inspired Bailey's love of nature. Her interest in wildlife was encouraged by her family who also loved natural history. Bailey was educated in private school and then attended Smith College from 1882 to 1886. Although she did not follow a degree course at Smith, she was later awarded a bachelor's of arts degree by Smith in 1921. While at Smith, Bailey organized one of the nation's first Audubon Societies and worked to end the era's fashion craze of decorating women's hats with bird feathers and even entire birds. She wrote many articles on birds for *Audubon Magazine*, and these articles formed the basis for her first book about birds, *Birds through an Opera Glass* (1889).

After college, Bailey traveled and dabbled in social work. However, contracting tuberculosis led her to travel west in 1893 to find a better **climate** in which to recover. She traveled and studied birds throughout Utah, California, and Arizona. Her first major western bird book was *A Birding on a Bronco* (1896). This book was aimed at beginners in ornithology and became one of the first popular American bird guides. She went on to write ten books altogether. In 1899 she married Vernon Bailey, a biologist who also studied animals, especially mammals. They traveled the country together, studying wildlife and helping each other write magazine articles and books that are considered classics on western natural history. Florence Bailey's book *Handbook of the Birds of the Western United States* (1902) became a standard reference book, documenting hundreds of species of birds. She became the first woman associate member of the American Ornithologist's Union in 1885, and its first woman fellow in 1929. In 1931 Bailey was the first woman recipient of the organization's Brewster Medal for her book *Birds of New Mexico* (1928).

climate long-term weather patterns for a particular region

naturalists scientists who study nature and the relationships among the organisms

When not traveling, the Baileys entertained amateur and professional **naturalists** in their home in Washington, D.C. Florence Bailey helped organize the Audubon Society of Washington D.C. and frequently taught its classes in basic ornithology. Although childless, Bailey spent her life educating young people about the value of birds. In 1908 a California mountain chickadee, *Parus gambeli baileyae*, was named in her honor.

Florence Augusta Merriam Bailey committed her life to educating others on the basic principles of ornithology through her prolific writing and teaching.

Denise Prendergast

Bibliography

McMurray, Emily J., ed. *Notable Twentieth-Century Scientists.* Detroit: Gale Research Inc., 1995.

Internet Resources

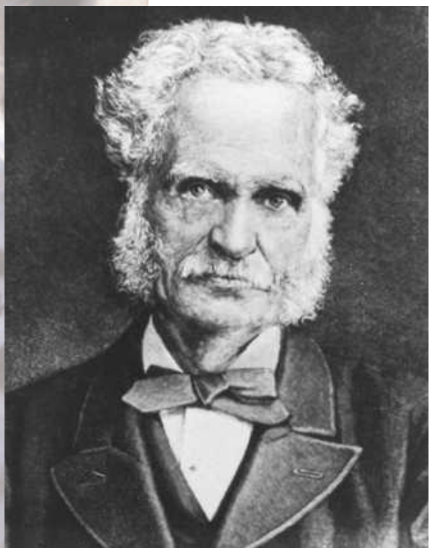
American Association of University Women. New York State, Saint Lawrence County Branch. <http://www.northnet.org/stlawrenceaauw/bailey.htm>.

Baüplan

See Body Plan.

Bates, Henry Walter

British Naturalist
1825–1892



A prominent entomologist, Henry Walter Bates developed the "Batesian mimicry" theory following his research in the Amazon.

naturalist a scientist who studies nature and the relationships among organisms

fauna animals

Batesian mimicry a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

Henry Walter Bates was born in Leicester, England. Bates was a **naturalist** who specialized in the study of insects.

Bates left school at the age of thirteen and worked in his father's stocking factory. He was an amateur botanist and entomologist. In 1844 Bates met Alfred Russel Wallace, who along with Charles Darwin originated the theory of evolution by natural selection. In 1847 Wallace suggested Bates accompany him on a trip to tropical jungles to study natural history. They would pay for their trip by collecting animal specimens and selling them in Europe. In 1848 Bates and Wallace arrived in Brazil at the mouth of the Amazon River. Wallace stayed for four years, and Bates for eleven years. During this time, Bates explored the entire valley of the Amazon and collected nearly 15,000 species, mostly insects. Of these species, 8,000 were previously unknown. Many of the specimens were sent back to museums and collectors in Europe to raise funds to pay for the trip.

After returning to England in 1859, Bates worked on his huge collections, classifying and describing the various species. He wrote a famous paper entitled "Contributions to an Insect **Fauna** of the Amazon Valley" and presented it to the scientific community in 1861. Bates also proposed a hypothesis about a certain type of mimicry which is now called **Batesian mimicry**. While in the Amazon valley, Bates observed that certain harmless butterflies looked very similar to other butterflies that were poisonous or distasteful to predators. Bates theorized that the harmless butterflies had evolved to look like the toxic butterflies. In this way, he believed that the harmless butterflies increased their chances of survival by taking advantage of the defenses of the toxic butterfly. A classic example of Batesian mimicry is the viceroy butterfly which looks very similar to the foul-tasting monarch butterfly. Bates was a strong supporter of evolution by natural selection, and his findings about mimicry supported this theory.

In 1864 Bates was appointed as the assistant secretary of the Royal Geographical Society in London. He held this position for twenty-eight years until his death. Bates is recognized among scientists for his contribution to the classification of scarabs, a type of beetle. He described over 700 new species of scarabs. Bates wrote *The Naturalist on the River Amazons* (1863) and many scientific papers on insects.

Denise Prendergast

Bibliography

Williams, Trevor I., ed. *A Biographical Dictionary of Scientists*, 3rd ed. New York: John Wiley & Sons, 1982.

Internet Resources

University of Nebraska State Museum. <http://www.museum.unl.edu/research/entomology/workers/HBates.htm>.

Behavior

Animal behavior includes the actions and reactions of animals to external stimuli. The study of animal behavior involves two main approaches: answering questions about how an animal does something (proximate questions) and why an animal does something (ultimate questions). Though humans have always observed animals behave, animal behavior did not become a field of study until the 1930s, when it was called **ethology**.

ethology animal behavior

Behavior is determined by both genetics and environmental factors, and is controlled by neural mechanisms. Thus, all animals with nervous systems are capable of behavior, including extremely simple ones such as the flatworm, *Caenorhabditis elegans*, which responds to light. The study of animal behavior is expanding rapidly and includes **taxa** and subjects too numerous to list here. Major divisions of the field include learning, cognition, and social behavior.

taxa named taxonomic units at any given level

Founders of animal behavior studies include scientists Karl von Frisch, Konrad Lorenz, and Niko Tinbergen, whose work in the 1930s won them a shared Nobel Prize in 1973. Their work focused on how animals can do things they have never before seen done, which is a proximate question relating to the genetics that determine some of an animal's makeup and the physiology that allows the animal to perform the feat.

Their work also included elements of ultimate questions, and it is the answers to these "why" questions that lead us to fully understand the driving force behind the evolution of the behavior. Using the *C. elegans* example given above, questions about how the flatworm avoids light will be answered by geneticists and physiologists studying light sensors and locomotion capabilities. Why the flatworm avoids light relates to things like evolution (its ancestors avoided light, and it increases an individual's fitness for survival to do so) and environment (predators can detect flatworms better in the light). These ultimate questions helped link the fairly new study of behavior to established disciplines of evolution and **ecology**, and gave birth to the field we know today as behavioral ecology.

ecology the study of how organisms interact with their environment

Behavior is a **phenotypic trait**, and, as with other such traits, an individual's behavior is determined through both genetics and environment. There are few examples of a trait that is strictly determined through just one of these routes, though through rigorous study we can tease apart the genetic and environmental components that determine a behavior.

phenotypic traits the physical and physiological variations within a population

For example, when a gene for a complex behavior such as alcoholism is reported, it usually means that there has been an abnormal allele of a gene found in some large percentage of alcoholics tested, and that the presence of this allele may somehow make the individuals with it more likely to be alcoholics. It does not indicate, however, that all people with that allele are alcoholics or that all alcoholics have that allele. There are many social factors such as depression and stress that contribute to alcoholism.

Behavior is controlled by the nervous system. Nerve cells acquire sensory cues from the environment, such as light in the case of *C. elegans*, and convert them to electrical signals that are transported to a central decision-making location, such as a nerve ganglion in *C. elegans* or the brain in a higher animal. There it will be determined whether the received stimulus

Worker bees surround their queen honeybee. The workers will feed and care for their queen, therefore helping to preserve their family's genetic information.

demands a reaction. From there, another electrical signal will be sent back out to the target where the response will occur, such as a muscle that controls locomotion and performs the actual behavior.

Learning

One loosely defined category of animal behavior is learning, and this includes imprinting, kin recognition, associative learning, and play. During learning, behaviors are changed based on what an individual sees or experiences.

Imprinting is irreversible learning that occurs during a specific time in an individual's development. Documented in both mammals and birds, one type of imprinting is the recognition and bond that develops between the parent and child in the first few days after birth. A famous example of this occurred when Konrad Lorenz divided a clutch of goose eggs in half, and allowed half of them to incubate with their mother and the other half in an incubation chamber. Those in the first half displayed normal behavior, following their mother around and ultimately interacting and mating with other geese. Those in the second half spent their first few hours with Lorenz and the baby geese imprinted on him. Even when these geese were later reintroduced to their mother and siblings, they showed no recognition but instead always followed Lorenz around and even later showed courtship behavior toward humans. This experiment shows the importance of the **critical period** in which imprinting occurs (the first few hours of life in this case) and the irreversibility of what is learned, even when the species that is imprinted (a human in this case) is incorrect.

critical period a limited time in which learning can occur

Another example of imprinting includes recognition of kin. At an early age, odors of the nest and early companions are used as cues that let animals recognize who their kin are. Documented even in insects, this kin recognition can be used to explain interactions later in life (significantly after separation from the nest) in which an animal treats another one like a relative if it smells like the nest from which it originated. This may be an important part of kin selection, which is discussed in the final, social behavior paragraph of this entry.

Other types of learning, such as associative learning, are not dependent on a critical period, though the learning may happen most efficiently if taught at a certain time. Associative learning is simply the ability to associate one stimulus with another. One example is trial-and-error learning, where as a result of a certain behavior and its outcome, a good or bad association is learned. Whether an association is positive or negative ultimately leads to the repetition or avoidance of the behavior. Food choices may fall under this category, where the sampling of different food types may lead to satisfaction and nourishment or bad taste and sickness.

Finally, play can be viewed as a type of learning in which capturing prey and social behavior are practiced. Though play is usually done with siblings and without the actual goals of hunting to kill or establishing social and mating hierarchies, the actions practiced in play allow these skills to be practiced for use later on.

Play time for these young lions teaches them essential survival skills. The hitting, biting, and roaring learned through playing may help these cubs in their later courtships of possible mates.

Cognitive Behaviors

A second group of behaviors that can be loosely gathered together are cognitive behaviors. These are complex behaviors that involve the perception, storing, processing, and use of information.

Long-distance travel is an example of this complex process. Whales, butterflies, and birds travel thousands of kilometers to return to the exact same spot they were the year before. Migrating animals use several mechanisms including orientation, piloting, and navigation. Orientation involves moving in a certain compass direction, which can be known from cues like stars and the Sun, although some animals can detect magnetic north without these cues.

Piloting is employed for short distances. It involves moving between landmarks such as rivers and mountains that are familiar from past migrations.

Navigation is the most complex. It involves both determining present location in relation to other known locations and using orientation to get to the next destination. This means the animal must create a mental map that is spatially correct in order to plot out the next course.

Social Behaviors

A third group of behaviors is related to social living. Examples include communication, cooperation, and competition. Communication can be between species, such as when a dog snarls to expose its teeth to warn a potential attacker what may be in store. Frequently, communication occurs among species and can be **aural** such as bird song or cricket chirp; **olfactory**, such as a spot where an animal urinates; visual; or **tactile**.

aural related to hearing

olfactory related to smell

tactile related to touch

Communication serves a myriad of purposes, including defining territories, attracting mates, telling where a food source is, or warning of impending danger. Cooperation is when two or more individuals work to perform a single task. Many times this task may seem more beneficial to one individual than the other, in which case the individual getting less or no benefit is termed altruistic. Examples of cooperation are in food finding, child rearing, and standing watch for predators.

In many cases of apparent altruism, it is found that the individual receiving the benefit is related to the one giving, such that the one giving is actually helping to preserve a genetically related line. This phenomenon is called kin selection and serves to propagate related **genomes**, an act that is not purely altruistic.

genomes the sum of all genes in a set of chromosomes

Competition occurs when a limited resource needs to be divided among individuals. An example of a resource to be divided is territory. Frequently, males must establish a territory that has good food or is a good mating or nesting spot so that they are preferentially chosen by females for mating. Those males who accomplish this are the most successful in passing on their genes. Competition for territory can take the form of violent contests with other males, and even after the territory is won it may need vigilant guarding to keep intruders out. SEE ALSO Acoustic Signals; Behavioral Ecology; Communication; Courtship; Social Animals; Sociobiology.

Jean K. Krejca

Bibliography

Alcock, John. *Animal Behavior*, 6th ed. Sunderland, MA: Sinauer Associates, 1998.

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Benjamin Cummings, 1999.

Halliday, Tim. *Animal Behavior*. Norman: University of Oklahoma Press, 1994.

Lorenz, Konrad. *King Solomon's Ring*. New York: Harper & Row, 1952.

Maier, Richard A., and Barbara M. Maier. *Comparative Animal Behavior*. Belmont, CA: Brooks/Cole Publishing, 1970.

Mellgren, Roger L., ed. *Animal Cognition and Behavior*. New York: North-Holland Publishing Company, 1983.

Wilson, Edward O. *Sociobiology: The New Synthesis*. Cambridge, MA: The Belknap Press of Harvard University Press, 1975.

Behavioral Ecology

Behavior is what animals do and why they do it. Behavioral ecology examines the evolution of behaviors that allow animals to adapt to and thrive in their habitats.

There are two broad categories of behavior—learned and instinctive. Instinctive behavior is a pattern passed genetically from one generation to the next. A spider, for example, never needs to see another spider weave a web to know exactly how, where, and when to do it. This information is carried innately with the spider and allows it to carry out many of its life processes without ever having to think about them. The disadvantage to instinct is that is inflexible and does not allow the animal to change when the behavior is no longer appropriate. The armadillo's instinctive upward leap when threatened worked fine until the animal encountered a new environmental hazard—the automobile. **Learned behavior**, in contrast, is the result of experience accumulated and assimilated throughout a lifetime that allows the animal to adapt to unpredictable changes.

learned behavior behavior that develops with influence from the environment

A behavioral ecologist studies patterns of behavior that fall somewhere between instinctive and learned. They include:

- Reflex: A rapid automatic response to a stimulus. Hedgehogs automatically curl into a ball when threatened.
- Conditioned reflex: An instinctive reflex that can be trained to occur under different conditions. A racehorse will go faster when flicked with a whip because it associates the whip with its traditional predator, a large cat, clawing at its back.
- Migration: A seasonal movement to a more favorable summer or winter environment. One of the most phenomenal migrations is that of the monarch butterfly, which spans thousands of miles and two generations. The young are genetically programmed to return to the fields their parents left.
- Hibernation and estivation: A state of torpor, or lowered metabolic rate resembling sleep, entered into by some animals in order to survive severely cold winters or hot, dry summers.
- Imprinting: Memorization by a young animal of the shape, sound, or smell of their parents or birthplace during a very brief period following birth. If the parent is absent, the baby will imprint on the first object it senses, giving rise to the sight of ducklings that think humans are their parents or kittens that have imprinted on dogs.
- Courtship: The special signals and complicated rituals that allow male-female bonds to occur for mating purposes. These behaviors assure the intentions and, consequently, the safety of both partners, who might attack or devour an approaching mate if the signals are unclear.
- Mimicry: The evolution of a harmless animal to look or behave like a dangerous animal. The viceroy butterfly mimics the coloration of the poisonous monarch, which most birds are genetically programmed to avoid.
- Preadaptation: A mixture of instinctive and learned behavior. Purple martins who once nested on cliffs have learned to use human-built structures to extend their ranges.

Behavioral ecologists who study animals closely in natural settings report numerous incidents of watching them encounter a new situation and think out a new response. Harvard biologist E. O. Wilson describes watching several beavers whose dam had been vandalized come up with a solution to the problem. Because the water flow was too strong to be stopped by their instinctive techniques, the beavers came up with a new and successful idea of patching the dam with gooey underwater mud and debris. Wilson is convinced that this showed the beavers' ability to evaluate a problem and solve it with reasoning.

For many years it has been taboo for scientists to propose the idea that animals consciously reason. As biologist Jane Goodall explained, "If you admit that animals have sentience and emotion, you have to take a long, hard look at how we abuse them." SEE ALSO Acoustic Signals; Behavior; Communication; Courtship; Social Animals; Sociobiology.

Nancy Weaver

Bibliography

Burnie, David. *Dictionary of Nature.* London: Dorling Kindersley Inc., 1994.

Binomial (Linnaean System)

Despite the overwhelming diversity of life that exists (and once existed) on this planet, it is clear that some organisms are more similar to each other than to others. Thus, organisms can be assigned to groups based on their overall similarity to other organisms. For example, humans belong to the group "mammals" as do all other organisms that possess mammary glands and hair. The grouping of organisms provides a convenient means of classification; that is, an organism can be described by the groups to which it belongs.

Carolus Linnaeus (1707–1778) is the naturalist responsible for developing the system still used in the twenty-first century for classifying animals.

The classification system that is used today is called the Linnaean System after its inventor, the Swedish naturalist Carolus Linnaeus (1707–1778). In his 1758 book, *Systema Naturae*, Linnaeus categorized all organisms into seven hierarchical groupings arranged from most inclusive to least inclusive. They are kingdom, phylum, class, order, family, genus, and species. Humans belong to the kingdom Animalia, the phylum Chordata, the class Mammalia, the order Primates, and the family Hominidae, and have been given the generic name (genus) *Homo* and the specific name (species) *sapiens.* The Linnaean System is hierarchical because there may be many species per genus, many genera (plural of genus) per family, and so on.

Because specific names are not unique (i.e., there may exist a plant with the specific name *sapiens*), the name of a species always includes both the generic name and the specific name, for example, *Homo sapiens*. This method of giving every species a unique combination of two names is called "binomial nomenclature," and is part of Linnaeus's classification system. By convention, these scientific names for organisms, as opposed to the common names, are always italicized. Furthermore, the generic name is capitalized while the specific name is not. Biologists prefer scientific names to common names because of their uniqueness, stability, and universality. Common names, on the other hand, often refer to more than one species and vary over time and from place to place. Biologists follow a certain Code of Nomenclature when deciding what to name a newly discovered species.

The practice of naming and classifying organisms is termed "**taxonomy**." Linnaeus classified organisms mainly by their physical (morphological) characteristics. He believed that his groups held theological significance, that is, that they revealed God's plan in creating life. However, with the recognition that species evolve, which led to Charles Darwin's *On the Origin of Species* in 1859, it became apparent that Linnaeus's classification system held biological significance as well. Organisms that are morphologically similar and consequently grouped together are usually similar because they share a common ancestry. The Linnaean System thus reflects evolutionary relationships among organisms. For example, humans are grouped with gorillas and chimpanzees in the order Primates because we are more closely related to gorillas and chimpanzees then we are to other mammals. Likewise, Primates are grouped with Rodentia in the class Mammalia because primates and rodents are more closely related to each other than they are to other organisms in the phylum Chordata, such as reptiles and fish. SEE ALSO LINNAEUS, CAROLUS.

taxonomy the science of classifying living organisms

Todd A. Schlenke

Bibliography

Darwin, Charles. *On the Origin of Species by Means of Natural Selection.* London: John Murray, 1859. Facsimile edition reprinted Cambridge, MA: Harvard University Press, 1975.

Jeffrey, Charles. *An Introduction to Plant Taxonomy.* Cambridge, U.K.: Cambridge University Press, 1982.

Linnaeus, Carolus. *Systema Naturae*, 10th ed. Stockholm, Sweden: Laurentius Salvius, 1758. Reproduced New York: Stechert-Hafner Service Agency, 1964.

Schuh, Randall T. *Biological Systematics: Principles and Applications.* Ithaca, NY: Cornell University Press, 2000.

Simpson, George Gaylord. *Principles of Animal Taxonomy.* New York: Columbia University Press, 1961.

Internet Resources

Maddison, David R., and Wayne P. Maddison. *The Tree of Life.* <http://phylogeny.arizona.edu/tree/phylogeny.html>.

Biodiversity

Biodiversity is the term applied to the variety of organisms that occupy a given region. This includes all organisms that live in the region, from microscopic protists to large mammals. The region can be a political unit such as a country, a geographic feature such as a mountain range, or the entire world.

The term "biodiversity" is a combination of two words, "biology" and "diversity." The union of these two words is fairly recent, being inspired by the growing realization that the number of species in the world is seriously declining. Used in this context, it has taken on a greater meaning than just the variety of species, having grown to include three closely related levels: genetic diversity, taxonomic diversity, and **ecosystem** diversity. Biodiversity is created by complex physical and biological environments (ecosystem diversity) that allow organisms to evolve specializations, and genetic barriers (genetic diversity) that allow them to speciate (taxonomic diversity).

ecosystem a self-sustaining collection of organisms and their environment

The importance of biodiversity has been recognized by people of many cultures and backgrounds who understand the multitude of functions it serves for humans, from providing food to filtering waste. Threats to biodiversity include direct killing of species by hunting, contaminating the environment with toxins, and **habitat loss**. The loss of biodiversity through extinction must ultimately be overcome by drastic changes of human behavior. Otherwise, humans will destroy the very environment that supports them.

habitat loss the destruction of habitats through natural or artificial means

Levels of Biodiversity

Genetic Diversity. The first level of biodiversity, genetic diversity, is the level at which we can most clearly observe the evolution of diversity. Genetic diversity includes the many kinds of genes that are available for given members of a species, such as a family, a population, or the entire species. This variety of genes allows the species to have many kinds of heritable traits that allow it to survive through changing environments.

For example, in a particularly cold winter, many individuals of a species may die from lack of insulation, but if the population as a whole has genetic diversity for a trait such as fat storage, then at least some members of the population will survive and the species will not become extinct. The next year, more offspring will have the valuable trait and the species will evolve to tolerate the cooler environment.

Species with little genetic diversity, such as farm hybrids (special breeds of crops or livestock that are all closely related), have limited ability to adapt to changing weather conditions or insect pests. Species lacking genetic diversity cannot adapt to a changing environment and may become extinct without help like the careful maintenance that goes into farm crops and animals.

At the opposite extreme, characteristics of genetically healthy populations are a high population size that includes many individuals that are unrelated to each other. Often, the existence of disjunct populations, those separated by some geographic barrier that only occasionally lets migrants through, ensures that there are always unrelated individuals.

Taxonomic Diversity. The next level of biodiversity, taxonomic diversity, refers to the variety of individuals at a given hierarchical level in the scientific naming system. This could be the number of different species, genera, families, or kingdoms. For example, a cornfield may have hundreds of birds living in it, but they may represent only three species that are all in one family, meaning that there is low taxonomic diversity. A similar-sized area in a nearby forest may also have hundreds of birds living in it, but these birds may be from twenty different species that belong to eight families and three orders, representing a higher level of diversity. Around the world, crops and livestock typically consist of only one species. These **monocultures** support a low level of biodiversity.

monocultures cultivation of single crops over large areas

habitat the physical location where organisms live in an ecosystem

Ecological Diversity. Ecological diversity is the variety of **habitat** types that are available in a given area. These habitats can have different physical characteristics such as temperature and soil type, as well as different organisms inhabiting them. When the habitat with all its organisms and their complex interactions are considered together, it is termed an ecosystem. Ecosystem diversity is typically the level that is discussed in relation to biodiversity.

Beyond ecosystems is a division termed "landscape" that consists of all of the ecosystems in a defined region, such as a drainage basin. **Biomes** are groups of similar landscapes, such as all the mountain ranges in the world. Finally, the largest division is the biosphere, which refers to all life on Earth.

biomes major types of ecological communities

A mountain range is as an example of ecological diversity that illustrates the evolution and patterns of biodiversity. Because of the latitude of the range selected as an example here, the temperatures are warm and plants grow throughout the year. The topography and weather patterns typically make one side of the mountain moist while the other is dry, meaning that each side grows its own kinds of plants. There will also be variation in soil type, as the soils are made from dead plants, and variation in insects because many insects can eat only certain species of plants.

Soil type will determine what kind of ground-dwelling invertebrates and other decomposers can live there, as well as providing habitat for reptiles, amphibians, and small mammals that build their burrows in the soil and feed on the invertebrates. This kind of variation at the base of the food chain determines that there will be variation at all the higher levels as well, including predators.

Another major habitat characteristic is elevation. Higher elevation means colder temperatures and less oxygen, which also dictates that tougher, scrubbier plants will live near the top and that there will be less soil and fewer species at high elevations. Barriers that are inhospitable to some taxa, such as a mountaintop, a river, or a deep canyon, add complexity to the habitat that consequentially creates separate populations that do not communicate very often. These separated populations allow for greater genetic, and ultimately taxonomic, diversity.

From these examples we can make the generalization that biomes in warmer **climates**, with greater energy from primary **producers** and with more varied and complex habitat types, have a higher biodiversity than those without those traits. For example, a mountain range of the same overall characteristics at a higher latitude will have less soil and less energy because there is less primary production from the plants, which go dormant for much of the year. This will cause the overall number of species and biodiversity to be lower.

climates long-term weather patterns within particular regions

producers organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

The Importance of Biodiversity

The value of biodiversity has been argued by many different people for a variety of reasons, but they all point to a unified ideal of conservation. Aldo Leopold is known as the father of environmental ethics in the United States. In books such as *Sand County Almanac and Sketches Here and There* (1949), he stressed that humans must change their role from consumer of the natural world to cohabitator of it. This change is needed to preserve biodiversity, which would ensure that natural resources are available for future generations.

The value of biodiversity is also recognized by various groups and organizations in modern society. They include waste managers who use wetlands to clean runoff; pharmacists who search for new drugs in rare species; a food industry that interbreeds wild species to improve domestic ones; a pet industry that imports and breeds rare animals; hobbyists who bird-watch,

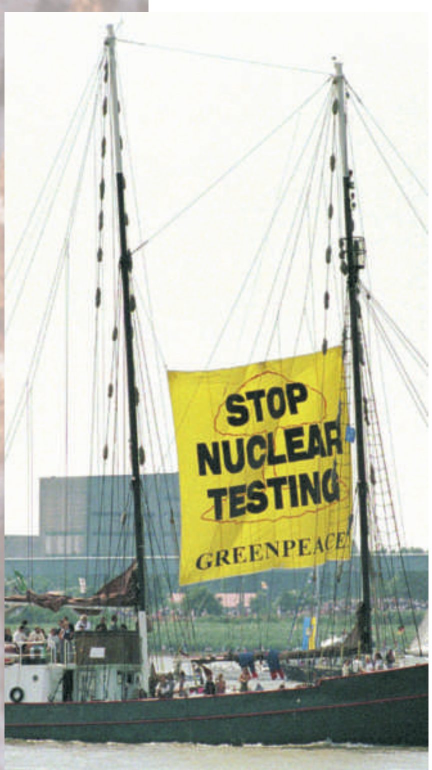
camp, and photograph in search of new species; hunters and fishermen who selectively harvest to eat and teach their families about the wilderness; scientists who use species to study evolution; and, finally, conservationists interested in preserving biodiversity not only for what it can do for them, but for its inherent value in that it lives and breathes as we do.

The Decline of Biodiversity

The decline of biodiversity is documented for prehistoric times and can be the result of natural events that may or may not be related to the fitness of the species that become extinct. A constant level of background extinction has always existed, but it is mass extinction events that cause concern about the future of biodiversity.

Extinction. The largest extinction event recorded occurred 250 million years ago, when 95 percent of marine species died in response to an uplift of the species-rich continental shelf that was caused by **plate tectonics**. Another famous example of mass extinction is the impact of the Chicxulub meteorite, which is thought to have left a dense cloud over the sky worldwide for a decade, causing a decrease in primary production (plant activity) and a subsequent extinction of many taxa. This impact coincides with the end of the dinosaur age and probably contributed to the extinction of many of those lines.

plate tectonics the theory that Earth's surface is divided into plates that move



Greenpeace, responsible for hoisting this large banner on this boat's masts, is one of the best-known organizations working to publicize and educate the public on current environmental challenges.

Extinction rates at the beginning of the twenty-first century are undeniably higher than background rates, but the exact rate calculated depends on what method of calculation is employed. Using estimates from recent past extinction rates based on fossils, mammal extinctions were once one per two hundred years, and most recently were twenty species in the twentieth century. At the turn of the twenty-first century, the rate of bird extinction is 1,000 times the average over the past 2,000 years. Combining the two calculations provides an estimate of a 1 percent loss of species diversity over the twentieth century, a number much greater than any prehuman impact. Using habitat loss as a predictor of species loss, it is estimated that between 2 and 25 percent of biodiversity will be lost over the twenty-first century.

Causes of extinction. Biodiversity decline can result from excessive hunting, environmental contamination, or habitat loss and there are a variety of ways to combat these sources of decline. Excessive hunting typically impacts large species that come into frequent contact with humans, usually because the humans are moving into the animal's habitat. These species are killed out of ignorance, because they are seen as a safety threat, or because they are desired for their fur or meat or as trophies. Many times these species are top predators, so their loss is felt throughout the food chain as populations of prey items go unchecked, which causes subsequent problems for the ecosystem and humans. The regulation of hunting, however, involves innumerable complications when impoverished people rely on hunting for their livelihood and when regulation is not well-funded.

Contamination of the air, land, and water results largely from the generation of energy and the use of machines such as the automobile. Power plants and cars produce huge amounts of pollution that have far-reaching impacts because the pollution is spread by wind and river to formerly pristine areas. Contamination of soils and waters also results from the use of

pesticides and fertilizers associated with farming as well as from human waste generated in large urban centers. However, the major threat to biodiversity is habitat loss. Human activities alter the environment to the degree that it can no longer sustain species where they once lived.

pesticides substances that control the spread of harmful or destructive organisms

The solution to these problems must start with global recognition of the importance of conservation. Biodiversity will need to be maintained in those places where it still exists by creating and managing large protected areas. Some species will need to be helped along artificially by maintaining them in captivity and creating seed banks. Previously destroyed habitat will need to be restored by revegetating and repairing the damage that has been done. Management strategies will have to be created that allow for the conservation of land in concert with human goals. To support all of these strategies, a financial, legal, and political infrastructure will need to be created.

It is important to recognize that Earth's declining biodiversity is a serious global problem. It will be up to educators and future generations to stress the importance of conservation and find means to preserve biodiversity, the immense variety of organisms and interactions that support life on Earth. SEE ALSO Ecology; Habitat; Habitat Loss.

Jean K. Krejca

Bibliography

Becher, Anne. *Biodiversity.* Santa Barbara, CA: ABC-CLIO, 1998.

Begon, Michael, John L. Harper, and Colin R. Townsend. *Ecology*, 2nd ed. Cambridge, MA: Blackwell Scientific Publications, 1990.

Dunell, Lee. *State of the Ark: An Atlas of Conservation in Action.* London: Gaia Books, 1986.

Elredge, Niles. *Life in the Balance: Humanity and the Biodiversity Crisis.* Princeton, NJ: Princeton University Press, 1998.

Jeffries, Michael J. *Biodiversity and Conservation.* London: Routledge, 1997.

Leopold, Aldo. *A Sand County Almanac and Sketches Here and There.* New York: Oxford University Press, 1949.

Miller, G. Tyler, Jr. *Environmental Science*, 3rd ed. Belmont, CA: Wadsworth, 1991.

Rosenzweig, Michael L. *Species Diversity in Space and Time.* New York: Cambridge University Press, 1995.

Bioethics

The term "bioethics" is derived from the Greek words *bios*, meaning life, and the Greek word *ethos*, meaning character. The meaning is essentially "life character." Today, ethics might be better described as applied morals or the philosophy of being moral, with bioethics being the discussion or application of morals within the diverse fields of the life sciences.

The quest for better health has guided scientists and researchers to develop many tools for analysis including organic chemical synthesis and improved genetic engineering. A significant aspect of contemporary medical research is the use of animals as test subjects. Many advances in personal care products, pharmaceutical drugs, and life-saving medical treatments have come about through the use of animals for testing and research. However, this practice is controversial.

Many people feel that animals are abused and mistreated for unnecessary research. The use of animals to test the safety of household or personal care products angers those who feel that humans are unfairly abusing animals for commercial gain. In contrast, scientists point out that animals are the most reliable indicators of potential human response to certain diseases and treatments, and that many successful, life-saving treatments and medical breakthroughs have emerged only because it is possible to test treatment options using animals, rather than human beings.

Unfortunately, some of these discoveries have come at the cost of the natural or induced death of test animals. So the ethical situation arises: Does the benefit of the new data outweigh the risk to the organism, or is the risk greater than the benefits? What may be considered unacceptable to one person may be an acceptable trade-off to another. To address this dilemma, bioethicists attempt to set reasonable restrictions and limits on experimentation so as to maintain a balance between the suffering of experimental animals and the research benefits that may be derived from animal experimentation.

During PETA's (People for the Ethical Treatment of Animals) worldwide campaign to educate the public about the treatment of animals on fur farms, many protestors posed dramatically in front of stores selling fur-trimmed products.

Ethics itself has long been coupled to philosophy and religion. Each person's moral viewpoint is constructed from a host of factors, including education, family background, religion, personal experiences, social level, economic standing, and profession. So if every researcher and every consumer can, hypothetically, hold different views about the relationship between risk and benefit, who is responsible for setting guidelines? And what is the foundation for such guidelines?

Bioethics and Research Institutions

A first step toward establishing ethical guidelines for animal testing has been taken by institutions in the United States that fund research, such as the National Institute for Health, the Food and Drug Administration, and the Agriculture Department. Their policies are primarily set by the public in the form of political action initiated by their elected representatives. The directors and boards of these institutions consider the opinions of their constituents when deciding what types of research to support.

Private institutions such as the Howard Hughes Foundation and Rockefeller Foundations set their policies through committee discussion groups and professional panels that make recommendations to the directors of the respective foundations. Their opinions are reflected in the programs the foundations choose to fund.

Finally, private businesses and corporations that fund this type of research generally use a board or panel approach and approve of experiments within the guidelines set forth in both state and federal law, with an eye to accommodating the general will of the public.

In each of these three cases, an advisory committee is usually composed of senior researchers of a particular discipline—for example, biotechnologists to examine biotechnology questions—plus a philosopher to provide some historical depth and background, and members of interest groups or other public representatives. These panels make their recommendations based upon consideration of current circumstances as well as the potential future impact of the relative costs and benefits of the proposed research.

What sorts of issues does a panel consider when looking at a given experiment? With regards to animal testing for a new pharmaceutical, the dialog generally contains several crucial elements. The first step is to identify an experimental need. For example, a company may wish to test a new drug that would destroy fatty deposits in coronary (heart) arteries. The pharmaceutical company needs to conduct experiments to ensure drug safety and identify any possible side-effects for humans. Since federal law requires that any drug be thoroughly tested with an accurate experimental model to understand its effects before it is approved, one of the first questions to consider is how this may be best accomplished.

A variety of systems are available to model a drug's behavior. These include microbial models (not suitable in this case); tissue models (the heart tissue model might provide very good information with no apparent negative effects); computer modeling (not always appropriate for finding actual data); and finally, animal models—which have the potential to provide the most accurate information about the drug's likely effect on human beings.

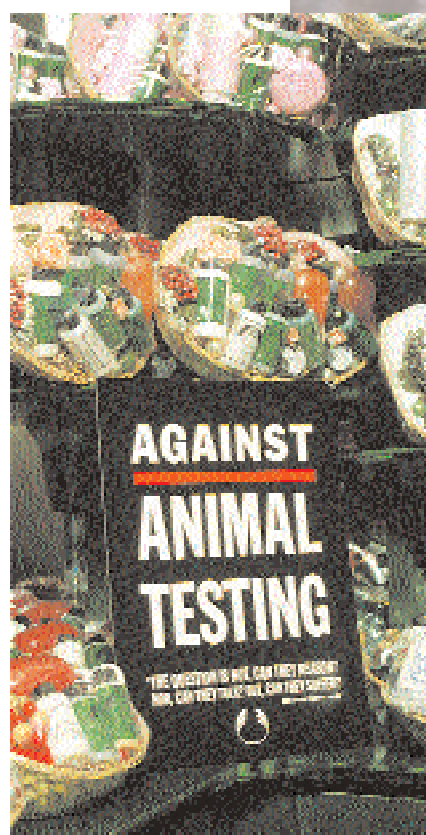
The question of ethics arises during this process. In contemporary American culture, we tend to value human life above the lives of animals. Supporting this view are such culturally accepted practices as the consumption of certain animals as food, the production of drugs such as insulin from animals, and the pursuit of the longstanding hobbies of hunting and fishing for recreation and relaxation. Not everyone agrees that all of these practices are acceptable, however.

controversy a discussion marked by the expression of opposing views

Animal Rights vs. Human Lifestyle

The widespread use of animal life to maintain human life or lifestyle is a growing point of **controversy**. An increasing number of consumers are voicing the opinion that the use of animals in the development of products for human use should be restricted. This is especially true in regard to the cosmetics industry where products are used for appearance rather than health purposes. For example, many consumers, investors, and animal rights activists are offended by the ways in which a product like mascara may be tested on animals before it can be approved for human usage.

There are those who believe that animal testing may be acceptable if used to develop new drugs that may save human lives. The necessary data regarding performance and safety cannot be gathered any other way. But the practice of killing an animal every time a shampoo changes its color is disturbing to many of these same people. While this may seem extreme, this happens under current law because every time something is added to an existing formula the new combination must be retested for safety and effectiveness, and animals do not always survive such testing.



The Body Shop, an international manufacturer of hair and skin products, publicizes its refusal to use animals in the testing of their products.

At first, one might question why it is necessary to go to such lengths to test a nonmedical product. But what if a shampoo's new color proved to harmful to human skin? Or caused hair to fall out? Most consumers agree that it is not acceptable to have less stringent safety standards for such products, and yet there is disagreement about what this means in regard to the ethics of animal testing. It is impossible to set absolute moral guidelines, since each case is unique, but for a variety of reasons, current law is set to err on the side of physical human safety.

Questions in Bioethics

Bioethics requires the asking of questions that go beyond current legal requirements. Are there ways to guarantee safe cosmetics and personal care products that do not involve the use of animals? If animal testing is the only sure way to guarantee product safety, are there ways to keep from harming animals in the process? One option gaining in popularity is to restrict animal testing to the most humane and painless tests possible. Restricting the use of animals to the final stages of testing is another way researchers are trying to balance human safety with animal comfort.

Another issue confronting bioethicists has to do with the removal of animals from the wild for research purposes. In particular, the use of wild chimpanzees and other primates is under scrutiny. The dilemma arises because the public does not appear to support continued harvesting of primates from wild habitats for research purposes, yet the chimpanzee, for example, is the animal most closely related to humans, and thus most desirable for testing potential medicines.

There is little disagreement that creative minds are needed to explore alternative methods of assessing the effects of chemicals on human beings. Increasing knowledge about the human genome, and the promise of genetic treatments for human disease, suggest that animals will continue to have a role in medical research. Those involved in the field of bioethics will constantly be challenged to assess how and when to use animals for this research.

The field of bioethics addresses more than just the question of how to manage conflicting priorities and approaches to animal testing. Now that geneticists have created clones of nonhuman species of vertebrates, there are increasing questions regarding the ethical use of human genetic material. Should researchers be allowed to try to clone human organs for life-saving transplants? Should human embryonic tissue be made available for stem-cell research? Should doctors be allowed to test **gene therapy** on human patients who have exhausted all other treatment options?

gene therapy a process where normal genes are inserted into DNA to correct a genetic disorder

Scientists search for ways to apply a growing body of knowledge to the betterment of human life. Philosophers and others pose ethical questions concerning scientific advancement. Sellers of goods and services depend on the advancements of science to create and fill market needs. Bioethics is the field where life science, philosophy, and commerce meet, where practitioners negotiate boundaries, wrestle with guidelines, and seek balance within the natural world in the quest to improve the quality and quantity of human life. SEE ALSO Animal Rights; Animal Testing.

Brook Ellen Hall

Bibliography

Kuhse, Helga, and Peter Singer, ed. *Bioethics: An Anthology.* Malden, MA: Blackwell Publishers, 1999.

Shannon, Thomas A. *Bioethics: Basic Writings on the Key Ethical Questions that Surround the Major, Modern Biological Possibilities and Problems.* Mahwah, NJ: Paulist Press, 1994.

Veatch, Robert M. *The Basics of Bioethics.* Upper Saddle River, NJ: Prentice Hall, 1999.

Biogeography

Why do different species occur in the places they do? Biogeography is the study of why animal species (and also plants) live in different regions on Earth. This includes both organisms alive today as well as those that have become extinct. Any particular animal species is found where it is because that species either evolved and originated there or came there from some other place. The two divisions of biogeography reflect these two ways that animals come to occupy an area. Biogeography can be broken down into historical biogeography, which studies the past history and evolution of a species, and ecological biogeography, which studies the environment of a species.

Ecological Biogeography

Ecological biogeography studies how animal species are distributed in relation to the environment. The environment that influences what animals are present in a region includes both nonliving, **abiotic** factors (such as climate or soil composition) as well as living, **biotic factors** (such as other plants and animals). Earth is divided into major ecological areas called **biomes**. Biomes are regions of distinct **climate** and plant life. There are several kinds of biomes. Examples include the dry, hot desert in which cactuses and other plants are adapted to low water conditions, and the tropical evergreen forest with heavy year-round rainfall and lush plant life.

abiotic nonliving parts of the environment

biotic factors biological or living aspects of an environment

biomes major types of ecological communities

climate long-term weather patterns for a particular region

Dispersal occurs when an animal moves away from the area in which it was born and lives in another area. Dispersal increases the biogeographic range of a species, spreading the population. However, the extent to which an animal can disperse may be limited by ecological factors. Animals that disperse into areas for which they are not adapted will not survive. For example, alligators cannot disperse into central North America because it is too cold during the winter. These ecological limits to dispersal help determine the range of an animal species.

Historical Biogeography

Historical biogeography is the study of how animals that are present in a geographical region today relate to the animals that lived there in the past. A major factor explaining why a species is present in a region today is the presence of the same species in the past, or the presence of a closely related species that once lived there and from which the current species has descended. That is to say, a species is located somewhere because it was there in the past, or because an ancestor of the species lived there.

Continental drift is a major factor in determining current species distributions. All the continents on Earth were once part of one single land mass called Pangaea. About 200 million years ago, this landmass began to drift apart to form the continents of today. There are correspondingly six major biogeographic regions. They are the Neararctic, covering North America; the Neotropical, covering South America; the Ethiopian, covering Africa; the Oriental, covering India and southeastern Asia; the Palearctic, covering Europe and northern Asia; and the Australian, covering Australia.

continental drift the movement of the continents over geologic time

Each of these regions has a group of animals that are more closely related to each other than to animals in other biogeographic regions. This is because of local diversification by speciation (the forming of new species) and the radiation (spread) of species within a biogeographical region; animals in a region are descendants from the ancestors that were previously there. The same is true for plants. Many animal species that are closely related stay in the same biogeographical region because it is hard to disperse or move between these regions. These regions are isolated from one another by an ocean or a very large mountain range, or are connected by only a narrow landmass (an **isthmus**). This isolation serves as a barrier to dispersal; most animals simply can not swim across the ocean to colonize another continent. Likewise, most animals that live in the Pacific Ocean cannot cross the land bridge that joins North and South America to reach the Atlantic Ocean, and vice versa.

isthmus a narrow strip of land

Sometimes a population of animals is split into two populations by the sudden appearance of a physical barrier across which no individual can disperse; this is called a vicariant event. These two populations can become separate species over time because of isolation. An example of a natural vicariant event is an earthquake making a new canyon that is too wide for mice on either side to disperse across. Humans create obstacles that can also cause vicariance, such as highways that would stop mice from dispersing.

> An example of a species that created an ecological impact through its migration is the brown tree snake. This species began invading Pacific islands late in the twentieth century by stowing away on shipping boats. As no snakes were native to the islands, the local animals, especially birds, became easy prey for them, and the native bird populations on the islands were negatively affected.

Humans can help promote dispersal. As technology has increased worldwide travel and transportation in the nineteenth and twentieth centuries, some animals have been able to disperse into new biogeographic regions on boats, trucks, or planes. How all the organisms in one place interact with each other and their environment is called the community ecology of an area. Biogeographic regions strongly determine the community ecology of an area. As a consequence, species that successfully disperse to new biogeographic areas can cause huge ecological impacts. For example, the brown tree snake began invading Pacific islands late in the twentieth century. The local animals, especially birds, are easy prey for brown tree snakes because they have not adapted to snake predators. The snakes can quickly wipe out the bird populations that can not adapt fast enough. SEE ALSO Living Fossils.

Laura A. Higgins

Bibliography

Brown, James H., and Mark V. Lomolino. *Biogeography*, 2nd ed. Sunderland, MA: Sinauer Associates, Inc., 1998.

Purves, William K. et al. *Life: The Science of Biology*, 5th ed. Sunderland, MA: Sinauer Associates, Inc., 1998.

Biological Evolution

Biological evolution is the change in the allele frequency of a gene in a population over time. That is to say some genetic change has happened in the population between generations. Only populations can evolve, not individuals. Individuals can not change their genetic makeup. Only between generations, is there the possibility for genetic changes due to the forces of evolution. These forces are natural selection, mutation, gene flow, nonrandom mating, and genetic drift. Evolution is a measure of a population, not of an individual. Genetic variation, genetic differences between individuals, must exist for evolution to occur.

Charles Darwin defined evolution as descent with modification. However, Darwin did not understand the genetic basis to evolution. Not until Gregor Mendel's work was rediscovered in 1900 could modification with descent be understood in terms of maintaining genetic variation. The mathematical proofs of Godfrey Harold Hardy and Wilhelm Weinberg, known as the Hardy-Weinberg theorem, started the field of population genetics, the integration of Darwinian selection and Mendelian genetics. Their proof showed how variation can be maintained because each individual had two **alleles** for each gene. This is in contrast to Darwin, who specified a kind of blending inheritance in which offspring were intermediate to the parents. Just as importantly, their work specified the forces (causes) of evolution. Population genetics is the foundation for modern evolutionary biology. Other population geneticists, such as Ronald A. Fisher, John B. S. Haldane, and Sewall Wright, contributed to the foundations of the theory of population genetics from the 1920s to the 1940s.

This 50 million year old fossilized spadefish is a part of the fossil record scientists use to study evolution. The detail is particularly good here; the impression of the fish's eggs is visible.

alleles one of two or more alternate forms of a gene

fossil record a collection of all known fossils

biogeography the study of the distribution of animals over an area

All animals are the descendants of a single common ancestor. Biological evolution has created the diversity of organisms we see today, as well as extinct animals such as dinosaurs for which we have the **fossil record**. The diversifying action of evolution to create new species is called speciation. Speciation is the splitting of one former species into two species that are reproductively isolated from each other such that they no longer successfully reproduce and exchange genes. Speciation is the result of a combination of **biogeography**, natural selection, adaptations, and the other evolutionary forces.

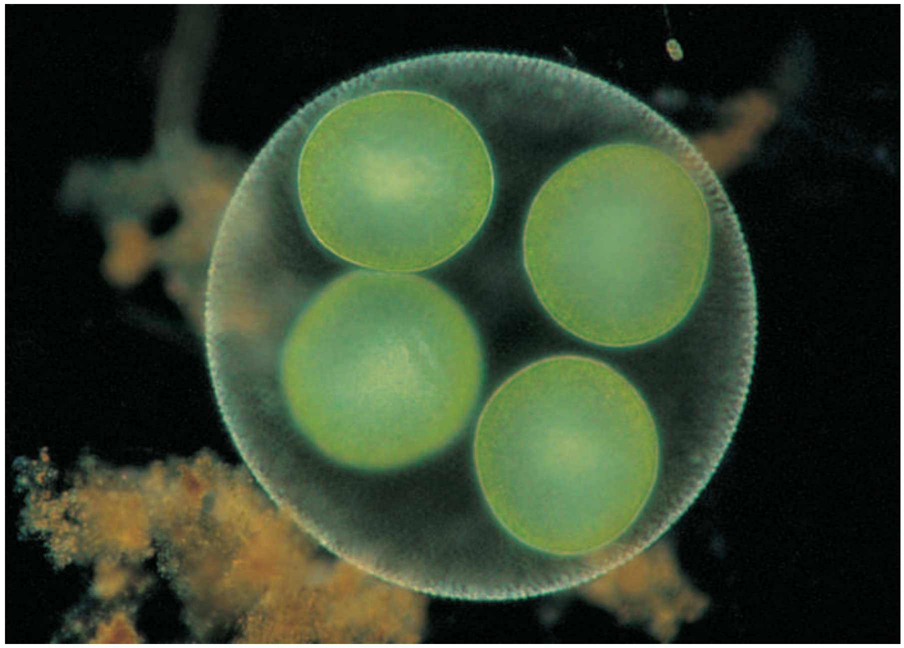
There are two main modes of speciation: allopatric and sympatric. Allopatric speciation is the division of one population into two populations because of some geographical barrier. While separated, each population evolves differently from the other population. When contact is restored between the two populations, they cannot reproduce, and so are unable to exchange genes because of the differences they acquired while separated. Sympatric speciation is when one population splits into two without any geographical barrier. While this mode of speciation was doubted for years, in the 1960s Guy Bush conducted experiments on fruit flies that supported this mode of speciation. In the early 1980s, Bill Rice conducted laboratory experiments in which he was able to cause sympatric speciation. Even though sympatric speciation is possible, it is not as common as allopatric speciation.

Causes of Biological Evolution

There are five forces that cause evolution: natural selection, mutation, gene flow, nonrandom mating, and genetic drift. All five depend on the existence of genetic variation, which is necessary for any evolutionary change. Natural selection is the differences in the survival and reproduction rates of individuals with different **phenotypes**. When phenotypes can be genetically inherited, natural selection produces adaptations as the population evolves. Natural selection can remove variation from a population if it is stabilizing selection. Diversifying selection can increase the amount of variation in a population. Directional selection changes the average trait in the population.

phenotypes the physical and physiological traits of an animal

Genetic mutations occur when errors are made in replicating (copying) and dividing DNA. Mutation is the ultimate source of genetic variation. Most of the time, mutations either have no effect on the phenotype, and



Reproduction—shown within this Chlorophyta Volvox protozoa that contains four daughter colonies—is a driving force behind biological evolution.

therefore are neutral, or have a harmful effect. Rarely, a mutation will create a phenotype that is better, and so natural selection will favor this beneficial mutation. Mutations happen naturally at low levels of frequency. These levels can be much higher under some conditions. For example, exposure to radiation and to some toxic chemicals produces higher mutation rates.

Gene flow is the exchange of genes among populations or species. The exchange of genes between species is called hybridization. Introducing new genes into a population changes the gene frequency and causes evolution. Gene flow can be positive or negative for a population. Lots of gene flow can prevent local adaptation because any evolution produced by natural selection is swamped by the invading genes. On the other hand, gene flow can introduce a new beneficial gene into a population. Natural selection can favor this new adaptation, and it can spread through the population.

Nonrandom mating changes what combinations of genes are mixed together in sexual reproduction. Sexual reproduction creates new individuals, half of whose genetic information comes from the mother and half from the father. If individuals within a population who have a particular **genotype** pair off and mate at a rate different from the occurrence of that gentotype in the population, then nonrandom mating is occurring. Nonrandom mating can be caused by mating among close relatives, or inbreeding, which can result from population subdivision. Nonrandom mating also happens when individuals choose mates based on particular phenotypes. In some animal species, a few males get most of the matings because they have some highly desirable phenotype. Assortative mating also produces nonrandom mating, which is the mating of males and females of the same phenotype. For example, large male frogs mate with large female frogs and small males mate with small females.

genotype the genetic makeup of an organism

Genetic drift causes evolution by random changes in the allele frequencies. One way for genetic drift to happen is for some of the alleles to be left after some kind of fluctuations in population size. For example, if

disease wipes out most of a population, only some alleles will be left in the population. Also, only some combinations of alleles for different genes will be left. If natural selection is not acting on a gene, then random genetic drift can be a stronger force than if selection is present. The impact of drift depends on the population size. Drift is stronger in smaller populations; they are more susceptible to random changes in allele frequencies since there are not as many alleles present.

Limits to Biological Evolution

What can limit evolution? Three main factors restrict the amount of change evolution can make in a population: the degree of genetic variation is limited; natural selection produces adaptations that are a compromise in form and function; and most forces of evolution are not adaptive.

First, genetic variation is the ultimate barrier to evolution. If there is no genetic variation, no evolution can happen. Genetic variation is limited to the history of the organism. A bear will not suddenly gain wings in a few generations of evolution. No bear has ever had wings, and it is unlikely that any bear will evolve them. An organism contains only so much DNA and the amount of existing genetic variation, the raw material for evolution, is restricted by the past history of the species. A bear does not have the underlying genetic variation necessary for a mutation to produce wings from the existing variation.

Second, adaptations are usually compromises and therefore limit evolution. Natural selection works on a whole organism rather than just single traits, so it is the combination of traits that natural selection favors. A cheetah is a fast runner but a poor swimmer. Any cheetah with webbed feet would be a better swimmer but could certainly not run as fast. Adaptations are trade-offs.

Third, many forces of evolution are not adaptive. Natural selection is the force of evolution that produces adaptations but the other forces of evolution are not necessarily adaptive. Gene flow can introduce genes into a population that are better suited to another environment. Nonrandom mating can break up existing combinations of genes that work well together. Mutation is typically harmful. Random genetic drift is frequently not beneficial. Most forces of evolution are random and can be working counter to natural selection.

Rates of Evolution

Does evolution proceed at a fast pace or a slow pace? How much of evolution can we actually observe? In 1972 Niles Eldredge and Stephen J. Gould wrote an article that presented the idea of punctuated **equilibrium**. Some organisms for which there are good fossil records show long periods of no morphological evolution (evolution in the form and structure of organisms); the animals remain unchanged over thousands of years. But then there suddenly appears what looks like a morphologically similar new species. The theory of punctuated equilibrium is that long periods of no change are followed by short periods of rapid transition. This is in direct contrast to gradualism. Gradualism suggests slow but continuous change over geological time. How is one to know if the fossil record is incomplete, and that the seemingly rapid change is accounted for by missing intermediate stages?

equilibrium a state of balance

This question has inspired research on the rate of evolutionary change. It is possible to calculate rates of morphological evolution from the fossil record. Evolutionary rates can be measured over several generations in natural and laboratory populations. It is also possible to measure the relative rate of change in molecules for which the gene sequence is known. The sequence of a gene is the order of nucleotides within it. Sexual reproduction can also increase the rate of evolution compared to asexual reproduction. This is due to increased genetic variation by recombination and independent assortment. Gene sequencing has made it possible to investigate how the rate of evolution changes with the degree of underlying genetic variation, also called genetic **polymorphism**. In 1991 the first important test of rates of molecular evolution and molecular polymorphism was conducted by J. H. McDonald and Martin Kreitman. As the entire genetic material (genomes) of more and more organisms are sequenced, we will understand more about the rate and mechanisms of evolution. SEE ALSO ADAPTATION; GENES; GENETICS; NATURAL SELECTION.

polymorphism having two or more distinct forms in the same population

Laura A. Higgins

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Endler, John A. *Natural Selection in the Wild.* Princeton, NJ: Princeton University Press, 1986.

Futuyma, Douglas J. *Evolutionary Biology*, 3rd ed. Sunderland, MA: Sinauer Associates, Inc., 1998.

Otte, Daniel, and John A. Endler. *Speciation and Its Consequences.* Sunderland, MA: Sinauer Associates, Inc., 1989.

Purves, William K. et al. *Life: The Science of Biology*, 5th ed. Sunderland, MA: Sinauer Associates, Inc. 1998.

Ridley, Mark. *Evolution*, 2nd ed. Cambridge, MA: Blackwell Science, Inc., 1996.

Biological Pest Control

Scientists use different pest control methods that range from choosing a pesticide that will be least harmful to beneficial insects to raising and releasing one insect to attack another. Biological control of horticultural pests is a subject of increasing interest, especially to people who prefer to use chemicals as little as possible. The traditional and familiar use of chemical pesticides sometimes has detrimental effects on the environment (such as with DDT) and harmful effects on humans (such as the increased risk of cancer in individuals exposed to certain pesticides). There are, however, alternative pest control methods, such as biological pest control, that are less harmful to the environment and humans. Unfortunately, biological pest control methods alone are rarely sufficient. Research suggests that an integrated approach, using pesticides, biological pest control, and other techniques may be the most effective.

In general terms, biological pest control is the use of a specifically chosen living organism to control a particular pest. This chosen organism might be a naturally occurring parasite, predator, or disease that will attack a harmful insect. Biological pest control is a way to manipulate nature to increase a desired effect. There are three main ways to use natural enemies against unwanted insect pest populations: classical biological control, augmentation, and conservation.

Classical Biological Control

Classical biological control involves releasing an imported organism that establishes itself and spreads to permanently control a pest. In 1889, for example, the release of 129 imported Australian vedalia beetles resulted in a dramatic reduction of cottony cushion scale disease, which had threatened California's citrus industry. Successful biological control means no further costs are required to keep the pest under control.

Classic biological control may also mean traveling to the country or area from which a newly introduced pest originated and returning some of the natural enemies that attacked it and kept it from being a pest there. New types of insects are constantly arriving, accidentally or intentionally. Sometimes they survive. When they come, their enemies are left behind. If the insects become a pest, introducing some of their natural enemies can be an important way to reduce the amount of harm they can do. Although simple in concept, the process of locating the place of origin of the nonnative pest and then finding and introducing natural enemies from its place of origin presents many ecological and logistical challenges. For example, any introduced pest predator or parasite must undergo exhaustive testing before being released to be sure it will not harm nontarget organisms. Even when challenges are successfully met, projects can fail because of problems relating to such factors as climate differences, prior or current pesticide use, disturbances of the habitat by other agricultural operations, and the removal of noncrop vegetation that might otherwise offer food and shelter to the natural enemies.

Augmentation

Augmentation is a method of increasing the population of a natural enemy that attacks pests. This can be done by mass producing a pest in a laboratory and releasing it into the field at the proper time or breeding a better natural enemy that can attack its prey more effectively. Mass rearings can be released at special times when the pest is most susceptible and natural enemies are not yet present, or they can be released in such large numbers that few pests go untouched by their enemies. In one study, for example, male insects were sterilized by gamma radiation, and large numbers were released into the environment to mate with wild insects. The pest population was dramatically reduced because they were unable to produce viable offspring.

Scientists also grow microbes, such as bacteria and fungal spores, in the laboratory and spray crops and lawns with large numbers of these natural organisms to bring certain pests under control. About 1,100 species of viruses, bacteria, fungi, protozoa, rickettsiae, and nematodes are known to parasitize insects. Japanese beetle populations, for example, once created major crop infestations here in the United States but have been decimated by treating crops and lawns at intervals with spores of a bacillus bacterium that causes milky disease, a lethal pathogen for these beetles. These spores

Farmers use the natural appetite of ladybug beetle larvae for aphids to help keep the population of aphids on their farms under control.

infect the Japanese beetle larvae but do not harm other animals in the environment.

Another bacterium, *Bacillus thuringiensis*, has been extensively exploited in the bacterial control of pest insect populations. Commercial preparations of *Bacillus thuringiensis* are registered by at least twelve manufacturers in five countries for use on numerous agricultural crops and forest trees for control of pests including the alfalfa caterpillar, bollworm, cabbage looper, fruit tree leaf roller, California oakworm, and fall webworms. Many other commercial bacterial products exist. For many years, a mixture of *Bacillus popilliae* and *Bacillus lentimorbus* has been marketed under the trade name Doom.

Viral diseases have also been studied as a means of controlling certain caterpillars and sawfly larvae. Crops are sprayed with a substance prepared from diseased insects in order to start an epidemic of a fatal disease in the pest population.

Augmentation is effective but it relies upon continual human management and does not provide a permanent solution, unlike importation or conservation methods.

Conservation

Conservation of enemies is an important part of any biological control effort. This strategy involves identifying any factors that limit the effectiveness of a particular natural enemy and changing them to help the beneficial species. Conservation of natural enemies involves either reducing factors that interfere with the natural enemies or providing needed resources that help natural enemies. Use of reflective aluminum strips mixed in with mulch in vegetable fields, for example, has reduced or prevented aphid attack and thus protected cucumbers, squash, and watermelons from infestation. The planting of cover crops, such as providing nectar-producing plants and sources of alternate hosts in and around fields, and the interplanting of different crops to provide habitat diversity are management techniques that lead to the buildup of natural enemy populations and result in enhanced biological control.

Other Alternative Nonchemical Control Methods

Physical energy is also known to kill insects. In a recent discovery, adult Indian-meal moths exposed to certain wavelengths of sound during their egg-laying period reduced their reproduction by 75 percent. These sound waves also had a similar effect on flour beetles. Light waves, high-frequency electric fields, and high-intensity radio frequencies also may offer helpful options. Sophisticated methods of pest control are continually being developed. Cutting-edge research with highly specific insect hormones was also underway at the beginning of the twenty-first century.

CASE STUDY

The battle against spotted alfalfa aphids in California began in the late 1950s when researchers noted growing damage among the crop. Initial tests showed that the aphids had developed a resistance to chemical sprays, and that beneficial insects were dying off because of the chemicals. Over the years, pesticide use was reduced and the aphid problem diminished as the natural predators regained their populations.

Integrated Pest Control Methods

Integrated pest control methods, which involve more than one method, may be the best answer. Combining disease-resistant plant varieties with an insecticide that leaves parasites and predators unharmed is one ideal strategy that seems to offer promise. It has been successful, for example, in combating the spotted alfalfa aphid in California. In other cases, first-line defenses such as chemical sprays combined with bait, followed by the sterile-insect technique were highly effective. The most important value of this control method is that far fewer chemical pesticides are used, and so the environment remains unaffected.

Biological pest control methods, in concert with proven agricultural practices such as destruction of crop residues, deep plowing, crop rotation, use of fertilizers, strip-cropping, irrigation, and scheduled planting operations, can further prevent or reduce crop damage. SEE ALSO DDT; PESTICIDE.

Stephanie A. Lanoue

Bibliography

Atlas, Ronald M. *Principles of Microbiology.* St. Louis: Mosby-Year Book, 1995.

McDermott, Jeanne. “Some Heartland Farmers Say No to Chemicals.” *Smithsonian* 21, no. 1 (1990):14–18.

Murphy, Terence M. “Herbivory, Predation, and Biological Control.” *American Biology Teacher* 54, no. 7 (1992):416–419.

Nester, Eugene W., C. Evans Roberts, and Martha T. Nester. *Microbiology: A Human Perspective.* Melbourne: William C. Brown Publishing, 1995.

Pickett, J. A. "Behavior Controlling Chemicals." *Education in Chemistry* 16, no. 2 (1979):44–47.

Singleton, Paul. *Bacteria in Biology, Biotechnology, and Medicine*, 5th ed. New York: Wiley, 1999.

Biomass

Suppose you take a walk in the forest one day and you look around you at all the trees and think, "That's a lot of wood, I wonder how much all these trees weigh?" Biologists ask the same question. Biomass is the total mass of all the trees (after the water has been taken out).

The term "biomass" is actually applied to three related but slightly different concepts. The total dry weight of all living organisms that can be supported at each **trophic level** in a food chain is known as the biomass. The term is also applied to the dry weight of all living organic matter in an entire ecosystem. Finally, people interested in alternative sources of energy use the term to apply to the total mass of all plant materials and animal wastes that can be used as fuel.

trophic level the division of species in an ecosystem by their main source of nutrition

Plants use a complex chemical process known as **photosynthesis** to combine carbon dioxide, water, and sunlight to produce carbohydrates (sugar and cellulose), fats, and proteins. The solar energy that drives photosynthesis is stored in the chemical bonds of these molecules. These carbohydrates, fats, and proteins make up biomass. Biomass, then, can be considered to be stored solar energy.

photosynthesis the combination of chemical compounds in the presence of sunlight

The energy stored in carbohydrates and other compounds by photosynthesis can be released by burning or by metabolism. When animals eat plants, their bodies slowly release the energy stored in the chemical bonds and this energy becomes available to the animals for muscular activity or maintaining body temperature. When biomass is burned, the water and carbon dioxide are released back into the atmosphere. Therefore, biomass is a renewable energy resource.

American Bioenergy Association

This interest group located in Washington D.C., works to promote the use of bioenergy resources as alternative energy sources. The ABA strives to gain support through the federal government by proposing policies such as tax incentives, increased budget allocations, and research funding. The ABA argues that using biomass would cut U.S. dependence on oil from the Persian Gulf, and fuel the nation's economy.

The total amount of biomass produced each year is about eight times the world's energy consumption. However, the energy density of each unit of biomass is much smaller than the energy content of fossil fuels ("old" biomass), so much more mass must be burned to produce the same amount of energy. Also, the world's biomass is widely distributed, so concentrating and transporting the biomass remains a problem. There are experimental projects that convert biomass into alcohol or natural gas. But worldwide, only about 7 percent of the biomass produced each year is used as fuel, so this energy resource remains underutilized.

The amount of biomass generally decreases at each higher trophic level. In a temperate grassland, for example, the amount of biomass at each trophic level is only about 10 percent of the biomass of the level below it. If there are 10,000 kilograms (22,000 pounds) of producers (grasses and other plants), there will be only 1,000 kilograms of primary consumers (grasshoppers, voles, bison), 100 kilograms of secondary consumers (shrews, hawks, small cats), and only 10 kilograms of tertiary consumers (large cats, wolves, humans).

The remaining 90 percent of the available energy from biomass at each level is converted to waste heat. This energy loss at each trophic level generally limits food chains to no more than four or five levels.

Marine environments usually reverse the amounts of biomass in the first two trophic levels. The mass of primary consumers (small fish and shrimp) is generally much larger than the mass of producers. This happens because the primary producers are tiny phytoplankton that grow and reproduce rapidly instead of large plants that grow and reproduce slowly. SEE ALSO Biomes; Food Web.

Elliot Richmond

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth Publishing Company, 1990.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates, 1987.

Biomechanics

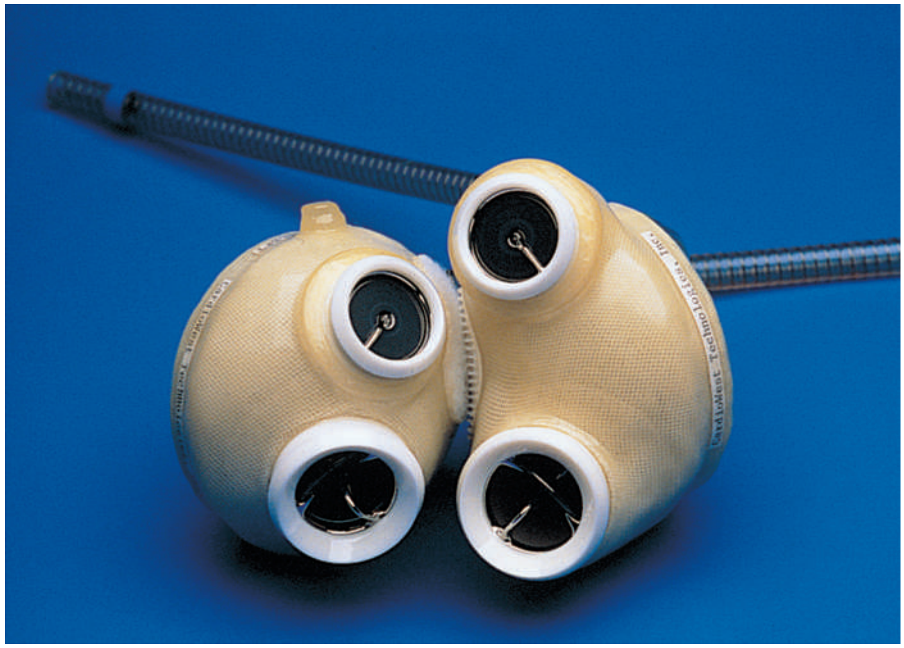
The science of biomechanics applies mechanical principles to the study of organisms. Biomechanics uses mathematical models and computer simulations to study living organisms, in addition to direct biological measurements.

Biomechanics helps us understand limitations on the size of organisms, problems with scaling, energy efficiency, the advantages of internal versus external skeletons, and other concepts. Biomechanics can even help biologists understand animal behavior, such as how a whale can remain submerged for extended periods of time.

For example, the largest single-celled organisms are protists about the size of the period at the end of this sentence. There are larger cells that are part of multicellular organisms, but no single-celled organisms. So why are there no large, single-celled animals? The primary restriction is surface-to-volume ratio. A cubical cell 100 μm on a side has a volume and mass 1,000 times as great as the volume and mass of a cell 10 μm on a side. This larger mass requires roughly 1,000 times as much oxygen, food, and water. It also produces 1,000 times as much waste that must be excreted.

Where does the cell exchange all this material? Exchange takes place through the cell membrane. But the cell membrane of the larger cell is only 100 times as large as the smaller cell, so 1,000 times as much material must pass through a membrane only 100 times as large. If the cell membrane is wrinkled and folded its area is increased, but the cell will ultimately reach a point where it will be unable to feed or breathe through the membrane. This places a practical limit on the maximum size a single-celled organism can attain. Large organisms must be multicellular and have a complex system of specialized cells that can transport food, oxygen, and waste.

If you compare a house cat (*Felis sylvestris*) and a Bengal tiger (*Felis tigris*), it is obvious that multicellularity is not a sufficient solution to the problems of scaling up an organism to larger size. Weight is proportional to volume, so weight increases with the cube of height. Muscle and bone strength is



Production of this artificial heart by Cardiowest Tech was made possible by the close study of the mechanics of the human heart.

proportional to cross-sectional area and increases with the square of height. This means the tiger requires much thicker legs than the house cat, relative to its overall size, to support its larger mass and move quickly.

A detailed biomechanical study of the effects of scale that considers factors such as weight, air resistance, muscle strength, heat loss, and bone stress can explain some surprising observations. For example, an impala, a domestic cat, a domestic dog, and a domestic horse can all jump to roughly the same height above the ground. Biomechanics helps us understand why. Biomechanics can also explain why large whales (air-breathing organisms) can remain submerged for a long time compared to small dolphins and seals. Underwater, body size is advantageous. In contrast, large hawks can only hover for a short time, whereas hummingbirds, kestrels, and kingfishers can hover for extended periods. In the air, large size is a disadvantage.

One of the most productive applications of biomechanics has been in the field of athletic competition. Coaches study the principles of biomechanics to learn how to improve the performance of the athletes they train. Ideas of conservation of angular momentum from physics can help coaches teach athletes how to improve their ability to throw a discus or put the shot. Energy conservation helps marathon runners learn how to train more effectively and run more efficiently.

The biomechanics of running, especially amateur running, has been an area of intense research and interest. Some sports doctors videotape their patients to study abnormalities in their gait that have the potential to cause injury. Doctors can then prescribe shoe inserts or other shoe modifications to help prevent injury. They may also recommend a change in running style or training regimen based on a runner's idiosyncrasies. For example, a doctor might notice that the runner is swinging his or her arms across the body. This causes an excessive rotation of the pelvis, which can lead to hip pain. If this is the case, the doctor may train the runner to move his or her arms parallel to the direction of motion.

Another important area of research in biomechanics is automobile safety design. Most people have seen films of crash-test dummies. Crash-test dummies are designed to simulate humans. Their joints move the same way that human joints move. By analyzing how car accidents affect the dummies, engineers can design safer automobiles.

More recently, biomechanics is moving toward computer models that can be used. The advent of fast, powerful computers and improved mathematical models make it possible to analyze the effects of a crash on humans with greater accuracy and less expense than is possible through mechanical simulations such as dummies.

Elliot Richmond

Bibliography

Cavanagh, Peter R. "Biomechanics: A Bridge Builder among the Sport Sciences." *Medicine and Science in Sports and Exercise* 22, no. 5 (1990):546–557.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Hubbard, Mont. "Computer Simulation in Sport and Industry." *Journal of Biomechanics* 26 (1993):53–61.

Huxley, Julian S. *Problems of Relative Growth*. New York: Dial Press, 1932.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology*. Sunderland, MA: Sinauer Associates Inc., 1987.

Shorten, Martyn R. "The Energetics of Running and Running Shoes." *Journal of Biomechanics* 26 (1993):41–51.

Thompson, D'Arcy W. *On Growth and Form*. Cambridge, U.K.: Cambridge University Press, 1942.

Biomes

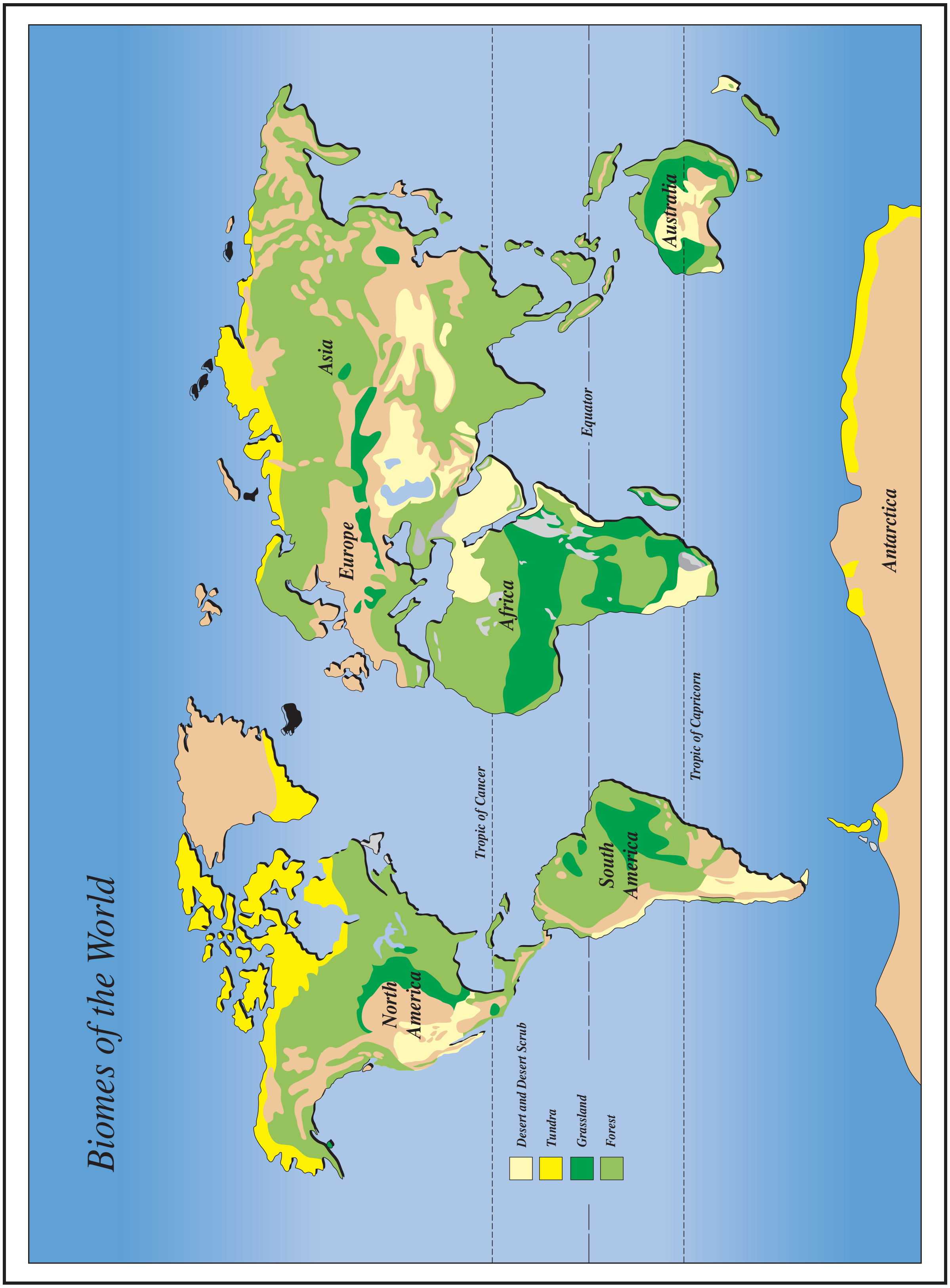
An ecosystem is a community of organisms that interact with each other and with the **abiotic** (chemical and physical) factors in their particular environment. A biome is the largest well-defined ecosystem. Biomes include vast grasslands, continent-wide deserts, and sweeps of arctic tundra. Biomes also include such well-defined ecosystems as coral reefs, lakes, and river systems.

abiotic nonliving parts of the environment

Biomes are characterized by climate, by typical vegetation, and by the way organisms have adapted to that environment. Biomes are not permanent. Grasslands can be transformed into deserts; forests can be converted into grasslands. Climate change at the end of the last Ice Age dramatically altered the biomes of North America because of natural changes in climate and the movements of land masses. Since the Industrial Revolution, human activity has become an increasingly important factor in alteration of biomes.

Biomes are usually classified on the basis of average temperature and precipitation. This classification scheme results in many different biomes. Five typical biomes are:

- Aquatic
- Deserts
- Forests
- Grasslands
- Tundra


Biomes of the World
Desert and Desert Scrub
Tundra
Grassland
Forest
North America
South America
Europe
Asia
Africa
Australia
Antarctica
Tropic of Cancer
Equator
Tropic of Capricorn

Aquatic Ecosystems

Water covers about 75 percent of Earth's surface (including both freshwater and marine environments). While some ecologists reserve the term "biome" to refer to terrestrial ecosystems, aquatic ecosystems play a very important part in the ecology of Earth. Aquatic ecosystems can be freshwater (such as ponds and lakes, streams and rivers, and wetlands) or marine (such as oceans, coral reefs, mangrove swamps, salt marshes, and **estuaries**).

estuaries areas of brackish water where rivers meet the oceans

Freshwater Regions. Water is classified as fresh if it contains less than 1 percent salt (sodium and potassium chloride and other salts) in solution. Most freshwater plants and animals are unable to tolerate higher concentrations of salt in the water.

Ponds may be only a few square meters, whereas the largest lakes cover thousands of square kilometers. Ponds and lakes are scattered all over Earth. Many important ponds are seasonal and last for only one or two months at a time. These seasonal ponds may still be important resting places for migrating birds and other animals. Some large lakes have lasted for tens of thousands of years.

Lakes and larger ponds can be divided into three different "zones," determined by depth and distance from the shore. The littoral zone is the top layer of water near the shore. It may be warmer than the average temperature of the lake, but it also may have wider seasonal temperature variation. This is generally the most biologically diverse community in the lake, including algae (like diatoms), rooted and floating aquatic plants, grazing snails, clams, insects, crustaceans, fishes, and amphibians. Insect larvae may also inhabit this zone. The vegetation and animals living in the littoral zone provide food for other creatures such as turtles, snakes, and ducks.

The open water surface of the lake is known as the limnetic zone. Since this zone receives the most sunlight, it is a rich source of plankton. These plankton are the base of the food chain for the whole lake. Small fish also inhabit the limnetic zone, where they eat plankton or food that falls on the surface of the lake.

The bottom of the open water portion of the lake is known as the profundal zone. Since little light penetrates this region, its inhabitants are **heterotrophs**, which eat the small fish and other animals from the littoral and limnetic zones. Other inhabitants are detrivores, subsisting on material falling into the deep water from the surface.

heterotrophs organisms that do not make their own food

The temperature of a pond or lake will vary seasonally. In colder climates, the surface of the lake may freeze solid. In large lakes the deep water will never freeze, remaining about 4°C (39° F) all winter. During spring and fall, substantial mixing of the lake water can occur (sometimes called "turning over").

A river is a long, narrow body of water flowing downhill. A river may start in the mountains and flow all the way to the ocean. Or it may start in a lake or spring and flow a short distance before joining another river or entering a lake. The start of the river will have a lower temperature, clearer water, and more oxygen. The middle part of the river will be wider and slower moving. The water will be warmer. There will be more species diversity,

The mountains and alpine meadow of Denali National Park, Alaska, are part of a larger ecosystem which is otherwise known as a biome.

including plants and algae. Close to the mouth of the river, the water may be filled with sediment. Fish that can tolerate less oxygen and warmer temperatures, such as carp and catfish, will be found near the mouth.

Wetlands are areas of standing water that support aquatic plants. Marshes, swamps, and bogs are all wetlands. The water in wetlands flows slowly or is still. Wetlands can be seasonal or permanent. Since the water in wetlands is often low in oxygen, plant species often require special adaptations. Wetlands have the highest species diversity of all ecosystems, with many species of amphibians, reptiles, birds, and fur-bearing mammals living in them.

Marine Regions. Marine ecosystems, which cover about three-fourths of Earth's surface, include oceans, seas, saltwater marshes, estuaries, and coral reefs. Because of their size, marine ecosystems are important parts of the atmospheric carbon dioxide cycle. Marine algae take in huge amounts of carbon dioxide from the atmosphere and release much of the world's oxygen supply. Marine ecosystems also supply most of the atmospheric water vapor that falls as precipitation on land.

Oceans are the largest of Earth's ecosystems. Like lakes, oceans are subdivided into separate zones: intertidal, pelagic, abyssal, and **benthic**. All four zones have a great diversity of species. The intertidal zone is the region along the shoreline between average low tide and average high tide. In other words, this region goes through cycles of submergence and being exposed to air. Animals in this zone must be able to survive the extended periods of exposure. The pelagic zone includes all the open ocean water. The abyssal zone is the deep ocean water, between 2,000 and 6,000 meters deep. The benthic ocean includes the deep ocean bottom inhabited by organisms.

benthic living at the bottom of a water environment

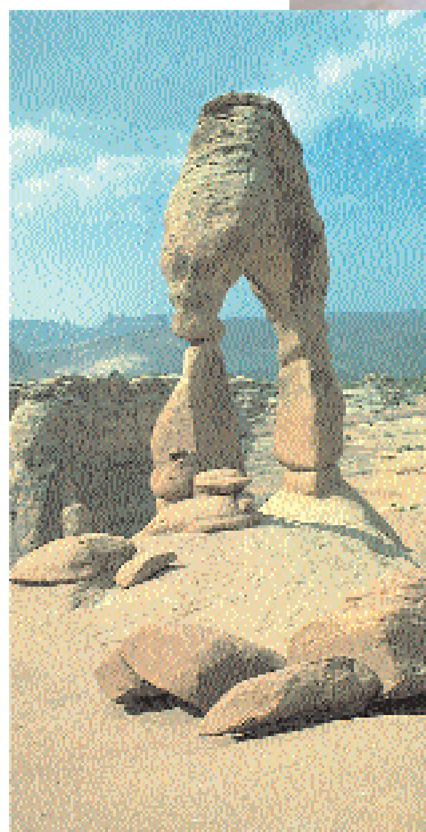
Deserts

Deserts cover about one-fifth of Earth's surface. The identifying characteristic of the desert biome is low annual rainfall. Some deserts receive large amounts of rain in the form of heavy thunderstorms, but these occur for a short time and run off rapidly. On average, any region that receives less than 50 centimeters of rainfall per year is considered a desert. The driest deserts receive less than 2 centimeters of rainfall per year. The Atacama in Chile may get no rainfall at all for years at a time.

Most of the world's deserts occur in a band between 10° and 40° of the Equator. Cold deserts, such as the basin and range area of Utah and Nevada and parts of western Asia, occur at higher latitudes. Most deserts have a wide variety of specialized vegetation, as well as many specialized animals. Because there is little rainfall, most desert soils have high nutrient levels. However, the humus (organic matter) in soils is very low.

Desert plants are typically low-growing shrubs and short woody trees. Leaves are of many different types, but all show various degrees of specialization because of the lack of rainfall. Many plants have small leaves that are covered with a waxy film to retain water. The thorns of cacti are highly modified leaves that shade and protect the plant. The thickened and often flattened stems of cacti have taken over the job of photosynthesis.

While mule deer, pronghorns (which resemble antelopes), desert bighorns (a type of wild sheep), and mountain lions are all found in the relatively humid deserts of North America, the dominant vertebrates of warmer and drier deserts are small reptiles and amphibians. Mammals are usually small, like the kangaroo mice of North American deserts. There are also insects, arachnids, scorpions, and birds. The animals stay inactive in protected hideaways during the hot day and come out to forage during twilight hours or at night.



The "Delicate Arch" of the Arches National Park in Utah sits on top of a large sandstone formation. The climate of the park is desertlike, with temperatures reaching highs of 38°C (100°F) in the summer months, and lows of 0°C (32°F) in the winter.

Forests

Forest biomes are ecological communities dominated by trees. There are three major types of forests distinguished by latitude: tropical, temperate, and boreal forests (taiga).

Tropical forests include the greatest diversity of species of any of the world's biomes. By definition, tropical forests occur in the tropics, within 23.5° of the equator. Instead of the four seasons typical of temperate regions, most tropical forests have two seasons, a dry season and a wet season. The temperature and amount of daylight are fairly constant. However, because of the heavy forest canopy, little sunlight reaches the forest floor.

The annual rainfall in tropical forests is generally 200 centimeters or more. This high amount of rainfall results in soils that have lost most of the nutrients. A square kilometer of tropical forest may contain 100 species of trees and thousands of species of insects. Orchids, bromeliads, ferns, mosses, and palms grow in the trees and on the forest floor. Birds, bats, small mammals, and insects live in and around the trees.

Temperate forests are characterized by four distinct seasons, including a winter season with extended periods below freezing. The tree canopy allows light to penetrate to the forest floor, so there is an understory of shade-tolerant trees and shrubs. This results in a stratification of the **flora** and fauna of the temperate forest, with distinct sets of plants and animals present in the treetops, the mid-levels, and on the forest floor. Most trees are broad-leaved **deciduous** trees that drop their leaves each fall; mixed in are some evergreen conifers. Typical tree species include oak, hickory, maple, elm, willow, and dogwood. Animals include rabbits, squirrels, skunks, many species of birds, deer, mountain lion, bobcat, timber wolf, fox, and black bear. Reptiles and amphibians inhabit the forest floor.

flora plants

deciduous having leaves that fall off at the end of the growing season

Boreal forests are cold forests of northern latitudes that experience many months of snow cover and below-freezing temperatures. Extensive boreal forests occur north of 50° north latitude to beyond the Arctic Circle. Boreal forests are found in a broad belt extending from Siberia across Alaska, into Canada and parts of the northern United States, and also in Scandinavia. These forests may also be found farther south at higher altitudes. Seasons are divided into short, moist, moderately warm summers and long cold, dry winters. The length of the growing season in boreal forests is very short, around 100 days. Precipitation is primarily in the form of snow, the equivalent of 40 to 100 centimeters of rainfall annually. Soil is generally thin, nutrient-poor, and **acidic**. The dense canopy permits little light to reach the forest floor, so the forest understory is limited. The trees are mostly evergreen conifers such as spruce, pine, and fir. Animals include woodpeckers, hawks, owls, many other bird species, moose, bear, weasel, fox, lynx, and deer.

acidic having the properties of an acid

Grasslands

Grasslands are lands dominated by grasses. Large shrubs or trees are restricted to stream banks and to isolated stands. There are two main divisions of grasslands: tropical grasslands, called savannas, and temperate grasslands.

Savanna. A savanna is grassland with widely scattered individual trees or small groups of trees. Savannas of one sort or another cover most of central Africa and large areas of Australia, South America, and India. A savanna is not as arid as a desert but receives roughly the same amount of rainfall as a temperate forest. The annual rainfall ranges from 50 to 130 centimeters per year. However, the rainfall occurs in a "wet" season of four to six months. The wet season is followed by a dry season. During the dry season, drought and fires can occur. The drought and fires suppress the growth of trees and shrubs. This cycle of wet and dry seasons, fires, and drought maintains the savanna conditions.

Human activity can inadvertently convert a forest into a savanna. If the trees are removed and grass grows rapidly enough to cover the bare ground before the trees can recolonize, then fires may become the dominant force, and the savanna will become more or less permanent. The relatively infertile soil of savannas has discouraged the conversion of savannas to farming of wheat and other grasslike crops. When farming is instituted, the organic material is quickly exhausted and the soil then requires the addition of chemical fertilizer to remain productive.

Fire is essential to the life of a savanna. Most animals killed by the fires are insects and small animals. Large animals are able to escape the fire. Birds and other opportunistic feeders move in quickly to eat the killed animals or to prey on the animals fleeing the fire. The grass quickly sprouts from the extensive root structure out of reach of the fire. Many shrubs and woody plants are killed by the fire.

The shrubs and trees that survive have special adaptations that allow them to survive the fire or to sprout quickly when the rains come. The life cycle of animals that live on the savanna is tied to this same cycle. Calves are born soon after the start of the rainy season, when plenty of new grass is available. Other animals that live completely or partly on the savannas around the world (not all in the same place) include giraffes, zebras, buffaloes, kangaroos, mice, moles, gophers, ground squirrels, snakes, worms, termites, beetles, lions, leopards, hyenas, and elephants.

Temperate Grassland. Temperate grasslands also have grasses as the dominant vegetation. Trees and large shrubs are restricted to the banks of streams. Temperatures vary widely from summer to winter. The amount of rainfall is less in temperate grasslands than in savannas. The plains and prairies of central North America were typical temperate savannas before the land was converted to farming. As in savannas, the cycle of seasonal drought and fire is essential to maintaining the **biodiversity** of temperate grasslands.

biodiversity the variety of organisms found in an ecosystem

The soil of the temperate grasslands contains a thick layer rich in organic matter from the growth and decay of grass roots. The organic material holds the soil together and provides nutrients for new growth. Seasonal drought, fire, and grazing by large mammals all prevent woody shrubs and trees from invading and becoming established. Some trees, such as cottonwoods, oaks, and willows, grow along streams and in river valleys. Many annual plants, such as wildflowers, grow among the grasses.

Temperate grasslands also experience a wet season and a dry season. Most precipitation occurs in the late spring and early summer. The rest of the year is relatively dry, with rainfall averaging 50 to 90 centimeters per year. The temperature range of temperate grassland is very wide. Summer temperatures can be well over 40°C (104°F), while winter temperatures can drop as low as -40°C (-40°F).

Animals found in temperate grasslands in different parts of the world include gazelles, zebras, rhinoceroses, wild horses, lions, wolves, prairie dogs, jackrabbits, deer, mice, coyotes, foxes, skunks, badgers, blackbirds, grouse, meadowlarks, quail, sparrows, hawks, owls, snakes, grasshoppers, leafhoppers, and spiders.

Tundra

Tundra is the coldest of all the biomes. "Tundra" is derived from the Finnish word *tunturia*, which means "treeless plain." Extremely low temperatures, little precipitation, poor nutrients, and short growing seasons characterize tundra. Dead organic material functions as a nutrient pool for nitrogen and phosphorus. Because of the constant freezing and thawing of the ground, the tundra is strangely humped into low mounds, often with a pentagonal or hexagonal shape.

In addition to the cold climate, tundra typically has low biological diversity, with only a few plants and animals present in any region. The vegetation is small and low to the ground. Drainage is very poor because there is frequently a layer of permafrost (permanently frozen soil) just below the surface. In the short summer after the surface ice melts, the tundra is covered with pools of water that provide breeding opportunities for millions of mosquitoes, blackflies, and other biting insects. Animals that live on the tundra often show large oscillations of population.

Arctic Tundra. Arctic tundra is found in the Northern Hemisphere between the taiga and the Arctic Ocean. The growing season is around fifty to sixty days. The average winter temperature is -34°C (-29°F), and the average summer temperature is around 10°C (50°F). Total precipitation varies widely but is typically quite low. The rainfall equivalent may be around 15 to 25 centimeters a year, about the same as a desert. The soil layer is thin. Soil forms very slowly and is somewhat acidic. Below the soil is a layer of frozen gravel and silt. During the short growing season, water saturates the upper surface, forming bogs and ponds. A wide variety of plants are nevertheless able to survive these odd conditions, including small willows only a few centimeters tall, sedges, reindeer mosses, liverworts, and grasses. More than 400 varieties of flowers take advantage of the short growing season.

All the plants have adapted to fierce winds and cold temperatures by growing close together and close to the ground. The tallest plants in the tundra are only a few centimeters tall. In the winter a protective blanket of snow covers the plants, which have evolved the ability to conduct photosynthesis with very little light and at low temperatures. Because of the short growing season, most plants reproduce by budding and division rather than by flowering. Arctic **herbivores** include caribou, arctic hares, squirrels, lemmings, and voles. These are preyed on by bears, wolves, and foxes. The birds are migratory, and include ravens, snow buntings, falcons, loons, sandpipers, terns, and various species of gulls. Insects include lots of mosquitoes, blackflies, moths, and grasshoppers.

herbivores describes animals that eat only plants

The animals all migrate south in the winter or hibernate. The mammals have developed the ability to breed and raise young quickly in the short summer. Almost no reptiles or amphibians live in the arctic tundra.

Alpine Tundra. Alpine tundra is generally similar to arctic tundra. However, alpine tundra has a longer growing season. Alpine tundra is found at high altitudes above the tree line throughout the world. The closer to the equator, the higher the altitude required. Even on the equator, there are still mountains high enough to have some areas of alpine tundra. Alpine tundra soils are generally well drained, but rocky subsoils serve the same function as arctic permafrost. Alpine tundra has a unique community of organisms different from arctic tundra. Animals include mountain goats, pikas, and marmots. Typical plants include heather, short bunchgrasses, and small trees. SEE ALSO Ecosystem; Habitat.

Elliot Richmond

Bibliography

Botkin, Daniel B., and Edward A. Keller. *Environmental Science: Earth as a Living Planet*, 2nd ed. New York: John Wiley and Sons, 1998.

Brown, Leslie. *The Life of the African Plains.* New York: McGraw-Hill, 1972.

Chernov, Yurii Ivanovich. *The Living Tundra*. Cambridge, U.K.: Cambridge University Press, 1985.

Costello, David Francis. *The Prairie World.* New York: Thomas Y. Crowell, 1969.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth, 1989.

Farb, Peter. *Ecology.* New York: Time, 1970.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth, 1990.

Odum, Eugene P. *Ecology and Our Endangered Life-Support Systems.* Sunderland, MA: Sinauer Associates, 1993.

Perry, David A. *Forest Ecosystems.* Baltimore, MD: Johns Hopkins University Press, 1994.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates, 1987.

Shelford, Victor E. *The Ecology of North America.* Chicago: University of Illinois Press, 1963.

Spurr, Stephen H., and Burton V. Barnes. *Forest Ecology.* New York: John Wiley and Sons, 1980.

Biometry

Biometry is the application of mathematical models to living systems. The use of statistics and mathematics as a tool for interpreting experimental data has proven invaluable to biologists, public health practitioners, researchers, and environmental scientists in areas such as genetics, toxicology, neurology, and clinical trials. Once considered a fledgling application of mathematics, biometry has proven to be a vital field playing a central role in substantive scientific and social issues of the day.

History of the Discipline

English scientist Francis Galton (1822–1911) is considered the founder of the biometric school. He strongly believed that virtually everything could be proven mathematically—that everything was quantifiable. Following this belief, Galton's first experiments (performed around 1850) included using statistical models to measure beauty and the effectiveness of prayer. Later, he came up with his own theory to explain inheritance: the theory of ancestral **heredity**. This theory held that each parent contributes one-half of the offspring's traits, each grandparent one-fourth, and so on.

heredity the passing on of characteristics from parents to offspring

It was not until the 1940s, though, that the application of statistics to biological questions began to have a profound impact on the scientific community. Scientific articles appeared in various journals, spurring the

biometrics section of the American Statistical Association to publish the *Biometrics Bulletin*, in 1945. Two years later the International Biometric Society (IBS) was established. According to its constitution, the IBS is "an international society for the advancement of biological science through the development of quantitative theories, and the application, development, and dissemination of effective mathematical and statistical techniques." Shortly thereafter, the IBS began publishing *Biometrics*, a journal directed toward biologists who saw statistics as a powerful tool in their work. Since its inception, *Biometrics* has been the premiere source for biometry-related scientific articles.

The first biometry studies were primarily concerned with agriculture in its broadest definition, specifically the design of experimental techniques. The first issue of *Biometrics* illustrates the type of analyses being performed in 1947. Articles included: "Some Uses of Statistical Methods in Plant Breeding," "Statistical Methods in Forestry," "Some Uses of Statistics in Plant Pathology," and "Some Applications of Statistical Methods to Fishery Problems." Biologists soon began writing articles relating more to the actual tools of their trade, such as the manipulation of slide rules, early calculators, and other devices. Indicative of the difficulty of applying complex statistical equations to biological queries in the days of clunky desk calculators, these reports attempted to ease the burden caused by less than stellar technological advances. Stressing the importance of collaboration between statisticians and researchers also became widespread, as the use of biometry in biological experimentation grew more commonplace. By sharing statistical methodologies, experimental designs, and the basic "how's" and "why's" of using appropriate mathematical models, both statisticians and researchers began to carve out a truly unique field of study.

The Expanding Field of Biometry

Medical uses, in the form of clinical trials, were part of the second wave of compelling applications of biometrical principles. The 1954 trial of the poliomyelitis vaccine, in the United States, was considered one of the largest experiments ever conducted. This was also a key precursor to the array of clinical studies conducted in later decades for diseases such as AIDS, cancer, influenza, measles, and malaria. Clinical trials paved the way for biological scientists to explore biometrical doctrines in such areas as social sciences, physical sciences, and engineering.

Human Genome Project a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

The widening scope of possibility for biometry has always been reliant on technology. New techniques in exploratory data analysis and computer graphics allow for statistical development in the areas of organismal, cellular, and molecular biology, neuroscience, and neural networks. Attracting enormous attention in the year 2000 was the **Human Genome Project**. Mapping and sequencing human genes would have been severely limited without the application of mathematical and statistical principles and computational advances. Additionally, the advent of the World Wide Web and expanded communication technologies have had an incredible impact on the sharing of information as well as locating research materials.

When issues involving the environment—ecology, global change, biological diversity, oceanography, and meteorological data—became widely apparent in the 1970s, biometrical principles arising mainly out of the geo-

sciences opened up new opportunities for biometricians. Similarly, changes in social and economic conditions, especially in developing nations, also provide a wealth of statistical problems that demand biometrical attention and expertise, much of which depends on new methodologies.

A new field of particular interest is that of "seafloor biology," the birth of which began with the launching of *Deep Flight I*, a kind of underwater aircraft that was sent to explore the ocean floor. This endeavor will certainly necessitate further innovative developments in statistical methodologies to process and learn from the resulting data.

Ann Guidry

Bibliography

Armitage, Peter, and Herbert A. David, eds. *Advances in Biometry: Fifty Years of the International Biometric Society*. New York: Wiley, 1996.

Ingelfinger, Joseph A. *Biostatistics in Clinical Medicine*, 2nd ed. New York: Macmillan, 1987.

McGrath, Kimberley A., ed. *World of Biology*. Detroit: Gale Group, 1999.

Biotic Factors

An ecosystem is a community of organisms that interact with each other and with the **abiotic** and **biotic** factors in their environment. Abiotic factors are chemical and physical factors such as temperature, soil composition, and climate, along with the amount of sunlight, salinity, and pH. Biotic means living, and biotic factors are the other, living parts of the ecosystem with which an organism must interact. The biotic factors with which an organism interacts depend on whether it is a producer, a consumer, or a decomposer.

abiotic nonliving parts of the environment

biotic pertaining to living organisms in an environment

Producers are also known as **autotrophs**, or self-feeders. Producers manufacture the organic compounds that they use as sources of energy and nutrients. Most producers are green plants or algae that make organic compounds through **photosynthesis**. This process begins when sunlight is absorbed by chlorophyll and other pigments in the plant. The plants use energy from sunlight to combine carbon dioxide from the atmosphere with water from the soil to make carbohydrates, starches, and cellulose. This process converts the energy of sunlight into energy stored in chemical bonds with oxygen as a by-product. This stored energy is the direct or indirect source of energy for all organisms in the ecosystem.

autotrophs organisms that make their own food

photosynthesis the combination of chemical compounds in the presence of sunlight

A few producers, including specialized bacteria, can extract inorganic compounds from the environment and convert them to organic nutrients in the absence of sunlight. This process is called **chemosynthesis**. In some places on the floor of the deep ocean where sunlight can never reach, hydrothermal vents pour out boiling hot water suffused with hydrogen sulfide gas. Specialized bacteria use the heat to convert this mixture into the nutrients they need.

chemosynthesis obtaining energy and making food from inorganic molecules

Only producers can make their own food. They also provide food for the **consumers** and decomposers. The producers are the source of the energy that drives the entire ecosystem. Organisms that get their energy by feeding on other organisms are called **heterotrophs**, or other-feeders.

consumers animals that do not make their own food but instead eat other organisms

heterotrophs organisms that do not make their own food

detritus dead organic matter

Some consumers feed on living plants and animals. Others, called detrivores, get their energy from dead plant and animal matter, called **detritus**. The detrivores are further divided into detritus feeders and decomposers. The detritus feeders consume dead organisms and organic wastes directly. Decomposers break the complex organic compounds into simpler molecules, harvesting the energy in the process.

The survival of any individual organism in an ecosystem depends on how matter and energy flow through the system and through the body of the organism. Organisms survive through a combination of matter recycling and the one-way flow of energy through the system.

Food Chain

The food chain begins with producers, living things that take minerals and gasses from the environment for support. Consumers feed off of producers. Herbivores are plant-eating animals, while carnivores eat other animals. Onmivores are people and animals who eat both plants and other animals. The last link on the chain contains decomposers, who feed off dead plants and animals, reducing their remains to gasses and minerals.

The biotic factors in an ecosystem are the other organisms that exist in that ecosystem. How they affect an individual organism depends on what type of organism it is. The other organisms (biotic factors) can include predators, parasites, prey, symbionts, or competitors.

A predator regards the organism as a source of energy and matter to be recycled. A parasite is a type of consumer organism. As a consumer, it does not make its own food. It gets its food (energy and matter to be recycled) from its host. The organism's prey is a source of energy and matter. A symbiont is a factor that does not provide energy to the organism, but somehow aids the organism in obtaining energy or matter from the ecosystem. Finally, a competitor reduces the organism's ability to harvest energy or matter to be recycled. The distribution and abundance of an organism will be affected by its interrelationships with the biotic environment.

Humans are one of the few organisms that can control how the other biotic factors affect them. Humans are omnivores, consuming both producers and other consumers. Humans can also adjust the length of the food chain as needed. For example, humans who must deal with shortages of food resources usually alter their eating habits to be closer to the energy source. This is sometimes called eating lower on the food chain. Since approximately 90 percent of the energy available at each level of the food chain is lost to the next higher level, shortening the food chain saves energy and uses food more efficiently.

Humans are also biotic factors in ecosystems. Other organisms are affected by human actions, often in adverse ways. We compete with some organisms for resources, prey on other organisms, and alter the environment of still others. SEE ALSO ECOSYSTEM; HABITAT.

Elliot Richmond

Bibliography

Allaby, Michael. *Dictionary of the Environment*, 2nd rev. ed. New York: New York University Press, 1984.

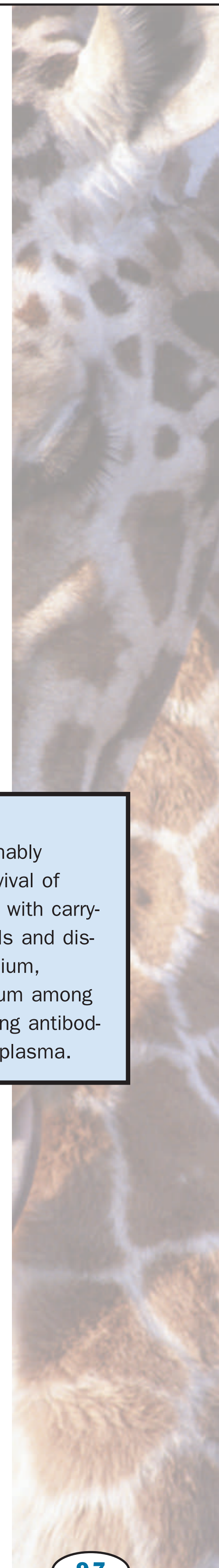
Caldwell, Douglas E., James A. Brierley, and Corale L. Brierley, eds. *Planetary Ecology.* New York: Van Nostrand Reinhold, 1985.

Jordan, William R., III, Michael E. Gilpin, and John D. Aber, eds. *Restoration Ecology: A Synthetic Approach to Ecological Research.* New York: Cambridge University Press, 1988.

Krebs, Charles J. *Ecological Methodology.* Menlo Park, CA: Benjamin/Cummings, 1999.

Rambler, Mitchell B., Lynn Margulis, and Rene Fester, eds. *Global Ecology: Towards a Science of the Biosphere.* San Diego, CA: Academic Press, 1989.

Worster, Donald. *Nature's Economy: A History of Ecological Ideas.* New York: Cambridge University Press, 1994.



Birds *See Aves.*

Blood

The life fluid of the body is blood. All animals, including humans, require that nutrients and oxygen be available for metabolism and that wastes be removed. In animals that measure 1 millimeter or less in diameter, these substances are transported within the body by diffusion between the cells and nearby body parts. In larger, more complex animals, circulatory systems have evolved with arteries, veins, and capillaries to transport respiratory gases, nutrients, waste products, hormones, antibodies, and salts to parts of the body.

Blood, the medium for transporting nutrients and waste products, is both a tissue and a fluid containing many specialized types of cells. It is a tissue because it is a collection of similar cells that serve a particular function. These cells are suspended in a liquid matrix called plasma, which allows the blood to act as a fluid.

Blood plays an important role in nearly all body functions. Oxygen is one of the crucial substances that enters the blood. Oxygen passes through the walls of the lungs, gills, or skin of the animal. The blood picks up and carries oxygen to all parts of the body. As the oxygen-laden blood moves through the circulatory system, it passes through cell walls and provides fuel for the working parts of the body.

Blood also carries digested food from the intestines to the muscle cells. When the muscles work, they produce waste products that must be disposed of. These waste products pass through the walls of the circulatory system into the blood. The blood then carries wastes to the kidneys, where they are eliminated from the body. The work of the muscles creates heat, which is transferred by blood throughout the body. In warm-blooded birds and mammals, blood maintains the temperature of the body.

Blood plays a critical part in the fight against diseases in animals. Blood contains many kinds of disease-fighting substances such as antibodies and white blood cells. Blood tests can reveal a great deal about how well the body is working.

> **Plasma**
> Plasma is unquestionably essential for the survival of human beings. Along with carrying important minerals and dissolved salts like calcium, sodium, and potassium among others, disease-fighting antibodies are contained in plasma.

Blood Composition

The blood of mammals—including humans—is complex. About half of the volume of blood is made up of blood cells, which originate in the bone marrow. Blood cells begin as stem cells, then develop into many other kinds of cells—red cells, white cells, and **platelets**. Blood is composed of 55 percent plasma and 45 percent other elements.

platelets cell fragments in plasma that aid in clotting

Plasma is the watery part of the blood. Plasma is 90 percent water and carries most of the chemicals in the blood. These chemicals include minerals such as sodium, potassium, vitamins, hormones, enzymes, and glucose. Some of these substances are manufactured in the body; others enter through the lungs or with food. Plasma also carries dissolved gasses, especially oxygen, carbon dioxide, and nitrogen.

Blood's red color, seen in the mosquito's "sac," arises from its oxyhemoglobin.

erythrocytes red blood cells, cells containing hemoglobin that carry oxygen throughout the body

hemoglobin an iron-containing protein found in red blood cells that binds with oxygen

leukocytes a type of white blood cells that are part of the immune system

granulocytes a type of white blood cell where its cytoplasm contains granules

monocytes the largest type of white blood cell

lymphocytes a type of white blood cells that completes its development in bone marrow

thromboplastin a protein found in blood and tissues that promotes the conversion of prothrombin to thrombin

Most stem cells become red blood cells, or **erythrocytes**. Human blood contains 4.8 to 5.4 billion red blood cells per milliliter of blood. Red blood cells' primary function is to carry oxygen from the lungs to every cell throughout the body. The outer layer, or membrane, of the red blood cell is flexible and can bend in many different directions without breaking.

Red cells have an iron-containing substance or pigment known as **hemoglobin**. As hemoglobin passes through the lungs, it picks up oxygen, forming a red-colored compound known as oxyhemoglobin, which gives the blood a distinctive red color. As the blood passes through body tissues, hemoglobin releases oxygen to cells throughout the body. During this passage, the hemoglobin gives up some of its oxygen. In response, the tissues send a waste gas, carbon dioxide, into the blood.

White blood cells, or **leukocytes**, form a wandering system of protection for the body. Composed of **granulocytes**, **monocytes**, and **lymphocytes**, these cells originate in the bone marrow, where there is a ratio of one white cell to 700 red cells. Two-thirds of white cells are granulocytes, which travel to places in the body where bacteria or other foreign substances are located and swallow up these invaders. Monocytes, another type of white cell, also swallow up foreign substances and assist the body in overcoming and resisting infections. Lymphocytes produce antibodies, which are released into the blood to target and attach to foreign substances.

The smallest of the blood cells are called platelets. These cells assist in blood clotting by sticking together and plugging small holes in the walls of the blood vessels. As these tiny platelets flow out of a cut on the wall of the blood vessel, they release a chemical known as **thromboplastin**. This self-sealing characteristic of blood is critical to an animal's survival.

Differences among Animals

One-celled organisms have no need for blood. They are able to absorb nutrients, expel wastes, and exchange gases with their environment through a

process called diffusion. In some invertebrates, such as flatworms and **cnidarians**, oxygen is dissolved in the plasma. Simple multicelled marine animals such as sponges, jellyfish, and anemones use seawater to bathe cells and perform the function of blood. The immune system of invertebrates is less developed than that of vertebrates, lacking the white blood cells and antibody system found in mammals.

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

Differing oxygen requirements play a significant role in the composition of blood and the design of animals' circulatory systems. Crustaceans and other arthropods have an open type of circulatory system, while more complex vertebrates—including humans—have a closed circulatory system. Larger and more complex animals have greater oxygen needs and have developed respiratory pigments to help transport oxygen in the blood. These specialized compounds, hemoglobin or **hemocyanin**, are able to carry greater amounts of oxygen because of the metal atoms in the pigments reacting with and transporting additional atoms of oxygen.

hemocyanin respiratory pigment found in some crustaceans, mollusks, and arachnids

The red pigment hemoglobin contains iron, transports oxygen, and is found in all vertebrates as well as some invertebrates with a closed circulatory system, such as earthworms. The blue pigment hemocyanin, which contains copper, is found in some animals with an open circulatory system, including some crustaceans such as crabs, and in some mollusks. This pigment transports oxygen to body tissues and gives the blood a bluish color. The blood of insects is clear or yellow. The red fluid from some squashed insects actually comes from blood they have eaten, not from their own blood, as they have no pigments.

Although the blood of complex animals tends to be similar to human blood, there are differences at the cellular level. For example, reptiles, fish, and amphibians have red blood cells with a nucleus, unlike humans and other mammals. Some arctic fish are able to produce a specialized protein that acts as a type of antifreeze, allowing them to survive where the blood of other animals would freeze. SEE ALSO Circulatory System.

Leslie Hutchinson

Bibliography

Hickman, Cleveland, Larry Roberts, and Frances Hickman. *Integrated Principles of Zoology*, 8th ed. St. Louis, MO: Times Mirror/Mosby College Publishing, 1990.

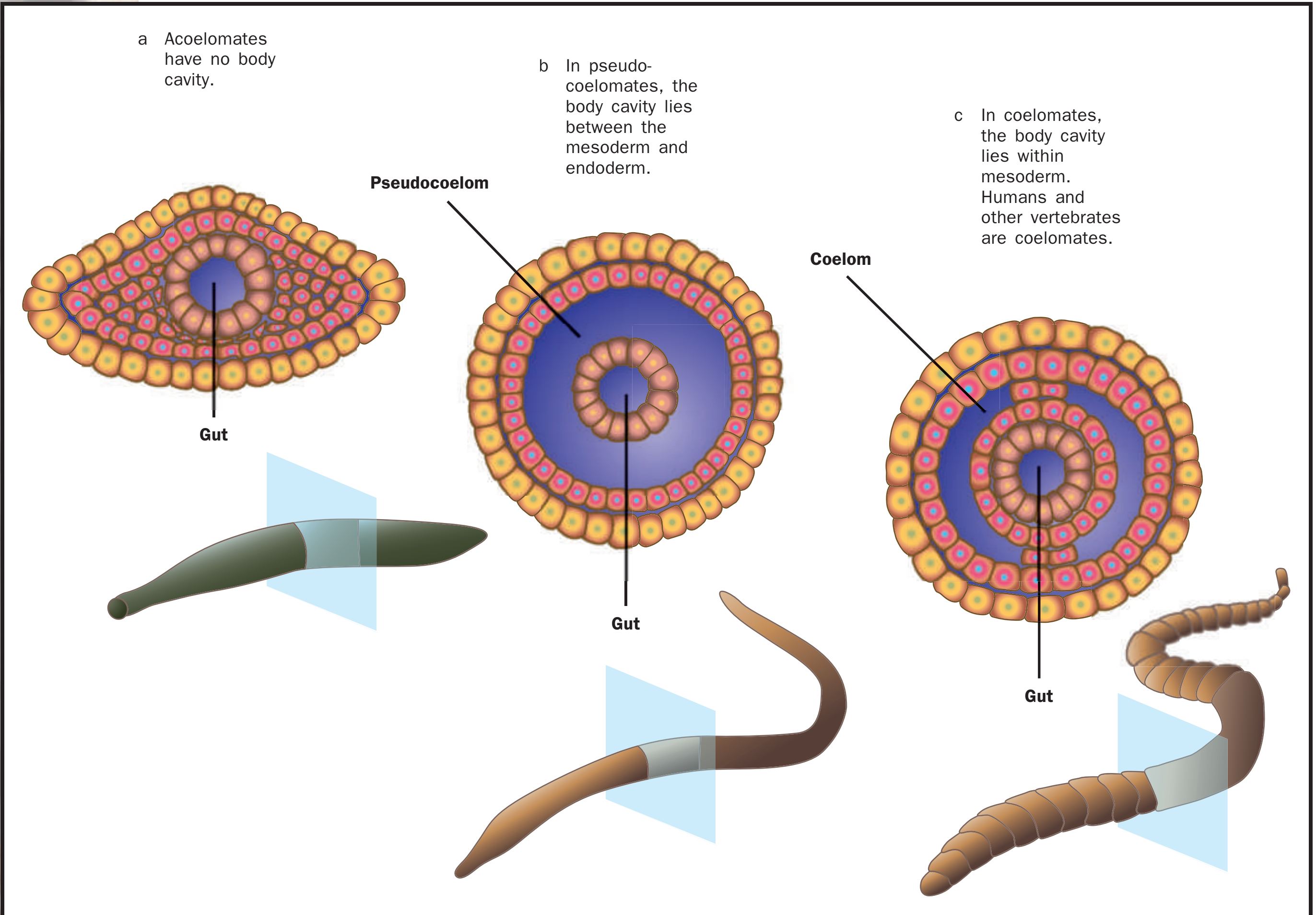
Mill, P. J. *Respiration in the Invertebrates*. London: Macmillan Press, 1972.

Randall, David, Warren Burggren, and Kathleen French. *Eckert Animal Physiology: Mechanisms and Adaptations*, 4th ed. New York: W. H. Freeman and Company, 1997.

Body Cavities

The evolution of body cavities within the kingdom Animalia has a very interesting history. In fact, the increasing complexity of animal form and function during the evolution of the group can be directly linked to the evolution of ever-more-sophisticated body cavities.

The most primitive animal phyla possess only a single body cavity, which typically has either digestive or circulatory functions, or both. There is no



The cross sections visually represent the structural differences between the acoelomate, pseudocoelomate, and the coelomate. Redrawn from Holt et al., 1998.

acoelomates animals without a body cavity

pseudocoelom a body cavity that is not entirely surrounded by mesoderm

coelom a body cavity

eucoelomates animals that have a true body cavity that is completely surrounded by meso-derm

spongocoel the central cavity in a sponge

secondary body cavity, or coelom, and consequently these phyla are referred to as the **acoelomates**.

Most animal phyla, however, have evolved a second body cavity of one form or another. The pseudocoelomates, which include a number of worm-like phyla, are characterized by a secondary body cavity known as the **pseudocoelom**. The pseudocoelom has some but not all of the characteristics of true coeloms. Finally, several animal phyla, including those that possess the most complex body plans in the kingdom, are characterized by a body cavity known as a true **coelom**. These phyla are known as the **eucoelomates**.

The Acoelomate Phyla

The most primitive animal phylum is that of the sponges (phylum Porifera). Sponges have a single body cavity known as the **spongocoel**. The spongocoel is critical to the food gathering strategy of sponges. Water enters the organism through numerous small pores known as ostia. Small food particles are filtered from the water by cells in the sponge walls. The water then flows through the spongocoel and leaves through a large opening known as the osculum. The one-directional flow of water through the sponge is controlled by special flagellated cells which line the spongocoel.

The second most primitive animal phylum is generally considered to be the cnidarians (phylum Cnidaria), which includes the jellyfish, sea anemones, and hydras. Cnidarians are diploblastic, meaning that they have two distinct tissue layers, an ectoderm and endoderm, separated by a third layer called the mesoglea. Cnidarians are characterized by a single **gastrovascular cavity**, an internal body cavity that functions in digestion. The gastrovascular cavity has a single opening that serves as both mouth and anus, and is typically surrounded by tentacles that are responsible for food gathering.

gastrovascular cavity a single cavity where digestion occurs

The other acoelomate phyla are more advanced than the sponges and cnidarians since their species are characterized by bilateral (left-right) symmetry, as well as the presence of three distinct tissue layers, the ectoderm, mesoderm, and endoderm. In these acoelomate bilatarian phyla, there is no body cavity other than the gastrovascular cavity. The mesoderm is solid. Bilaterally symmetric acoelomates include such taxa as the flatworms (phylum Platyhelminthes) and the ribbon worms (phylum Nemertina).

The "Tube-within-a-Tube" Body Plan

Animal species with a secondary body cavity, either a pseudocoelom or a true coelom, have what is called a "tube-within-a-tube" body plan. The secondary body cavity lies between the two tubes. The outer tube (also called the body wall or the **somatic** tube) typically contains the sense organs and muscles. Structures of the body wall are generally under voluntary control and are most often involved in mediating between an organism and its external environment. The inner tube (also called the gut tube or visceral tube) typically includes structures that control an organism's internal environment. These tubes perform functions such as digestion, blood circulation, the maintenance of internal homeostasis, and reproduction. The functioning of elements of the visceral tube is generally under involuntary control.

somatic having to do with the body

monophyletic a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

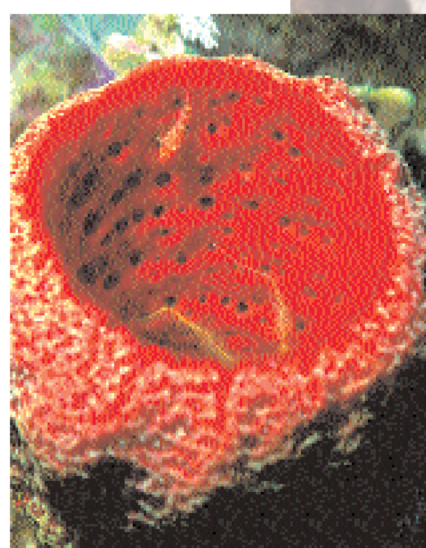
Both the pseudocoelom and the coelom are fluid-filled body cavities that lie between the outer body wall and the inner tube of the digestive tract. The distinction between the two lies in the tissue layer origin of the walls of the cavity.

The Pseudocoelomates

The pseudocoelom is an internal body cavity that develops between the mesoderm and the endoderm. Developmentally, the pseudocoelom is the persistent blastocoel, or fluid-filled cavity, of the developmental stage known as the blastula stage.

Several phyla of invertebrate animals are characterized by pseudocoeloms. These include the roundworms (phylum Nematoda) and the rotifers (phylum Rotifera), as well as a number of lesser-known phyla of wormlike animals.

At one point, all the pseudocoelomate taxa were grouped together in the phylum Aschelminthes. However, recent phylogenetic studies have shown that in all likelihood they do not form a **monophyletic** taxon (one that shares a common ancestor), and the group has since been split into numerous separate phyla. It is even possible that the pseudocoelom has evolved more than once.



A member of the phylum Porifera, this vase sponge uses its spongocoel to gather food.

The pseudocoelom serves many of the same functions as the true coelom, which is discussed below. However, certain complex physiological systems are found only in the eucoelomates. Unlike the eucoelomates, for example, the pseudocoelomates lack circulatory systems. Nevertheless, certain innovations made possible by a true coelom can also be found among the pseudocoelomates. In roundworms, for example, the pseudocoelom is fluid-filled and pressurized and functions as a hydrostatic (fluid dependent) skeleton.

The True Coelom and the Eucoelomates

The true coelom differs from the pseudocoelom in that it is lined on either side with cells originating from the mesoderm. It is filled with a fluid known as the coelomic fluid. The surfaces of the coelom are covered with a slick epithelial layer known as the **peritoneum**.

peritoneum the thin membrane that lines the abdomen and covers the organs in it

The cells of the peritoneum are responsible for regulating the transport of substances into and out of the coelom. The visceral peritoneum covers the viscera (internal organs). The parietal peritoneum lines the outer body wall. The lubricated surfaces of the peritoneum allow for the smooth, sliding motion of the organs within the coelom. The internal organs are suspended from the walls of the coelom by membranous sheets called **mesenteries**.

mesenteries the membranes that suspend many internal organs in the fluid filled body cavity of vertebrates

pericardial cavity the space within the membrane that surrounds the heart

pleural cavity the space where the lungs are found

peritoneal cavity the space within the peritoneum membrane that surrounds the abdomen and covers the organs within it

The coelom may be a single body cavity or may be divided into separate compartments during the course of development. In humans, the coelom is divided into three separate coelomic cavities. The **pericardial cavity** contains the heart, the **pleural cavity** contains the lungs, and the **peritoneal cavity** contains the rest of the viscera, including the digestive organs, liver, kidneys and excretory organs, and reproductive organs. The pleural and peritoneal cavities are separated by the pleuroperitoneal membrane and the diaphragm (which has a critical role in respiration), while the heart and lungs are separated by the pleuropericardial fold.

Species with a true coelom are called eucoelomates. Within the eucoelomates, two different groups may be distinguished based on the way in which the coelom forms during development. The protostomes are characterized by one method, called schizocoely, while the deuterostomes are characterized by another, called enterocoely. The method of coelom formation is in fact one of the key characteristics that separate these two important phylogenetic groups.

Two rival theories attempt to explain the evolutionary origin of the coelom. The acoelomate theory argues that the coelom evolved in an acoelomate ancestor. The enterocoel theory suggests that the coelom evolved from the gastric pouches of cnidarians. Current evidence appears to favor the enterocoel theory. It is unclear whether the pseudocoelomates represent an intermediate evolutionary stage between acoelomates and taxa with a true coelom, or whether pseudocoelomates evolved from an eucoelomate ancestor.

Development of the True Coelom

Among the eucoelomates, the coelom develops differently in the protostomes, which include the Annelida, the molluska, and the Arthropoda, and the deuterostomes, consisting of the Echinodermata, Hemichordata, and

Chordata. This is one of a few key characteristics distinguishing these two subkingdoms.

In both protostomes and deuterostomes, coelom formation occurs directly after gastrulation, the developmental stage in which the three tissue layers—the ectoderm, mesoderm, and endoderm—become distinguished. In both groups, coelom development is closely linked to the origin of the mesoderm.

The protostomes are **schizocoelous**. In protostomes, the mesoderm develops during gastrulation as cells migrate from the already existing ectodermal and endodermal layers to form a solid mesodermal layer that lies between the ectoderm and endoderm. This solid mesodermal mass subsequently splits ("schizo-" = "split") to form a hollow cavity that becomes the coelom.

schizocoelous the mesoderm originates from existing cell layers when the cells migrate

The deuterostomes are **enterocoelous**. In deuterostomes, the mesoderm originates as outpocketings of the endodermal archenteron, or embryonic gut. The mesodermal pouches extend toward one another as they grow, ultimately joining to form a single cavity that becomes the coelom.

enterocoelous a cavity formed by the in-folding of the wall of the intestinal cavity in a gastrula

The Importance of the Coelom

The evolution of the coelom was a crucial step in the history of the Animalia. The presence of a secondary body cavity, and the acquisition of the tube-within-a-tube body plan, was critical for the evolution of increasing size and complexity within the animal kingdom.

One major disadvantage of having only a single body cavity is that muscle contractions, such as those necessary for locomotion, cause the gastrovascular cavity to become squeezed and distorted. This not only restricts the flow of nutrients and other materials but also makes the evolution of an effective circulatory system impossible. As a result, acoelomate taxa must rely either on diffusion or on muscle contractions for the transport of nutrients, respiratory gases, and waste products around the body. Both these transport strategies are considerably less efficient than those permitted by the evolution of a coelom.

Consequently, the body sizes, shapes, and complexities that can be supported are severely constrained. Many acoelomate groups are small in size and characterized by a flattened, elongated morphology, or shape, one that is suited to diffusion as a transport mechanism, and that makes a complex circulatory system unnecessary. Not surprisingly, the result is that acoelomate phyla all have comparatively simple body plans. Even the pseudocoelomates are generally fairly small in size and lack circulatory systems. They have only simple locomotory behaviors, which in addition to motion, help to circulate nutrients in the pseudocoelom.

With the evolution of the coelom, the digestive and circulatory functions are separated, which allows for the possibility of separate specialization and improvement in efficiency. The evolution of the coelom permits the internal organs to grow, change shape, and shift in position. The coelom provides not only space but also protection for complex organ systems, because the fluid-filled environment helps to shield the internal organs from injury. The gastrovascular cavity becomes specialized for digestion alone, and the different portions of the digestive system can expand and contract

during the processes of feeding and digestion. This increase in efficiency in both digestion and circulation allows for the support of larger body sizes and increased metabolic rates, both of which are prominent features in the evolution of the Animalia.

In some taxa, the coelom can serve other functions as well. In many species, the fluid-filled, pressurized coelom is important in providing hydrostatic support. This is important in the Annelida, for example, which have evolved a compartmentalized coelom, with one coelomic compartment present in each segment of the organism. Slugs are another example of a group that uses the coelom as a hydrostatic skeleton involved in support and locomotion. Echinoderms such as starfish are characterized by a well-developed water vascular system derived from the coelom, which functions in the locomotion of the tube feet.

Modification and Reduction of the Coelom

The coelom has been modified in different ways in different phyla. The compartmentalization of the coelom in some vertebrates, including humans, has already been discussed. The creation of the pleural cavities, which contain the lungs, through the development of the muscular diaphragm is essential to the respiratory strategy of mammals, providing yet another example of a physiological function for which the evolution of the coelom has been necessary.

The unusual segmented coelomic compartments of annelids have also been mentioned. In this case, segmentation affects numerous components of annelid anatomy, and the coelom is only one more instance of this.

In addition, the coelom has been reduced in several other phyla that have evolved other structures to perform its usual functions. Arthropods, for example, have a hard chitinous exoskeleton (external skeleton) that provides support. The coelom is significantly reduced in the group, persisting only as a cavity around the gonads and excretory organs. (The **hemocoel**, a component of the arthropod's open circulatory system that bathes the internal organs in blood, is unrelated.)

hemocoel a cavity between organs in arthropods and mollusks through which blood circulates

Mollusks also have a body plan in which the coelom is reduced, in this case to a small body cavity that encloses only the heart. It is likely that the sedentary lifestyle of mollusks such as bivalves made a fully developed coelom unnecessary. Like arthropods, mollusks also possess a large hemocoel that bathes the organs in nutrients. SEE ALSO Body Plan.

Jennifer Yeh

Bibliography

Biology: Visualizing Life. New York: Holt, Rinehart and Winston, Inc., 1998.

Gilbert, Scott F. *Developmental Biology*, 5th ed. Sunderland, MA: Sinauer Associates, 1997.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Hildebrand, Milton, and Viola Hildebrand. *Analysis of Vertebrate Structure*. New York: John Wiley, 1994.

Karp, Gerald, and N. J. Berrill. *Development.* New York: McGraw-Hill, 1981.

Larson, William J. *Human Embryology*. New York: Churchill Livingstone, 1997.

Moore, Janet. *An Introduction to the Invertebrates.* Cambridge, U.K.: Cambridge University Press, 2001.

Body Size and Scaling

See Functional Morphology.

Body Plan

The term "body plan" refers to the general similarities in development and form and function among members of a particular phylum. Another name for these similarities is *baüplan*, which is the German word for "body plan."

A body plan is a group of structural and developmental characteristics that can be used to identify a group of animals, such as a phylum. All members of a particular group share the same body plan at some point during their development—in the embryonic, larval, or adult stage. Biologists have long observed that anatomy and embryology reflect shared underlying structural plans. These plans can be used to define taxonomic groups (usually phyla) and to construct hierarchical classifications within groups (organisms with similar body plans tend to be more closely related).

Similarities and differences in adult shape and form, as well as the developmental pattern of embryos, provide the framework for modern taxonomic classification. These comparisons are the basis of phylogenetic systematics. Embryonic development is relatively consistent among animals with similar body plans, although similar larval forms may give rise to very different adults in some groups. The timing, pattern, and scale of developmental events determine the shape of an organism, and closely related groups are more likely to share structural and developmental similarities than those that are more distantly related. Homologous structures and developmental stages—those that are similar among related groups because they are inherited from a common ancestor—are the basis of modern biological classification.

The fossil record suggests that **metazoans** (organisms with multiple cell and tissue types) first appeared about 500,000 years ago early in the Cambrian period. It is likely, however, that soft-bodied forms were present well before this but left no fossilized remains. Metazoans rapidly diversified into myriad forms that eventually gave rise to the diversity of metazoans we have today. Biologists refer to this historic event in the history of animal life as the Cambrian Radiation, sometimes referred to as the Cambrian Explosion. All living animals are descendents of a common ancestor that existed at the beginning of the Cambrian period, and their various evolutionary paths were established by the end of this biological supernova. A few body plans did not survive into the present, but the majority of readily fossilized metazoan body plans can still be found today. The distribution of diverse body plans among living metazoans provides a record of the evolutionary history of this group that dates back to its origin.

metazoans a subphylum of animals that have many cells where some are organized into tissues

Multicellularity in organisms permits specialization of cell structure and function. During the Cambrian Radiation, an increased overall complexity and the subsequent **differentiation** of embryonic and adult cells and tissues, a widespread phenomenon among metazoans called compartmentalization, provided the opportunity for evolutionary experimentation and innovation.

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

Animal Characteristics

Parazoa	Phylum Porifera (sponges)	No true tissue or loose tissue organization. Body is asymmetrical or radially symmetrical.
Eumetazoa – Radiata	Phylum Cnidaria (anemones and jellyfish)	Diploblastic—two layers: gastrodermis (derived from endoderm) and epidermis (derived from ectoderm). Radial symmetry, planula larva, dimorphic life cycle: polyps and medusa. Oral and aboral, no cephalization. Gastrovascular cavity: mouth opening, no anus. Specialized stinging cells (cnidocytes and nematocysts), muscles and nerves.
	Phylum Ctenophora (comb jellies)	Diploblastic, "mesoglea," eight rows of fused cilia, balance sense organ, two tentacles, bioluminescence.
Eumetazoa – Bilateria – Acoelomates	Phylum Platyhelminthes (roundworms)	Triploblastic (endoderm, mesoderm, ectoderm), bilateral symmetry, acoelomates, cephalization. Larval stages, no respiratory or circulatory system, incomplete digestive system (no anus).
Pseudocoelomates Characteristics: eumetzoa, bilateral symmetry, body cavity other than digestive cavity (pseudocoele).	Phylum Rotifera (wheel-bearing animals)	Triploblastic, complete digestive tract, pseudocoele, hydrostatic skeleton, organs located in pseudocoele, parthenogenesis, crown of cilia.
	Phylum Nematoda (roundworms)	Triploblastic, complete digestive tract, tough cuticle, only longitudinal muscles, pseudocoele, hydrostatic skeleton.
	Phylum Nemertea	No pseudocoele, body is acoelomate, has coelom-like structure for storing proboscis, complete digestive tract, circulatory system with hemoglobin.
Eucoelomates-Protostomes Characteristics: eumetazoa, triploblastic, bilateral symmetry, cephalization, blastopore becomes mouth, eucoelomates, schizocoelous, spiral cleavage, determinate cleavage.	Phylum Molluska (chitons, snails, slugs, clams, oysters, octopuses, and squids)	Most have external shells of calcium carbonate, although some have internal shells and some have none. Three body parts – foot, visceral mass, and mantle. Mantle cavity – houses gills and other organs, no body segmentation.
Coelomates have internal body cavities (coeloms) which contain digestive organs, some of the excretory and reproductive organs, and a thoracic cavity that contains the heart and lungs. Coelomates also form a variety of internal and external skeletons.	Phylum Annelida (earthworms, polychetes, and leeches)	Triploblastic, segmentation and body segment specialization, coelom.
	Phylum Arthropoda (crustaceans, insects, and spiders)	Triploblastic, segmentation, hard exoskeleton, jointed appendages, specialized appendages, antennae, mouthparts, legs, molting, variety of gas exchanges or respiratory structures.
Deuterostomes Characteristics: bilateral symmetry, some have secondary radial symmetry, enterocoelous, blastopore becomes anus, radial cleavage, indeterminate cleavage.	Phylum Bryozoa (moss animals)	Exoskeleton, sessile, and a lophophore, a ring of ciliated tentacles centered on the mouth. The mouth opens into a U-shaped gut; the anus is located just outside the lophophore. The body also contains a coelom and gonads; there is a small central ganglion, or "brain," but no specialized excretory or respiratory systems.
	Phylum Brachiopoda	Resemble bivalve clams with two shells surrounding a lophophore.
	Phylum Phoronida (tube-dwelling marine worms)	Lophophore present; three body parts in larval and adult forms, each containing its own coelom; prosome, mesosome, metasome. U-shaped digestive track, nervous system, specialized excretory organs, closed circulatory system.
	Phylum Echinodermata (sand dollars, urchins, and sea stars)	Calcareous endoskeleton composed of separate plates or ossicles, bilateral symmetry in larval stage, radial symmetry as adults (pentagonal), endoskeleton, water vascular system; regeneration, decentralized nervous system.
	Phylum Chordata (amphioxus, sea squirts, and vertebrates)	Bilateral symmetry; segmented body; three germ layers; well-developed coelom. Notochord present at some stage in life cycle. Single, dorsal, tubular nerve cord; anterior end of cord usually enlarged to form brain. Pharyngeal gill slits present at some stage in life cycle. Postnanal tail, usually projecting beyond the anus at some stage but may or may not persist. Segmented muscles in unsegmented trunk. Ventral heart with dorsal and ventral blood vessels; closed circulatory system. Complete digestive system. Cartilaginous or bony endoskeleton present in the majority of members (vertebrates).

New combinations of cells and tissues led to greater complexity and the exploitation of new ecological resources.

Important differences among body plans are present in the embryo although they may be apparent at any stage during the development of a given group. Conditions presented early in development set in motion a cascade of changes in cell growth, proliferation, and differentiation that operate throughout development to produce the body plans specific to a particular group of organisms.

Body plans vary among phyla in terms of egg-cleavage patterns (how the egg divides in early development), **gastrulation**, axis specification, and embryonic cell structure. The egg may be completely divided by the cleavage furrow (holoblastic cleavage), or only a portion of the **cytoplasm** may be cleaved (meriblastic cleavage) as in bird eggs. **Deuterostomes**, such as **echinoderms** and chordates, develop by radial cleavage. In this form of cleavage, the daughter cells sit on top of previous cells. **Protostomes**, such as mollusks, annelids, and arthropods, develop by spiral cleavage (the daughter blastomeres are not direclty over or beside each other but are tilted to the left or right 45 degrees).

gastrulation the formation of a gastrula from a blastula

cytoplasm fluid in eukaryotes that surround the nucleus and organelles

deuterostomes animals in which the first opening does not form the mouth, but becomes the anus

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

protostomes animals in which the initial depression that starts during gastrulation becomes the mouth

Gastrulation is the coordinated movement of cells and tissue in the embryo that determines later cell and tissue interactions. Gastrulation involves the combination of cell and tissue. These combination types differ among phyla.

Axis formation in the embryo is responsible for determining patterns of symmetry and polarity. Organisms may be **asymmetrical** (no symmetry) or **symmetrical** (a single line, or plane, of symmetry). Symmetry may be spherical, radial, or bilateral. Animals with spherical symmetry, like sea urchins, have a hollow globe of cell layers organized around a central point. Animals with radial symmetry, like jellyfishes, have body parts that radiate from a central point, like the spokes of a wheel. Animals with **bilateral symmetry**, like earthworms, have bodies that if cut lengthwise, form right and left halves that are mirror images.

asymmetrical lacking symmetry, having an irregular shape

symmetrical balanced body proportions

bilateral symmetry characteristic of an animal that can be separated into two identical mirror image halves

Bilateral symmetry is a critical prerequisite for the concentration of sensory organs and the development of the head. **Dorsal**-ventral (back-belly), **anterior-posterior** (mouth-anus), and right-left axes are specified in different ways among phyla. The primary body axes of annelids and vertebrates, for example, are determined by different mechanisms during early development. In most cases, the presence of multiple embryonic developmental axes is associated with cell diversity and tissue complexity. Cells and tissues in the embryo give rise to all classes of cells, tissues, and structures present in the adult stage. The specific fate of embryonic cells and tissues is determined early in development and varies among body plans.

dorsal the back surface of an animal with bilateral symmetry

anterior referring to the head end of an organism

posterior behind or the back

Most metazoan body plans can be described as a "tube-within-a-tube," with a body wall made up of layers of different tissue types surrounding a central cavity. In almost all metazoans, the body wall has three cell layers (ectoderm, mesoderm, and endoderm), although some, such as sponges (Porifera), have no organized cell layers, and others, such as jellyfishes (**Cnidaria**) have only two layers in the adult. Multicellular metazoan ancestors had an inside-outside, two-layered organization with an endoderm and ectoderm. In **triploblasts**, such as flatworms, a middle layer of mesoderm also evolved.

Cnidaria a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

triploblasts having three germ layers, ectoderm, mesoderm, and endoderm

The body wall surrounds a coelum (central cavity) between the digestive tract and body wall that is completely lined by mesoderm. The coelom allows the digestive system and body wall to move independently. Because of this, internal organs can be more complex. The coelom may also serve as a storage area for eggs and sperm, facilitating development of these gametes

within the animal body. Coelomic fluid helps in respiration and circulation by diffusing nutrients and in excretion by accumulating wastes. This fluid has the same function as several organ systems in the higher animals. In addition, coelomic fluid protects internal organs and serves as a hydrostatic skeleton. Metazoans have a mouth at one end of the coelom and an anus at the other. Protostomes develop so that the first opening in the embryo is the mouth (the word "protostome" means "first mouth"). Deuterostomes develop an anus first, then a mouth.

Of the thirty-five living phyla of metazoans, the ten largest contain nearly 2.5 million species in total, the other twenty-five account for only 5,000. Although some phyla have obviously been more successful than others in terms of the sheer number of species that they contain, all existing metazoan body plans are survivors of the Cambrian Radiation. The following is a description of the body plans of the ten most diverse metazoan phyla, presented in order of increasing complexity.

Porifera: Sponges

sessile immobile, attached

Sponges have a diploblastic embryo, which means they have a two-layered body wall (ectoderm and endoderm but no mesoderm). Adults are **sessile** (nonmobile and usually fixed to a single point) and have no coelom. Sponges have flagellated cells that move water around the body, and an internal skeleton with spicules, needle-shaped skeletal elements that occur in the matrix between the epidermal and collar cells. Adult sponges have no definite nervous system.

Cnidaria: Corals, Jellyfishes, and Anemones

Cnidarians have a body that is a simple, soft-walled sac. Cnidarians have two distinctive body forms, a mobile, bell-shaped medusa (jellyfish, for example) or a sessile polyp (sea anemones, for example). Either or both forms may be present during development, depending on the species. Cnidarians may live on their own, as do anemones, or live in colonies, as do corals and jellyfishes.

diploblastic having two germ layers; ectoderm and endoderm

All cnidarians have radial symmetry. They are **diploblastic**, which means they have two embryonic tissue layers, the ectoderm and endoderm, which give rise to the ectodermis and gastrodermis of the adult. The latter layers enclose a single opening, the enteron, or "inner cavity."

They have a mouth but no anus; and have a central body cavity called a coelenteron (hollow gut), and a nerve net, which serves as a primitive nervous system. Cnidarians are the only metazoans that have tentacles with nematocysts (stinging cells) and statocysts (organs that sense orientation).

The shell on this snail—a member of the phylum Molluska—has been formed by the secretions of its mantle. The mantle is a characteristic feature of mollusks.

Platyhelminthes: Flatworms

Flatworms are bilaterally symmetrical and have flattened, wormlike bodies. All platyhelminthes are triploblastic. They have unique flagellated cells called flame cells, which regulate the contents of extracellular fluid and are used for excretion, and a nervous system with a simple brain.

Rotifera: Wheeled Animals

Rotifers have several complex traits that are further developed in other phyla. The rotifer body is unsegmented, bilaterally symmetrical, and spherical with a bifurcate (split) foot and anterior wheel organ and a cuticle (extracellular protective layer). Rotifers feed using a pharynx with jaws. They have protonephridia, a primitive excretory organ, and a simple nervous system with vision receptors.

Nematoda: Roundworms

Nematodes have triploblastic embryos and cylindrical, unsegmented bodies in the adult stage. They have a **pseudocoelom**, a closed, fluid-containing cavity that acts as a hydrostatic skeleton to maintain body shape, circulate nutrients, and hold the major body organs. Nematodes also have a cuticle without cilia, longitudinal muscle fibers, a triradiate (three-chambered) pharynx, and an excretory system that consists of gland cells and canals.

pseudocoelom a body cavity that is not entirely surrounded by mesoderm

Molluska: Slugs, Snails, and Clams

The mollusk body has a head and a foot, and a **mantle**, a membranous or muscular structure that surrounds the visceral mass (internal organs) and secretes a shell if one is present (as in clams and branchiopods). Mollusks have an alimentary canal, a relatively complex nervous system, respiratory gills, and an active circulatory system with blood and a hemocoele, an enlarged, blood-filled space. Some groups of mollusks have a reduced coelom.

mantle the tissue in mollusks that drapes over the internal organs and may secrete the shell

Annelida: Segmented Worms

The annelid body is bilaterally symmetrical, segmented, and fluid filled. Annelids have a hydrostatic skeleton, which supports the body through the pressure of fluid contained within body cavities. The external surface of the body is protected by a cuticle. Annelids also have chaetae, or bristles, and a triploblastic body wall. The annelid nervous system consists of paired nerves and ganglia (clusters of **neuron** bodies or soma) arranged along the length of the body. They have simple excretory organs called nephridia, or coelomoducts, and a closed, tubular circulatory system.

neuron a nerve cell

Arthropoda: Crustaceans, Spiders, and Insects

Arthropods have triploblastic embryos. Their bodies are bilaterally symmetrical, with metameric segmentation, in which each repeating segment is similar to the next. Arthropods have an exoskeleton, a hard, jointed, external covering that encloses the muscles and organs, made of chitin (a tough, flexible carbohydrate); paired, jointed appendages; and one or more pairs of jaws. The digestive system consists of a tubular gut. Arthropods have **striated muscles**, a ventral nerve cord of segmental ganglia, ciliated sense organs, a reduced coelom, a haemocoel, and a heart that pumps a circulatory fluid called haemolymph.

striated muscles a type of muscle with fibers of cross bands usually contracted by voluntary action

Echinodermata: Sea Urchins, Starfishes, and Sea Cucumbers

Echinoderms have a swimming larval stage called a pluteus and a non-swimming, headless adult stage with pentamerous (five-sided) symmetry.

Echinoderms have a coelom that is divided into three sections, and an internal mesodermal skeleton (a supportive framework of **connective tissue**) with calcium carbonate spicules (conical masses of hard, shell-like matrial). Echinoderms have digestive systems but lack excretory organs. They have a water vascular system (also called the ambulacral system), which is a set of hydraulic canals derived from the coelom and equipped with tube feet, and which is used for gas exchange, movement, food handling, and sensory reception.

connective tissue cells that make up bones, blood, ligaments, and tendon

Chordata: Chordates, Including Vertebrates

Chordate embryos (and adults) are triploblastic. Chordate larvae and adults are bilaterally symmetrical and have a well-defined anterior-posterior axis (the "head" is easily identified from the "tail"). Adults have a complex nervous system with a dorsal nerve chord and **notochord** (some groups, including vertebrates, have a brain), various sense organs, gill slits, and a well-developed digestive tract. Chordates reproduce sexually. SEE ALSO ALLOMETRY.

notochord a rod of cartilage that runs down the back of chordates

Andrew G. Gluesenkamp

Bibliography

Gilbert, Scott F. *Developmental Biology*, 5th ed. Sunderland, MA: Sinauer Associates, Inc., 1997.

Gilbert, Scott F., and Ann M. Raunio, eds. *Embryology: Constructing the Organism.* Sunderland, MA: Sinauer Associates, Inc., 1997.

Kalthoff, Klause. *Analysis of Biological Development*, 2nd ed. Boston: McGraw-Hill, Inc., 2001.

Raff, Rudolph A. *The Shape of Life.* Chicago: University of Chicago Press, 1996.

Raff, Rudolph A., and Thomas C. Kaufman. *Embryos, Genes, and Evolution: The Developmental-Genetic Basis of Evolutionary Change.* New York: Macmillan, 1983.

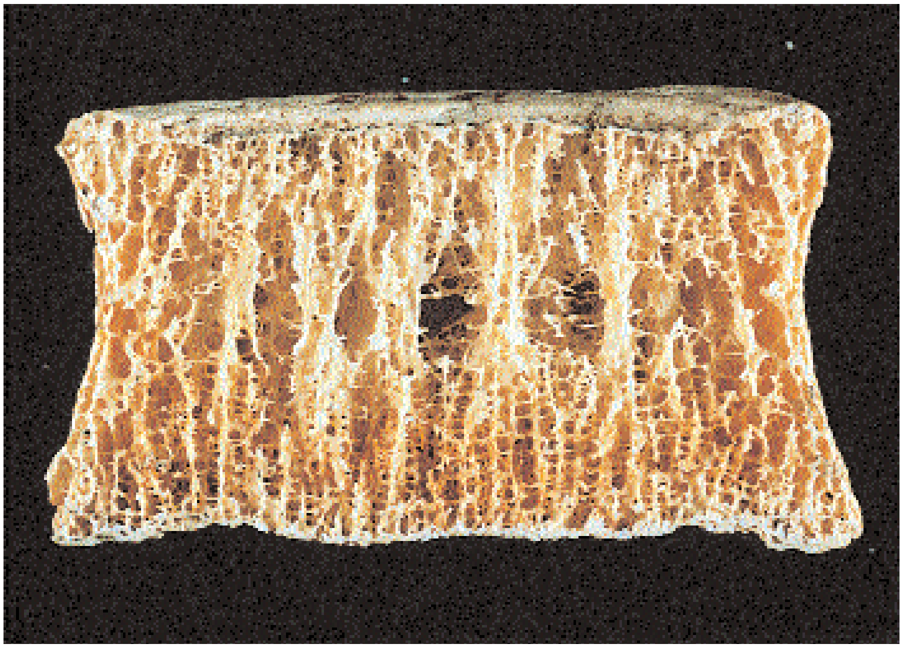
Bone

Bone is the major component of the adult vertebrate skeleton. It is a hard connective tissue comprised of living material, including bone cells, fat cells, and blood vessels, and an inorganic matrix, which is made up largely of water and minerals.

All connective tissues support and connect various parts of the body, and the specific functions of bones are diverse. As the main element of the skeleton, they provide structure and support to vertebrate bodies. They also act as levers for body movement, their position controlled by the muscles attached to them. Bones also protect the delicate internal organs from external impact. For example, the skull encases and protects the brain, and the rib cage houses the lungs and heart.

As well as serving these structural and protective functions, bones play two important physiological roles. They serve as deposits for calcium, a mineral that makes the bones stronger and is essential for the operation of nerves and muscles. Red blood cells, white blood cells, and **platelets** are all manufactured in the core of the bone, or bone marrow.

platelets cell fragments in plasma that aid in clotting



Cross section of a lumbar vertebra showing spongy bone tissue. The spongy bone consists of a honeycomb of small bone pieces called trabeculae that are filled with red or yellow bone marrow.

Bones change and develop along with the rest of the body. During the early stages of embryonic development, the vertebrate skeleton consists entirely of cartilage. As the fetus grows, calcium and phosporous deposits form around the cartilage as the mineralization process begins. At birth, the skeleton still consists mostly of cartilage and experiences further changes as the child matures. For instance, the bones of an infant's skull do not fuse until several months after birth. A newborn human has over 300 bones, which over time fuse into the 206 bones of an adult. Cartilage gradually replaces bone through the process of **ossification**, which is achieved through the activity of **osteoblasts**, the bone precursor cells.

ossification deposition of calcium salts to form hardened tissue such as bone

osteoblast potential bone forming cells found in cartilage

Bone is made up of osteocytes, living bone cells that are surrounded by the matrix. Osteoblasts secrete the matrix and collagen, a protein that gives bone a slightly elastic quality and prevents it from shattering when bearing weight. The osteoblasts also secrete mineral salts, which harden the bone. As the bone matures, the osteoblasts are transformed into osteocytes, and new osteoblasts are released into the system to build more bone.

Bone tissue can be categorized as compact or spongy. Compact bone, also called cancellous bone, has a honeycomb structure that is designed to withstand stress from multiple directions. Compact bone is denser and harder than spongy bone, and is present in the main bones of the arms and legs. It is made up of long, cylindrical units called osteons, which help the bone bear weight. Blood vessels and nerves run through the center of each osteon.

Many bones are composed of an outer layer of compact bone and an inner core of spongy bone. The skull, pelvis, ribs, breastbone, and vertebrae all contain spongy bone, as do the ends of the arm and leg bones. Trabeculae are the bony struts that create the criss-cross formation of spongy bone. Bone marrow fills the spaces between the trabeculae. A thin, two-layered membrane called the periosteum surrounds and protects both bone types. Nerves and blood vessels run throughout the outer layer of the periosteum into the bone. Osteoblasts are the main constituent of the inner layer.

Bones are connected to each other at junctions called joints. There are several types of joints, each with a different range and pattern of movement. The fused joints of the skull do not permit movement, the hinge joints of the elbow and knee allow movement in one direction, and the pivot joints found between certain neck vertebrae permit side-to-side twisting motions. The ball-and-socket joint in the shoulder allows a wide range of movement.

Bone is a dynamic tissue with a structure and composition that adapt to environmental stresses. It undergoes constant breakdown and rebuilding. As a calcium deposit, bone is responsible for maintaining required levels of this mineral in the blood. When calcium levels drop, cells called osteoclasts break down bone to release calcium into the blood. Through the activity of osteoblasts, bones also thicken in response to exercise and impact.

When a bone breaks, several processes contribute to its repair. First, cells from the periosteum transfer to the site of the break and create a fibrous network. Then other cells produce cartilage around this network. In the final step, osteoblasts arrive and convert the cartilage into bone. This healing process may take weeks or months, depending on the severity and location of the injury and the individual's age and general health.

As an individual ages, the rate at which bone breaks down slowly begins to exceed the rate at which it is formed. The bone is weakened, and its size reduced. Developing and maintaining proper exercise and nutrition habits at an early age ensures that bones remain healthy in old age. SEE ALSO Skeletons.

Judy P. Sheen

Bibliography

Harris, William H., and Judith S. Levy, eds. *The New Columbia Encyclopedia.* New York: Columbia University Press, 1975.

Parker, Sybil P., ed. *Encyclopedia of Science and Technology*, 8th ed. London: McGraw-Hill, 1997.

Burgess Shale and Ediacaran Faunas

The Burgess Shale was one of the most famous and important fossil localities known at the end of the twentieth century. Charles Walcott, who at the time was secretary of the Smithsonian Institution, discovered this fossil-rich rock bed in 1909 while exploring the Canadian Rockies of British Columbia. The Burgess Shale, which is now a part of Yolo National Park, is famous for the wide diversity of fossils of soft-bodied marine animals that are embedded in it. These fossils are approximately 530 million years old, and represent an array of life-forms present during the early–middle years of the Cambrian period (545–495 million years ago). The area originally quarried by Walcott is surprisingly small given the array of unique animal forms found in it. His initial survey covered an area that is only 10 feet tall and 200 feet long, the length of one city block.

The fossils of the Burgess Shale are significant for a number of reasons. The quality of their preservation provided the first opportunity to examine, in astonishing detail, the morphology (form and structure) of early soft-bod-

Many fossils from the early–middle Cambrian period have been uncovered at Burgess Shale sites such as this one in Yoho Valley, British Columbia, Canada.

ied life forms. In addition, these fossils are an early record of the novel body plans that were created during the Cambrian Explosion (approximately 570–540 million years ago), a geologically abrupt time period during which multicellular forms organized in a variety of new ways. The Burgess Shale does not depict the Cambrian Explosion itself, but the aftermath. The fossils are impressive not only for the novelty of the body plans represented, but also for the diversity of body plans.

Fossils of soft-bodied forms are rare because the process that creates fossils works better at preserving bones and hard structures. Before the discovery of the Chingjiang fossils in Yunnan Province, China, in the late 1980s, the Burgess Shale fossils provided the only evidence of the early soft-bodied animals that appeared during the Cambrian Explosion. The quality of these fossils indicates that they were created under **anoxic** (low oxygen) conditions. Many millions of years ago, the site of the Burgess Shale was underwater and located near the equator. Soft-bodied marine animals were carried by strong currents from surrounding highly oxygenated areas to the site of the Burgess Shale and were buried in an underwater mudslide. The

anoxic an environment that lacks oxygen low oxygen content of these waters killed the animals and protected their remains from decay.

Classifying the Burgess Animals

Approximately 120 species are found in the Burgess Shale, including familiar forms as well as several species belonging to previously unknown phyla. Some of the fossilized species are members of groups (phylum) that still exist. These species can be categorized as members of the phyla Porifora (sponges), Annelida (segmented marine flatworms), Arthropoda (insects, crabs, and trilobites), and Echinodermata (sea urchins, sea fans, and sea lilies), and one species is the earliest representative of the phylum Chordata (which includes vertebrates). Most of these animals were scavengers, and a few were predators. Of these Burgess Shale animals, the aptly named *Hallucigenia* (phyla Annelida) is probably one of the most famous for its bizarre morphology. Seven pairs of stiltlike legs support its long, cylindrical body. It is hard to tell for certain which end is "head" and which end is "tail," but most scientists designate the head end by the bulbous projection that is prominent on one end of its body.

The previously unseen animal forms found within the Burgess Shale include a number of wormlike and segmented organisms, some of which were assigned to novel phyla (phyla Priapulida and Onychophora) while others remain "unclassified to this day." *Opabinia* was a five-eyed, 3-inch-long creature with a frontal "nozzle" that was presumably used in its search for worms and other fossorial (living in burrows) prey. *Anomalocaris* ("unusual shrimp") was a fierce, 2-foot-long predator with robust forelimbs for grasping its prey and a square-shaped mouth rimmed with multiple rows of sharp teeth. Because *Anomalocaris* existed in the Burgess Shale only as separate pieces, Walcott first reconstructed it as two animals: a bivalved (having two symmetrical, shelled parts joined by a hinge) arthropod and a jellyfish. Fossils of related species later found in China reached a length of up to 6 feet! *Wiwaxia*, a spike-covered, sluglike animal, was a bottom feeder that was protected from hungry predators by its scaly back.

In attempting to fit these new forms into the preexisting classification scheme, which included only phyla Porifora, Annelida, Arthropoda, Echinodermata, and Chordata, Walcott erroneously classified these animals as worms and arthropods. His categorization of the Burgess animals as ancestors of modern-day animals conformed to the idea that the diversity of life-forms arose in a manner resembling the shape of an inverted cone, with the large number of species that exist today arising from a small number of ancient organisms.

It was not until H. B. Wittington of Cambridge University examined the fossils forty years later that these forms were placed into unique phyla. Whittington's reclassification caused a major upheaval in the way people thought about the origin of animals. Instead of the popular view that a small number of general body plans originated during the Cambrian period and gave rise to all the animals seen today, Whittington contended that the body plans evident today represent only some of the novel forms that were created during the Cambrian period. He argued that many different body plans were created then, a number of which went out of existence while the remainder continued and gave rise to the forms we see today. This premise formed the basis for his reclassification of the Burgess animals.

Ediacaran Fauna

Before the Cambrian Explosion and the associated appearance of new animal forms, there existed the Ediacaran Fauna (also known as Vendian Biota), a group of multicellular organisms with relatively simple body plans. Geologist Reginald Sprigg first discovered the fossil traces of these organisms in 1946 while exploring the Ediacara Hills of Australia. Since the initial discovery of the Australian fossils, additional Ediacaran fossils have been found on every continent except Antarctica. The age of the rocks containing these fossils range from 600 million to 544 million years old. Before the discovery of the Ediacarans, it was believed that animals did not exist before the Cambrian Period (before 545 million years ago).

In contrast to the Burgess Shale fossils, most of the Ediacaran fossils are burrows and trace fossils—casts and molds of the organisms they depict. The fossil traces of these simple animals can be broadly divided into those that are **radially symmetric** and those that are segmented. The radially symmetric traces are believed to have been formed by polyplike and disk-shaped organisms. The more complex, segmented forms are traces of tubelike units. The shape of these soft-bodied forms was preserved during rapid burial under sand on the ancient marine floor bed.

radially symmetric wheel-like symmetry in which body parts radiate out from a central point

The classification of the Ediacarans as animals remains controversial. The superficial similarity that some of the Ediacaran forms bear towards sea anenomes and jellyfish led some scientists to conclude that they are true animals, precursors to the animals that exist today. Various Ediacarans have also been mistakenly classified in the past as algae, lichens, or giant protozoans.

However, some scientists believe that the Ediacarans were not animals as we know them, and they did not evolve into such animals. These scientists focus upon characteristics of the Ediacarans that are not found in the body plans that evolved during the Cambrian. Based on information gleaned under close examination of the fossil traces, they concluded that the Ediacarans underwent a set of embryonic/morphological development processes that differs radically from the normal pattern of development experienced by true animals. SEE ALSO CAMBRIAN EXPOLSION; CAMBRIAN PERIOD; GEOLOGICAL TIME SCALE.

Judy P. Sheen

Bibliography

Erwin, Douglas, Jim Valentine, and David Jablonski. "The Origin of Animal Body Plans." *American Scientist* 85 (1997):126–137.

Knoll, Andrew H., and Sean B. Carroll. "Early Animal Evolution: Emerging Views from Comparative Biology and Geology." *Science* 284 (1997):2129–2137.

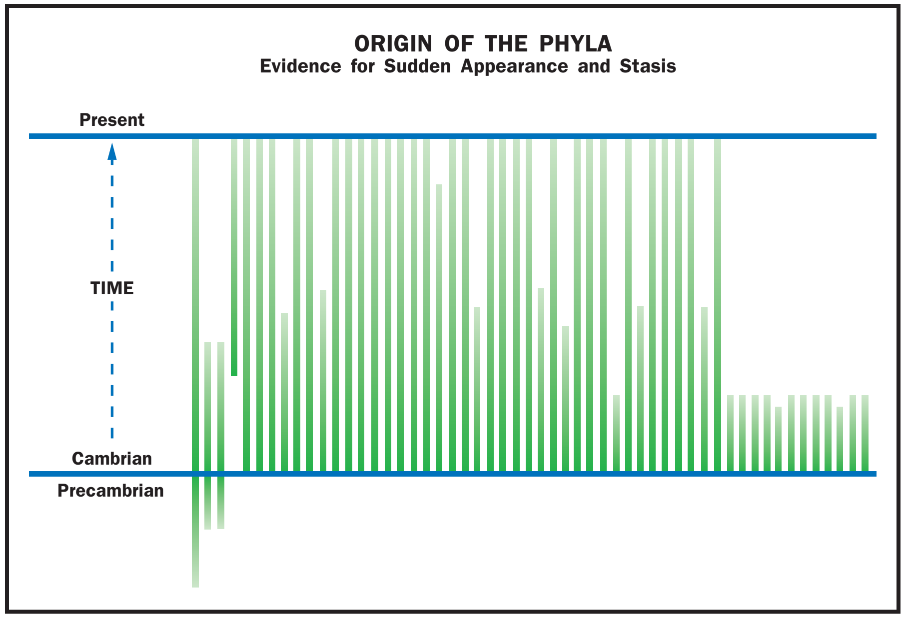
Gould, Stephen Jay. *Wonderful Life: The Burgess Shale and the Nature of History.* New York: W. W. Norton and Co., 1989.

Cambrian Explosion

C

The Cambrian Explosion, known informally as Biology's Big Bang, refers to the event that greatly increased the variety of animal species and created the major types of animals that exist today. Scientists refer to this event as an "explosion" not because it was a period of violent activity, but because

Study of fossils provided the information to create this chart.

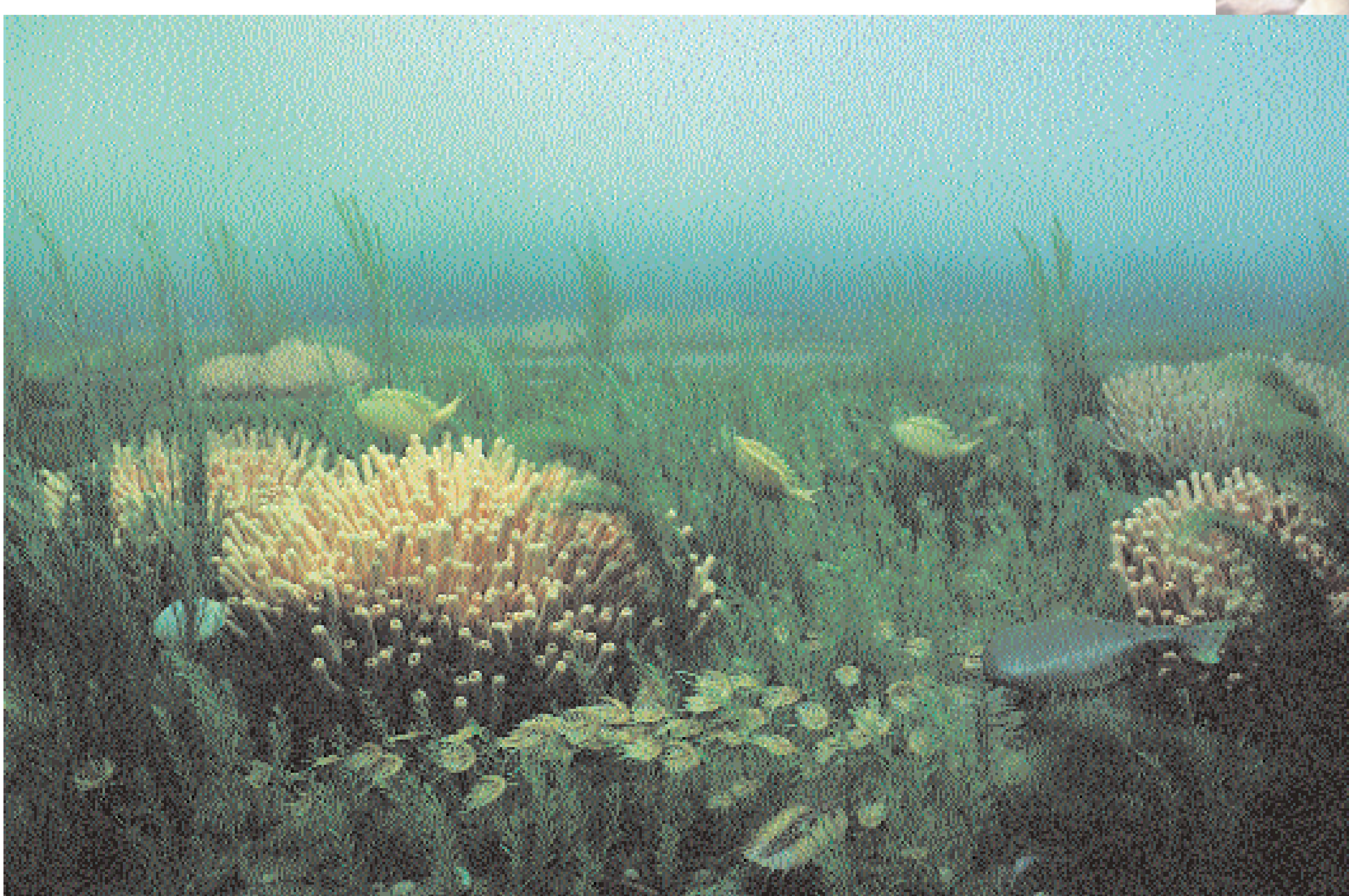


an incredible amount of evolutionary activity occurred in a relatively short length of time. This burst of evolution occurred during the early years of the Cambrian period (approximately 570 million to 495 million years ago). The Cambrian Explosion ran its course over several tens of millions of years, but this time period is quite brief considering the length of time that multicellular life has existed on Earth (about 600 million years).

In addition to the phyla that are still present today (phyla Porifera [sponges], Cnidaria [jellyfish], Platyhelminthes [flatworms], Nematoda [nematode worms], Molluska [clams], Annelida [roundworms], Arthropoda [insects, spiders], Echinodermata [sea urchins], and Chordata [vertebrates]), a number of other phyla were created and have since become extinct (including phyla Priapulida, Onychophora, and some unclassifiables).

The Burgess Shale (in British Columbia, Canada) and the Chingjiang (in Yunnan Province, China) provide fossil evidence for the outcome of the Cambrian Explosion. The fossils of both localities are impressive for the details they provide of early, soft-bodied marine organisms, and for the diversity of animal forms they display. Prior to Charles Walcott's 1909 discovery of the Burgess Shale in the western Canadian Rockies, life was thought to have evolved at a gradual, constant rate. The Burgess Shale fossils, formed 530 million years ago, shortly after the Cambrian Explosion, showed that the diversity of animal forms arose abruptly relative to the age of animal life as a whole.

No one knows exactly how the Cambrian Explosion started, but a number of theories have been offered. Many scientists believe that violent and abrupt changes in climate forced animal life to diversify and adapt to new and harsh conditions. Prior to the Cambrian Explosion, the present-day continents of Africa, South America, India, Antarctica, and Australia formed a giant landmass called Gondwana. Shortly before the Explosion, the abrupt shifting of Gondwana and Laurasia (ancestral North America) across Earth's surface caused volcanic eruptions and earthquakes, creating a hostile environment in which marine animals had to compete for survival.



Many of the marine-based life-forms recognized today originated in the Cambrian period.

These dramatic geological events mixed more oxygen dissolved into the water, which helped make possible processes such as respiration, cell division, and the synthesis of proteins that are important in body structure and support. In this respect, the movement of tectonic plates that resulted in an upheaval of Earth's geology contributed to the creation of complex body plans. The evolution of organs such as brains, digestive guts, and shells opened the door for the new creatures to increase in complexity. These animals were then able to forage more effectively, move more efficiently, and protect themselves.

The tectonic shift created a new ecological battleground for these animals to compete. The breakup of Gondwana and its subsequent reorganization created a larger area of marine habitat in which the new creatures would compete. This competition catalyzed the adaptive radiation (evolution of a large variety of specialized forms) of the lineages into their respective niches.

Another mystery surrounding the Cambrian Explosion is why new phyla, or major lineages, have not evolved since then. Some scientists assert that after successful body plans arose during the Cambrian, genetic limitations dictated that change occur only within the set lineages. Rather than create dramatically new body forms, these existing forms were modified into more complex animals. Because modern animals have been evolving and adapting for millions of years since their ancestors first appeared, they would have an advantage over any new "hopeful monsters" that may come about through mutation. Hopeful monsters are forms that are so different from the "tried and true," existing with low chances of survival.

Late twentieth-century efforts to solve the mysteries of the Cambrian Explosion focused on molecular genetic techniques. New technology allowed scientists to extract DNA from fossils of the first Cambrian animals and to study certain aspects of these animals' biology. In this manner, scientists can learn about the development and evolutionary relationships of these animals. SEE ALSO Burgess Shale and Ediacaran Faunas; Cambrian Period; Geological Time Scale.

Judy P. Sheen

Bibliography

Erwin, Douglas, Jim Valentine, and David Jablonski. "The Origin of Animal Body Plans." *American Scientist* 85 (1997):126–137.

Gould, Stephen Jay. *Wonderful Life: The Burgess Shale and the Nature of History.* New York: W. W. Norton and Co., 1989.

Knoll, Andrew H., and Sean B. Carroll. "Early Animal Evolution: Emerging Views from Comparative Biology and Geology." *Science* 284 (1997):2129–2137.

Cambrian Period

The Cambrian period (570 million years ago) marks an extraordinary shift in the evolution of life. It ushers in the beginning of the Paleozoic Era (the age of ancient life).

Cambrian period and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

prokaryotes single-celled organisms that lack a true cell nucleus

In the Precambrian, a three-billion-year period of evolutionary stasis, the dominant life-forms were **prokaryotes** (tiny one-celled bacteria) and blue-green algae, both of which thrived in the steaming waters and nitrogen- and sulfur-rich air of a geologically turbulent Earth. Prokaryotes are the simplest forms of life, undifferentiated cells with no nucleus that reproduce by fission, the splitting of the parent cell into two. Prokaryotes live off hydrogen, sulfur, and nitrogen and they release free oxygen as a waste product. The prokaryotes' leisurely existence continued for five-sixths of recorded time, during which their massive colonies of cyanobacteria, fossilized as stromatilites, bubbled out enough oxygen to form eventually an atmosphere and a corresponding ozone shield against sterilizing ultraviolet radiation. This development appears to have set the stage for what has been described as the Big Bang of Biology, the Cambrian Explosion.

This trilobite fossil is one of 120 different fossilized species found in the Burgess Shale in Yoho National Park, British Columbia, Canada.

Cambrian rock is named after the Latin "Cambria," meaning Wales. It was there that Cambrian rock was first studied for fossils in the late 1800s. Since then it has been found on every continent, with a particularly fertile deposit having been discovered in British Columbia, Canada. The latter is known as the **Burgess Shale**, a fine-grained, mudstone siltstone rock unit only about 200 feet long and 8 feet thick. Stephen Jay Gould has described it as the most important fossil deposit ever found. Dating to the mid-Cambrian of about 520 million years ago, the Burgess Shale has more than 120 animal species represented in it. The Burgess fossils demonstrate that the Cambrian period was a riot of experimentation in size, shape, and abilities. Animals that swam, that burrowed, and that foraged appeared at this time. A huge diversity of forms emerged. Some would succeed and continue to exist, while many others would disappear forever. The beginnings of every existing major **phyla** of animals can be found in the Burgess Shale and in other layers of Cambrian rock in Greenland and China. Over 900 species of marine life have been discovered at these locations, including sponges, jellyfish, annelids, mollusks, arthropods, and chordates with rudimentary backbones. One of the most interesting innovations found in Cambrian period animals was their ability to secrete a mineralized skeleton.

Burgess Shale a 570 million year old geological formation found in Canada that is known for well-preserved fossils

phyla broad, principle divisions of a kingdom

What could have caused this remarkable outburst of evolutionary life? The single most galvanizing event of the late Precambrian was the appearance of **eukaryota**, life-forms that stored DNA in a nucleus and were capable of organizing bodies consisting of more than one cell. Eukaryotes allowed for the possibility of specialization, since the individual cells did not each have to perform every task as long as they could communicate chemically with one another. This cooperation between cells set life-forms free to explore every design and variable in size and shape imaginable. Eukaryotes also developed the capability for sexual reproduction, which increases genetic diversity. Rather than duplicating the genetic material exactly as simple **fission** does, sexual reproduction ensures that a constant shuffling of genetic material will maximize the number of mutations and variations possible. This again allows for radical divergences in the exploration of the environment. These

eukaryota a group of organisms containing a membrane-bound nucleus and membrane-bound organelles

fission dividing into two parts

advances in eukaryote organisms, combined with the new, oxygenated atmosphere of the planet, would appear to have allowed for the outburst of metazoans—multicelled animals—in the Cambrian rocks. SEE ALSO Geological Time Scale.

Nancy Weaver

Bibliography

Fortey, Richard. *Fossils: The Key to the Past.* Cambridge, MA: Harvard University Press, 1991.

Friday, Adrian, and David S. Ingram, eds. *The Cambridge Encyclopedia of Life Sciences.* London: Cambridge University Press, 1985.

Lambert, David. *The Field Guide to Prehistoric Life.* New York: Facts on File, 1985.

McLoughlan, John C. *Synapsida: A New Look into the Origin of Mammals.* New York: Viking Press, 1980.

Steele, Rodney, and Anthony Harvey, eds. *The Encyclopedia of Prehistoric Life.* New York: McGraw Hill, 1979.

Camouflage

Predation is an instinctive animal behavior that involves the pursuit, capture, and immediate killing of animals for food. Birds that capture insects in flight, starfish that attack marine invertebrates, and tigers that pursue gazelle are all examples of predators. Predatory animals may be solitary hunters, like the lion, or they may be group hunters, like wolves. Natural selection favors the development of a variety of quick defenses against predators including camouflage and predator avoidance behaviors.

Camouflage is a form of deceptive coloration that is essential to the survival of most animals. Camouflage can make it extremely difficult to spot an animal in its natural habitat because the animal appears to blend into its surroundings. This adaptation is beneficial because it can provide protection from predators. At the same time, it can also conceal an animal and allow it to be a stealthy predator able to inconspicuously hunt down or snatch its unsuspecting prey.

This walking stick insect hides from its predators by blending into its environment. The insect's slow walk mimics the movement of branches swaying in the wind.

Types of Camouflage

Animals camouflage themselves in many ways, including background matching, color changing, disruptive coloration, and countershading.

Background matching. Background matching is probably the most common type of concealment. The animal and its surroundings are so close in color that they appear as one. Fish eggs, for example, often have very little pigmentation and appear transparent against the blue of the open sea. Polar bears appear to merge into the ice and snow of the Arctic, and grasshoppers blend perfectly with green grasses and shrubs.

Color changing. Color changing is another way to achieve camouflage. Emotion seems to play a role in color change in some animals, such as cephalopods and certain fish, which are capable of rapid color changes completed in a half-second or less. These animals, when excited, can exhibit spectacular displays of color, with waves of color rippling across their bodies. As the animal's eyes register the colors in its immediate environment, hormonal reactions send chemical messages to chromatophores, pigment-bearing cells in the animal's skin. The chromatophores undergo rapid changes in pigment concentration, distribution, and position, allowing the animal to seemingly change color almost instantly. Most vertebrates, however, undergo color changes less rapidly, requiring several minutes to several hours.

Disruptive coloration. Disruptive coloration may appear as patterns in which an animal's markings do not coincide visually with its body shape or outline. Flatfish, for example, are marked in such a way that their skin patterns do not reveal their contour when they rest on the ocean bottom. Many reef fish also have disruptive patterns in their coloration, which enable them to school safely over reefs during daylight hours. When a predator approaches, the fish form dense schools in which all of the individual fish orient themselves in the same direction. The movement of many fish, coupled with their similar disruptive coloration of vertical banding or horizontal stripes, presents an extremely confusing spectacle. This makes it difficult for a predator to attack any individual fish.

Some forms of disruptive coloration also function to hide movement. Forward movement of concentrically banded snakes, for example, is difficult to perceive when the animal moves between reeds or tall grasses.

Countershading. Countershading, a type of camouflage coloration in which the upper surfaces of an animal's body are more darkly pigmented than the lower areas, gives the animal's body a more uniform darkness and lack of depth relief because the underside of the body is shadowed. Light-producing organs found in some deepwater fish provide a unique form of countershading. The light-producing organs often occur in bands along the fish's undersides and are directed downward. This unique arrangement, coupled with the utter darkness of the ocean at deep depths, may provide camouflage by obliterating the fish's silhouette when a predator views it from below.

Some animals camouflage themselves through mimicry by showing an imitative resemblance to inanimate objects in their environment, such as the leaves or twigs of a tree. Stick insects, for example, may resemble twigs when resting on trees.

Predator Avoidance Behaviors

In addition to camouflage, animals use predator avoidance behaviors or protective adaptations to avoid being killed. Warning calls and visual and chemical signals that are unique to different animal species may evoke avoidance behaviors such as freezing, crouching, fleeing, escaping, and stinging. For example, many perching birds will gather in a mob when stimulated by the sight of an owl.

Freezing or immobility usually makes detection less likely. Many animals, such as rabbits and squirrels, exhibit this reflex-like behavior when startled. Some groups of animals commonly keep in touch by calls or by movements such as tail flicks, which are exhibited during freezing.

Many animals posses protective reflexes, armor, and spines that enable them to avoid predation. Stick insects resembling twigs and leaves, for example, exhibit unusual reflex behaviors, such as swaying to imitate moving foliage. Mollusks, like oysters and clams, may retract their soft bodies into their shells when disturbed. Turtles and other slow moving animals may retreat into their armor for protection. Still other animals, such as porcupines, protect themselves from predators with a thick coat of sharp quills.

Chemical means of defense may help an animal escape predators. An animal may eject a poisonous substance from a body reservoir or spine. Jellyfish, for example, may sting to avoid being captured. Snakes may inject venom through their fangs to kill or deter menacing predators. Some animals, like skunks, may even squirt substances at their enemies. The skin of some toads contains substances that make them distasteful to predators. Ants produce strong substances that attract other ants at low concentrations and in high concentrations produce fast movement, defense postures, and even fleeing.

Fleeing and escaping are two of the most common predator avoidance reflex behaviors. When an animal is startled or subjected to pain, it may run or jet away. Squids, for example, use jets of water to propel themselves quickly out of danger. Bony fish have structures that initiate escape-swimming when agitated. SEE ALSO HABITAT; MIMICRY.

Stephanie A. Lanoue

Bibliography

Brum, G., and Larry McKane. *Ecology and Animal Behavior*. London: Cambridge University Press, 1999.

Grier, James, and Theodore Burk. *Biology of Animal Behavior*. Chicago: McGraw-Hill, 1992.

Hanlon, Roger, and John B. Messenger. *Cephalopod Behavior*. London: Cambridge University Press, 1998.

Slater, P. *Essentials of Animal Behavior*. London: Cambridge University Press, 1999.

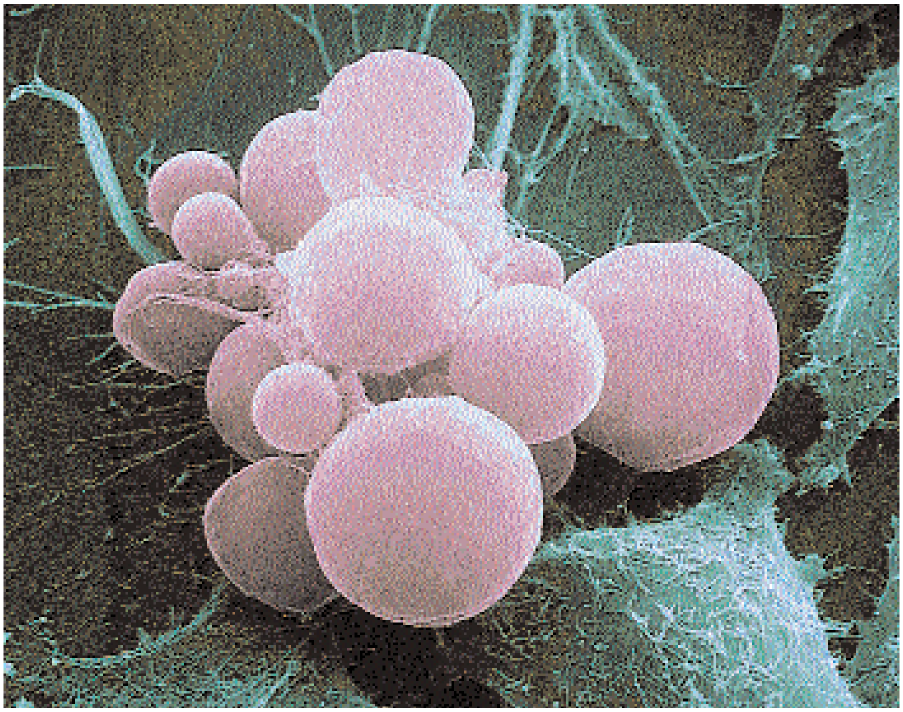
Cancer

Cancer is the uncontrolled growth of cells. This abnormal growth is the result of mutations in the genetic material of the cells, either spontaneous or brought on by environmental factors such as ultraviolet radiation or asbestos. This growth leads to a collection of mutated cells called a tumor. The tumor can be benign, meaning that it is comparatively harmless and restricted to one type of tissue. Alternately, it can be malignant, which means it can grow into surrounding tissue or migrate to different parts of the body. When a malignant tumor spreads to other tissues, this is known as metastasis.

Cell replication

Normally, animal cells grow with a variety of checkpoints. For example, when a person cuts her finger, skin cells will divide and grow to fill the opening, but they will stop growing once the cut is closed. The body has a number of mechanisms to prevent unchecked cell growth, and in order to become cancerous, abnormal cells must defeat several of them. Some of these mechanisms determine division rates; others manage DNA repair. Like any other controls in the body, these can go awry when a mistake arises in the DNA encoding them.

Excessive cell division. Suppose, again, that a person gets cut. First, skin cells must decide when it is time to divide and when it is time to rest. Of-



A scanning electron microscope magnifies mammalian cancer cells 7,500 times. These cancer cells could quickly reproduce, creating enough cells to form a tumor.

ten cells will receive signals from outside their membranes instructing them what to do, and the signals must pass down a cascade of messengers inside the cell for them to be conveyed. Each step along the cascade, then, can be a control point: a surface molecule on a skin cell is told that it must divide to heal a cut, and the surface molecule sends a signal to a protein inside the cell, which sends the signal to a different protein, and so on, all the way to the nucleus, which then initiates **DNA replication** and cell growth. At each step, it is possible that a mistake might start or halt the cell replication process. For example, overexpression of ras, an intracellular messenger that resides in the pathway between the surface and the nucleus, can lead to excessive cell division.

DNA replication the process by which two strands of a double helix separate and form two identical DNA molecules

Viruses and cancer. There are a number of ways that a protein such as ras can be overexpressed, including the involvement of a virus or a genetic mutation. Certain viruses are associated with cancers: for example, sexually transmitted human papilloma virus has been known to increase rates of cervical cancer. Out of all cancers, 10 to 15 percent are thought to be virus-related. Alternately, the genetic mistake might be spontaneous in one of three ways. A gene encoding the protein could be accidentally copied more than once, and, as a result, each copy would churn out the protein when activated. The gene could be misplaced and put near a region of DNA that encourages protein expression. Lastly, a mutation inside the gene might make it unusually active or resistant to later degradation. When such errors initiate uncontrolled cell growth, the gene involved is called an oncogene (*onco* is Greek for "tumor"). Before the mutation occurs, the gene may be called a proto-oncogene. Proto-oncogenes usually have the important function of controlling cell-cycle function, as is the case with ras, or may be involved in keeping the cell alive during times of stress, as in the case of Bcl-2, a molecule that prevents stressed or damaged cells from committing apoptosis (cell suicide). Certain viruses can cause these mutations and make oncogenes out of the protoncogenes.

How Cells Curb Their Own Growth

Mutations in cell-cycle control genes can obviously be a problem for an individual, so there are mechanisms in place to prevent this from happening. As mutations can happen during DNA replication, DNA copying is a tightly controlled process. Additionally, there are genes that have the task of DNA repair and mutation surveillance. One such gene is p53. If there is genetic damage, p53 will halt the cell cycle, may initiate DNA repair mechanisms, and may activate cell suicide if repair is not feasible. P53 and other genes that conduct DNA repair and damage surveillance are called "tumor suppressor genes."

organelles membrane bound structures found within a cell

cytosolic the semifluid portions of the cytoplasm

macrophages a type of white blood cells that attacks anything foreign such as microbes

Apoptosis. Apoptosis is a way for damaged cells to prevent themselves from causing more problems. Once apoptosis is initiated, the cell cleaves its own DNA and falls apart in a tightly regulated fashion. The dying cell will pinch off into small pockets of membrane and **organelles**, known as apoptotic bodies, in order to prevent toxic **cytosolic** compounds from being released. Then the apoptotic bodies will be swept up and cleared from the area by **macrophages** or other cells.

"Slipperiness." Aside from cell-cycle control and tumor suppressor genes, there are other means by which cells curb their own growth. For example, if one grows ordinary skin cells on a plate with growth media, the cells will grow until a bed covers the entire plate. But the cells will not grow beyond that; nor will they grow on top of one another. This is why a cut on one's finger will not grow into a huge lump after it closes. Normal cells will also adhere tightly to one another by secreting proteins that stick to other cell surfaces, whereas many cancer cells do not. Medical doctors use this lack of adhesion, this slipperiness, as one way of distinguishing cancerous tumors from other kinds of lumps.

nucleotide chain a chain composed of five-carbon sugar groups that forms the basis for nucleic acid

nucleotides the building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

Telomerases. Another common mutation seen in cancers is the activation of telomerases. When DNA divides, the replication machinery moves down the **nucleotide chain** until the very end. It is unable to copy the very end of the molecule (the telomere), however, so with each successive round of replication, the DNA chain gets shorter. In mammals, the telomeres contain repetitive DNA sequences that encode no protein; the idea is that these useless **nucleotides** can be discarded as cells divide. As the telomeres get shorter, though, the cell will eventually start deleting useful DNA. Some scientists think this is a reason animals grow old: The more cells divide, the greater the likelihood that certain genes will be eliminated and that the new cells will be dysfunctional.

Cancer Cells

Cancer cells, on the other hand, have no such problem. They usually express telomerases, which are enzymes designed to prevent the elimination of the telomeres during cell division. Cancer cells can therefore divide many times and not delete any genetic information crucial to their survival.

Cells require more than one mutation to become cancerous. Mutations in cell-cycle control and tumor suppressor genes are usually required for a tumor to be considered a full-fledged cancer. While many of the tumor suppressor genes are dominant traits (requiring only one allelic deletion to deactivate), many proto-oncogenes are **recessive**, meaning that both **alleles** must be destroyed in order for the cells to grow improperly. Such a combination of mutations in a single cell is unlikely, which is why some scientists think that cancers do not begin to show in humans until late in life, when repeated cell division has had a chance to accumulate a number of mistakes in the DNA.

recessive a hidden trait that is masked by a dominant trait

alleles one of two or more alternate forms of a gene

After p53 or other genes that screen DNA get deleted, the cells begin to spin out of control genetically and produce many different kinds of mutations. Like most mutations, the majority of these will simply kill off the cells possessing them. But as tumor cell division is unchecked, other cells will quickly replace them. As the tumor grows and accumulates more mutations, it may gain the ability to grow in different types of tissue.

Cancers may acquire a number of traits useful for their own growth. For example, certain tumors are angiogenic, meaning they draw blood vessels toward themselves to feed the growing tumor. The malignant cells do this by secreting certain hormones necessary for vessel formation. These new vessels also provide conduits for cancer cells to spread throughout the body. In the early twenty-first century, researchers also found that some tumor cells can create new lymphatic vessels, a process called lymphangiogenesis. These newly generated vessels may make it easier for the cancer to spread itself to other parts of the body.

Cancer Treatment

As one might predict, cancer treatment primarily seeks to stop the division of the cells. One method is radiation, which disrupts DNA replication entirely. Other pharmacological means seek to do the same. As cancers are usually the only collection of rapidly dividing cells in the body, halting replication can slow them down, although such treatments can impede healing or immune system function.

More recently, researchers have been using compounds designed to prevent angiogenesis to curb tumor growth. In the early twenty-first century, the National Cancer Institute was conducting clinical trials of anti-angiogenic compounds in a variety of cancers, including stomach, breast, prostate, lung, brain, and ovary, and in some leukemias and lymphomas.

Certain cancers produce tumor antigens, proteins recognizable by the body as hailing from a cancer. Prostate cancer, for example, generates tumor antigens specific enough to be used as a diagnostic tool in patients. Thus, it is theoretically possible to create a prostate cancer vaccine by teaching the body to recognize these antigens before cancer ever arrives and to fight off malignant cells, just as antivirus vaccines fight off virally infected cells. By the beginning of the twenty-first century, however, researchers had found vaccines to be of little use in specifically stimulating the body's immune system to reject tumors.

Cancers, ordinary cells gone wrong, defy normal biological conventions of regulation and **homeostasis**. As they can quickly reproduce and replace lost daughter cells, they are ripe for rapid mutation and evolution within the body. A variety of treatments exist, but cancers vary widely in origin and nature, as there are different regulatory mechanisms that control different cell

homeostasis a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

HELA CELLS

Although Henrietta Lacks died of cancer in 1951, little bits of her are alive everywhere. She is the originator of the first immortal cell line, HeLa cells. These are cancer cells scraped from her cervix, and they grew so well that they proved ideal for study in laboratories all over the world. Unfortunately, they grew so well in culture that they invaded other cell lines and ruined countless experiments. It became such a problem that in 1968, the premier standard-bearer of cell lines in the world, the American Type Culture Collection, tested all thirty-four of its "pure" cell lines and found that twenty-four of them were HeLa cells instead.

types. A more detailed understanding of cell-cycle regulation and mutation surveillance may yet unlock the secrets to curing the disease. SEE ALSO CELLS.

Ian Quigley

Bibliography

Scientific American. Special Topic Issue: "What You Need to Know about Cancer." September 1996.

Internet Resources

Cancernet. National Cancer Institute. <http://cancernet.nci.nih.gov/>.

Carboniferous

The Carboniferous period dates from 360 million to 280 million years ago. It gets its name from the vast deposits of coal produced when fluctuating seas drowned the tropical forests that covered much of North America and Europe.

Carboniferous period and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

amniote a vertebrate that has a fluid-filled sac that surrounds the embryo

CARBONIFEROUS OR MISSISSIPPIAN AND PENNSYLVANIAN?

In the United States, the Carboniferous Period is usually broken down into two periods—Mississippian and Pennsylvanian. Sedimentary rocks that formed in shallow oceans characterize the Mississippian or "Lower Carboniferous." These rocks are usually found along the Mississippi River. Coal bearing sedimentary rocks that formed in swamps and river deltas characterize the Pennsylvanian or "Upper Carboniferous. These rocks are usually found in the northeastern United States.

The later Paleozoic (286 million to 570 million years ago) was a world that would be recognizable to us. By this time the teeming marine and land plants had expelled enough oxygen to produce an atmosphere very similar to our own. Vast forests greened the supercontinent Pangaea and supported a thriving animal population. We would be struck by the sheer size and variety of the flora and fauna: horsetails and scale trees that stood from 50 to 100 feet tall and dragonflies with 2-foot wingspans. Drippingly humid and silent, the monotonously green rain forest abounded with scuttling creatures familiar and unfamiliar. Animals that swam, crawled, and flew populated the tropical swamps of the forest. Snails and cockroaches and myriapods made a living on the rich forest floor, along with 6-foot centipedes and crocodile-like amphibians.

By this time all the major characters of evolution had come into being. There would still be millennia of ingenious refinements of size and shape and function, variations on the main themes to exploit the new Devonian (408 million to 438 million years ago) environment of land and air. The Phylum Chordata, comprised of animals with backbones, had previously experimented with fishes and amphibians; now, in the Carboniferous period, the chordates would diverge into reptiles.

In a remarkable adaptation referred to as the **amniote** radiation, amphibians had evolved from needing large bodies of water in order to reproduce. The method was a semipermeable, shelled or leathery skinned egg filled with enough nutrients to sustain an embryo until it was fully developed. This dry-land form of reproduction necessitated yet another biological innovation, namely internal fertilization. These two features enabled the former amphibians to radiate out into every **niche** of the giant land mass, in turn encouraging further evolutionary branching. As the tetrapods (four-limbed animals) spread through the luxuriant vegetation, they made adjustments in their dentition and digestive tracts to take advantage of the untapped food source on land.

niche how an organism uses the biotic and abiotic resources of its environment

Three distinct groups of reptiles emerged, differentiated by the number of small holes in the skull located behind the eyes at either side. Anapsids had no holes and included the turtles and their now-extinct relatives. Synapsids, with a single pair of temporal openings, included all of the mammal-like reptiles, now extinct, and their distant relatives, the true mammals. Diapsids were reptiles with two pairs of openings. Petrocalosaurus was a rapid, 16-inch **insectivore** whose genes gave rise to lizards, snakes, crocodiles, dinosaurs, and birds.

insectivore an animal that eats insects

By the Carboniferous period, the constant ebb and flow of **continental drift** had once again pushed the land masses back together into one supercontinent, Pangaea, whose northern forests were periodically flooded by shallow tropical seas. The cycle of vegetation and flooding produced organic beds of peats that were compressed into coal layers over 3,000-feet thick. Exquisitely preserved fossils appear in this coal, especially near the Czech mining town of Nyrany. Here, hundreds of specimens have been collected, representing twenty amphibian and four reptile species as well as unusual fishes and small, shrimplike creatures.

continental drift the movement of the continents over geologic time

In the Carboniferous seas, huge limestone reefs were being laid down by limy coral, brachiopod, and crinoid skeletons. These reefs were home to starfish, **gastropods**, and sea urchins, while giant coiled nautiloids and bony fish swam overhead. SEE ALSO GEOLOGICAL TIME SCALE.

gastropods mollusks that are commonly known as snails

Nancy Weaver

Bibliography

Asimov, Isaac. *Life and Time.* Garden City, NY: Doubleday and Company, 1978.

Fortey, Richard. *Fossils: The Key to the Past.* Cambridge, MA: Harvard University Press, 1991.

———. *Life: A Natural History of the First Four Billion Years of Life on Earth.* New York: Viking Press, 1998.

Friday, Adrian, and David S. Ingram, eds. *The Cambridge Encyclopedia of Life Sciences.* London: Cambridge University Press, 1985.

Gould, Stephen Jay, ed. *The Book of Life.* New York: W. W. Norton and Company, 1993.

Lambert, David. *The Field Guide to Prehistoric Life.* New York: Facts on File, 1985.

McLoughlan, John C. *Synapsida: A New Look into the Origin of Mammals.* New York: Viking Press, 1980.

Steele, Rodney, and Anthony Harvey, eds. *The Encyclopedia of Prehistoric Life.* New York: McGraw Hill, 1979.

Wade, Nicholas, ed. *The Science Times Book of Fossils and Evolution.* New York: The Lyons Press, 1998.

Rachel Carson alerted the world to the dangers of environmental pollutants with works like the ground-breaking *Silent Spring.*

Carson, Rachel

Biologist and Author
1907–1964

Rachel Louise Carson was born on May 27, 1907, the youngest child of farming and teaching parents in Springdale, Pennsylvania. The 24-hectare (60-acre) homestead was an oasis of orchards, streams, and woods in the grimy Allegheny River Valley, which had been heavily polluted by the coal and steel industries. Carson's parents were a particularly gentle couple who encouraged in their daughter a love of books and nature and a deep belief in sharing Earth with all other living beings. She became a published author for the first time at the age of eleven and later said that the thrill of seeing her story in print and the princely prize of ten dollars set her on her life's course.

Carson received a scholarship to Pennsylvania College for Women and made the shocking decision to major in biology at a time when there were virtually no jobs for women scientists. Upon graduation, she was offered a summer internship at Woods Hole, Massachusetts—a famous ocean research center—and a full scholarship to John Hopkins University, where she earned her master's degree in biology. During the massive unemployment of the Great Depression of the 1930s, Carson took the civil service exam and became the first woman to be hired as a biologist by the U.S. Bureau of Fisheries. During World War II (1939–1945) she was assistant to the chief of the office of information at the newly renamed U.S. Fish and Wildlife Service. During this period she began a series of books about the ocean and how the lives of its inhabitants—birds, fish, eels, and crustaceans—are intricately linked to one another and to the sea around them. All three of the books—*Under the Sea-Wind*, published in 1941, *The Sea Around Us*, published in 1951, and *The Edge of the Sea*, published in 1955—became best-sellers, and they catapulted Carson into national celebrity and allowed her to become a full-time writer.

pesticide any substance that controls the spread of harmful or destructive organisms

In 1962 the publication of her fourth book, *Silent Spring*, caused a nationwide uproar over the dangers and benefits of unregulated **pesticide** use. Government study panels were convened, grassroots conservation and environmental movements were organized, and laws were passed in the wake of this latest Carson best-seller, which was promptly translated into over a dozen languages. Despite vicious attacks by the chemical interests, other scientists validated the warnings in *Silent Spring*, and Carson became a national hero. She was awarded numerous honors by such groups as the American Academy of Arts and Letters, the National Wildlife Federation, and the Animal Welfare Institute. She was the first woman to be awarded the Audubon Medal, and she received a posthumous Medal of Freedom. Carson died of breast cancer on April 14, 1964, with the hope that she would be remembered in connection with all that is lovely and beautiful. SEE ALSO DDT; PESTICIDE; SILENT SPRING.

Nancy Weaver

Bibliography

Harlan, Judith. *Sounding the Alarm.* Minneapolis: Dillon Press, 1989.

Jezer, Marty. *Rachel Carson.* New York: Chelsea House, 1988.

Cartilage

Cartilage is a fibrous and rubbery connective tissue found throughout the vertebrate skeletal system. As with other connective tissues, the general function of cartilage is to support and connect different parts of the body. Connective tissues originate from cells in the embryonic mesoderm, the middle layer of embryonic tissue.

Cartilage is made up of specialized cartilage cells called chondrocytes, which are suspended in an acellular matrix made up largely of a protein called collagen. All connective tissues have a **matrix**, and in the case of cartilage, the matrix is solid. A protective membrane named the perichondrium covers the surface of the cartilage and gives the subtance a shiny, cloudy-white appearance.

matrix the nonliving component of connective tissue

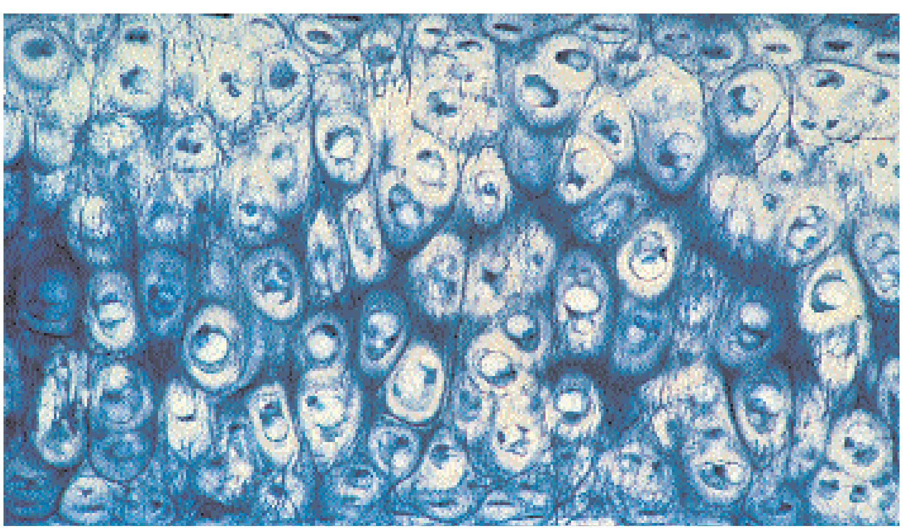
Early in development, cartilage makes up most of the vertebrate skeleton. As an individual grows older, calcium deposits form around the skeleton, and bone eventually replaces most of the cartilage. This process is called ossification. Ossification begins in humans when the fetus is still in the womb and is not complete until early adulthood. The skeleton of a young child tends to be less brittle than that of an adult because a certain amount of cartilage is still present.

This cartilage-to-bone conversion occurs in all vertebrates except for sharks, rays, and skates. These related "cartilaginous fishes" maintain a completely cartilaginous skeleton through adulthood. Cartilage is also found in branchiostomates such as tunicates, sea squirts, and **lancelets**, the closest relatives of the vertebrates. These animals have a cartilaginous rod called a notochord, which runs along the length of their back.

lancelet a type of primitive vertebrate

Cartilage is softer, more compressible, and more elastic than bone. In vertebrates whose skeletons do undergo ossification, cartilage is maintained in certain areas of the body that require this flexibility. Adults have cartilage in joints, in the nose, ears, breastbone, trachea, and larynx, and at the ends of bones.

Cartilage also helps to reduce friction between the bony elements of a joint. A lubricating liquid called synovial fluid helps the cartilage-covered



A photomicrograph of elastic cartilage. Cartilage is a fibrous and rubbery connective tissue that is found throughout the vertebrate skeletal system.

bones of the shoulder slide over each other more easily. Cartilage found in joints with a large range of motion is called smooth cartilage. In joints that experience more limited motion, cartilage plays a different role. In this kind of joint, the cartilage that holds the bones together is called elastic cartilage. Immovable joints are held together by fibrous cartilage. SEE ALSO Bone; Skeletons.

Judy P. Sheen

Cartilaginous Fishes *See Chondricthyes.*

Catadromous—Diadromous and Anadromous Fishes

Diadromous fishes describe species that spend part of their lives in freshwater and part in saltwater. There are two categories of diadromous fishes, **catadromous** and **anadromous**.

catadromous living in freshwater but moving to saltwater to spawn

anadromous moving from the ocean up a river to spawn

Catadromous fishes hatch or are born in marine habitats, but migrate to freshwater areas where they spend the majority of their lives growing and maturing. As adults they return to the sea to spawn. The word "catadromous" means "downward-running," and refers to the seaward migration of adults. The best-known group of catadromous fishes are the true eels. In these species, females spend their lives largely in freshwater, while males live primarily in the brackish water of estuarine areas. Individuals breed in the seas and die after spawning once.

Anadromous fishes are the opposite of catadromous fishes in that hatching and a juvenile period occur in freshwater. This is followed by migration to and maturation in the ocean. Adult fish then migrate back up rivers—"anadromous" means "upward-running"—in order to reproduce in freshwater habitats. The length of the initial freshwater period and of the oceanic period vary greatly by species. Similarly, the length of the migration can vary tremendously. Some species travel hundreds of kilometers between their marine habitat and their breeding grounds, while others migrate only a short distance upstream from brackish water to reach freshwater spawning grounds.

There are approximately 100 known species of anadromous fishes. Several of these are well-known and of great commercial value, including many species of salmon along with striped bass, steelhead trout, sturgeon, smelt, shad, and herring. Salmon in particular have long been admired for their lengthy, arduous migrations up rivers to their original spawning grounds, as well as for the unusual homing ability that allows them to accomplish this. Their ability to navigate back to appropriate breeding areas is particularly impressive since migration often follows a lengthy period at sea, often as long as four or five years. Chemical cues are believed to guide them in this journey.

In some anadromous species, the majority of individuals die immediately after spawning, with only a few returning downstream and surviving to spawn again. In other species, multiple migrations and spawning bouts are common.

The Rigors of Making Freshwater–Saltwater Transitions

Diadromous fishes are of particular interest to physiologists because of the great challenges posed by freshwater-saltwater transitions. In particular, freshwater and saltwater environments make strikingly different demands on water-balance systems, so these fishes must make the necessary **physiological** adjustments whenever they pass from one type of **aquatic** habitat to the other. Every diadromous species migrates at least twice, once from freshwater to saltwater, and once in the other direction. Because of their ability to tolerate a variety of salinity regimes, diadromous species are also described as **euryhaline**, meaning "broadly salty."

physiological the basic activities that occur in the cells and tissues of an animal

aquatic living in water

euryhaline animals that can live in a wide range of salt concentrations

Freshwater fish are in an environment in which they are hyperosmotic. That is, the concentration of salts and ions in their bodies is greater than that in the external aquatic environment. As a result, they have a tendency to lose important ions through **diffusion** across the skin and **gills**, and simultaneously to gain water from the environment. To maintain **homeostasis**, freshwater species have special adaptations for retaining ions and getting rid of excess water. First, they actively take in ions across their gills and skin, a process that requires energy. Second, to get rid of excess water they excrete nitrogenous waste products in great quantities, in the form of a highly diluted urine.

diffusion the movement of molecules from a region of higher concentration to a region of lower concentration

gills site of gas exchange between the blood of aquatic animals, such as fish, and the water

homeostasis a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

In marine environments the challenges are the opposite. Saltwater species must deal with an environment in which their salt and ionic concentrations are significantly lower than that of the surrounding aquatic environment. Saltwater species tend to lose water to the ocean and to gain ions from it. To obtain and conserve water, saltwater species increase their drinking rate, and excrete smaller amounts of a highly concentrated urine. In addition, they eliminate excess ions through specialized salt-excretion cells in the gills and in the lining of the mouth.

Euryhaline species must adopt the tactics of freshwater species while in freshwater environments, and those of marine species in saltwater environments. Frequently, physiological adjustments are made while organisms are in the intermediate, brackish waters of estuaries. These include changing their drinking rate, the degree of concentration of their urine, and the direction of ion-pumping in the gills and **integument**.

integument a natural outer covering

In addition to these physiological changes, associated with osmoregulation, other changes are made by diadromous species during transitions between freshwater and saltwater habitats. In some diadromous species, external features such as coloration change. For example, in some salmon species, individuals lose their typical red coloration before migrating to sea, where they take on a more silver-colored form. They regain their freshwater coloration when they reenter the freshwater environment.

Considering both the rigors of the long migratory journey and the serious physiological challenges faced by diadromous species, it makes sense to ask why these species have evolved a complex life cycle that requires multiple transitions between salt and freshwater environments. The likely answer is that species are able to take advantage of the benefits offered by each habitat, and that these benefits overshadow the burdens of the repeated migrations. For anadromous species such as salmon, for example, there appears to be a significantly greater safety for eggs in freshwater habitats yet the possibility for much faster growth in the ocean, where the food supply is more plentiful. The increase in growth rate that salmon exhibit once they have migrated to the ocean is dramatic.

The Benefits of Transitions

The rigors of the journey from saltwater to freshwater habitats, or vice versa, including the stresses related to physiological adjustment, is likely linked to the observation that many diadromous species are **semelparous**, that is, they reproduce in one large reproductive bout and then die. This is also known as "big-bang" reproduction. Semelparity is contrasted with the reproductive strategy of **iteroparous** species, which reproduce multiple times. Iteroparity characterizes numerous species, including humans.

semelparous animals that breed only once and then die

iteroparous animals with several or many reproductive events in their lives

Some formerly anadromous species have lost anadromy, having evolved to remain in freshwater habitats throughout the entire life cycle. For example, some species of salmon use lakes rather than oceans for the period of growth and maturation. However, they continue to migrate up rivers in order to find appropriate spawning grounds.

In other species, such as the steelhead trout, anadromy appears to be optional. Individuals that are spawned farther from the ocean have a tendency to remain in freshwater habitats during maturation, while those closer to river mouths have a tendency to retain the anadromous condition. This probably relates to differences in the costs of migration.

Perils to Diadromous Fishes

Diadromous fishes are particularly dependent on estuarine areas, the brackish areas linking freshwater rivers and saltwater environments. It is within the estuaries that diadromous species make the physiological adjustments necessary for transitioning between fresh and salt water. Unfortunately, many of these estuarine habitats are under threat. This is only one factor responsible for the dangerous declines in the **populations** of many anadromous species. Others include increasing river pollution that damages critical spawning habitats, the building of dams and other man-made barriers that make the upward migration difficult, and the overfishing of commercially important species. However, the release of young salmon into reclaimed rivers has met with some success, and in some areas special passages for migrating salmon allow individuals to get upstream to the spawning grounds. SEE ALSO Excretory and Reproductive Systems.

populations groups of individuals of one species that live in the same geographic area

Jennifer Yeh

Bibliography

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Withers, Philip C. *Comparative Animal Physiology*. Fort Worth, TX: Saunders College Pub., 1992.

Internet Resources

Oregon Coast Aquarium. <http://www.aquarium.org/education/spotlight/anadromy/anadromy.htm>.

Cell Division

Cell division is the basis of life itself; it is how animals grow and reproduce. When cells divide, two daughter cells are produced from one mother cell. Each new cell has exactly the same genetic material (DNA) as the cell that produced it.

Cellular division has three main functions: (1) the reproduction of an entire unicellular organism, (2) the growth and repair of tissues in multicellular animals, and (3) the formation of **gametes** (eggs and sperm) for sexual reproduction in multicellular animals. The process of **mitosis** produces identical cells for the first two functions listed above; the process of meiosis forms gametes.

gametes reproductive cells that only have one set of chromosomes

mitosis a type of cell division that results in two identical daughter cells from a single parent cell

Cellular division has two steps. First, the genome is divided up inside the nucleus by either mitosis or meiosis. Second, the **cytoplasm** (the rest of the content of the cell) is divided. The cell is actually split in two in a process called cytokinesis, in which the cellular membrane is pinched in the middle like a balloon squeezed in the center.

cytoplasm fluid in eukaryotes that surround the nucleus and organelles

Most of the life of a cell is spent growing and replicating DNA. This phase in the cell cycle is called interphase. Cells grow with materials produced from within the cell, using specialized structures called **organelles**. Before cell division takes place, the entire genome (the genetic material) has been copied, and there are now two complete copies in the cell nucleus.

organelles membrane-bound structures found within a cell

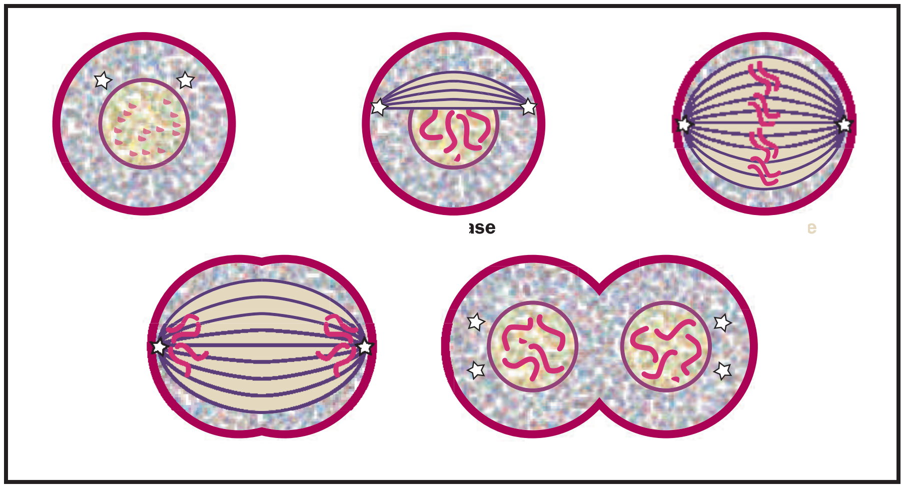
Diploid eukaryotes have two copies of DNA on two sets of chromosomes. The DNA of eukaryotic animals is packaged into chromosomes. Chromosomes come in pairs. Like pairs of shoes, they are almost the same but with slight variations. Humans have forty-six chromosomes, or twenty-three pairs. When DNA is replicated before the cell divides, each chromosome has two identical copies of DNA called sister chromatids. Sister chromatids can be compared to two left and two right shoes.

Mitosis

Mitosis is the process of cellular division that produces identical daughter cells from one mother cell. In single-cell organisms like protists, mitosis produces two whole organisms. In multicellular organisms, mitosis is the process by which the animal grows and repairs its tissues.

There are five steps in mitosis.

1. Prophase. The shape of the DNA changes. Other changes take place in the cytoplasm.
2. Prometaphase. Chromosomes start to move because microtubules are attaching to them.
3. Metaphase. Chromosomes line up in the middle of the cell, pulled there by microtubules. Sister chromatids line up on each side of the metaphase plate. This can be compared to putting one left shoe on one side of the plate and one right shoe on the other side of the plate.



The phases of mitosis.

4. Anaphase. Pairs of sister chromatids split and are pulled to opposite sides of the cell by the microtubules. This is like putting the left shoes into different sides of the cell; the same thing happens with the right shoes. At the end of anaphase, there is one complete set of chromosomes on each side of the cell and the sets are identical.
5. Telophase. DNA returns to the state it was in during interphase.

Cytokinesis then divides the rest of the cell, and two identical cells result.

Meiosis

Meiosis is the process of cellular division that produces the gametes which take part in sexual reproduction. Where mitosis produces two daughter cells from one mother cell, meiosis produces four daughter cells from one mother cell. The end products of meiosis, the gametes, contain only half the genome of a organism. This is like each cell ending up with only a single shoe; there are not pairs in these cells anymore. The two gametes fuse to produce a **zygote**. Because each gamete has half the genetic material of the mother cell, this **fusion** results in a zygote with the correct amount of genetic material.

zygote a fertilized egg

fusion coming together

There are two stages in meiosis, meiosis I and meiosis II. There are five steps in meiosis I.

- Interphase I. Chromosomes replicate, resulting in two identical sister chromatids for each chromosome.
- Prophase I. Chromosomes change shape. Homologous pairs of chromosomes, each with two sister chromatids, come together in a process called synapsis. This tetrad of chromatids is joined in several places, called chiasmata, and crossing-over occurs.
- Metaphase I. Tetrads line up on the metaphase plate, still joined.
- Anaphase I. Homologous chromosomes split apart. Sister chromatids remain together. Microtubules pull each homologue to opposite sides of the cell. This is like putting the left shoes on one side and the right shoes on the other.
- Telophase I and Cytokinesis. The cell divides. Each cell contains a pair of sister chromatids.

Meiosis II is similar to mitosis—sister chromatids split apart into new cells—and the same steps occur in the same order. Pairs of chromosomes were split in meiosis I, and sister chromatids are split in meiosis II. Meiosis II results in four separate chromosomes (two pairs of sister chromatids), each packaged separately. Crossing-over produces slight variations among all four cells. These four cells are gametes, either eggs or sperm.

Laura A. Higgins

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Griffiths, Anthony J. F., Jeffrey H. Miller, David T. Suzuki, Richard C. Lewontin, and William M.Gelbart. *An Introduction to Genetic Analysis*, 6th ed. New York: W. H. Freeman and Company, 1996.

Purves, William K., Gordon H. Orians, H. Craig Heller, and David Sadava. *Life: The Science of Biology*, 5th ed. Sunderland, MA: Sinauer Associates Inc. Publishers, 1998.

Cells

All living organisms are comprised of one or more cells. Most animal cells range in size between 10 and 100 micrometers and have several key elements.

The outer layer of a cell, the cell membrane, consists of a **phospholipid** bilayer, which serves primarily as a barrier from the external environment, and integral proteins which function mainly to regulate transport. The cell membrane creates an enclosed space in which the chemical processes, or metabolism, of the cell can occur. It also serves as a gatekeeper for the cell, carefully regulating what passes in and out. For example, nutrients pass in, and metabolic waste passes out.

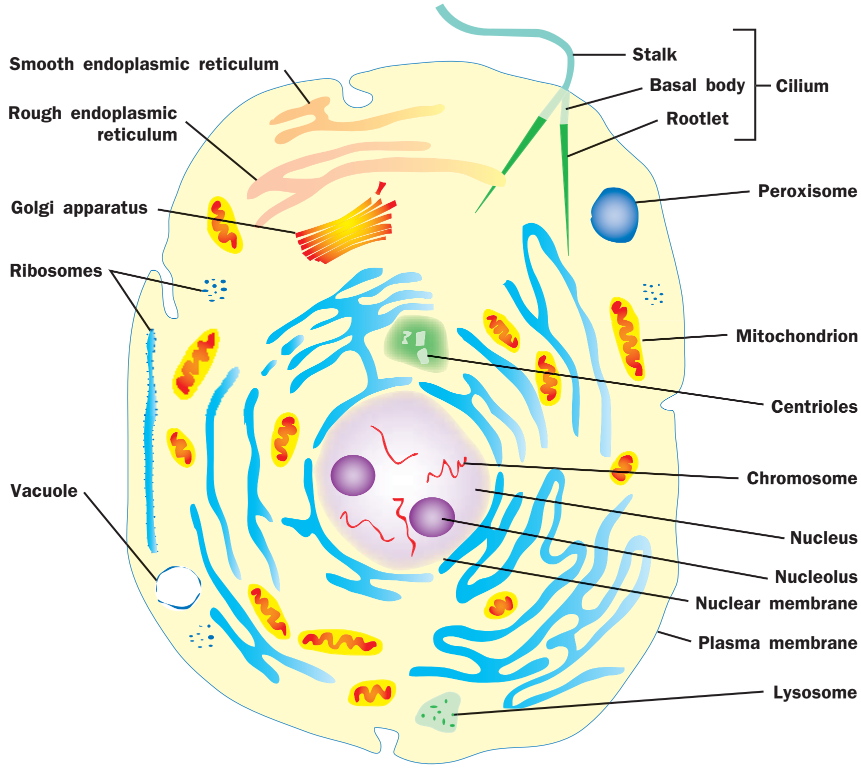
phospholipid molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water

The inside of an animal cell contains several **organelles**, specialized structures that perform specific functions for the cell. These organelles are suspended in a thick aqueous solution, the cytoplasm. The coordinated activity of the organelles is required for the survival of the cell. Many organelles are enclosed by membranes that generate separate compartments within the cytoplasm. One of the most important compartments is the nucleus. The nucleus contains genetic material, which acts as a blue print for the production of the proteins that perform most cellular functions. Protein synthesis is performed by ribosomes and takes place in the cytoplasm. Ribosomes attach to the endoplasmic reticulum (ER) during synthesis of those proteins that are to be exported, incorporated into the membrane, or placed into organelles. These proteins are then shipped from the ER to another compartment, the Golgi apparatus, where they are modified and then shipped to their final destinations. In recycling compartments, known as the lysosomes, old proteins and other molecules are broken down so that their components can be reused. Diverse chemical processes (e.g. the synthesis of the gas Nitric Oxide that functions as an important signal between cells) that produce toxic molecules (peroxides) as side products, take place in specialized chemical compartments of the cell which are called peroxisomes. As

organelles membrane-bound structures found within a cell

Redrawn from *New York Public Library Desk Reference*, 1998.

A TYPICAL ANIMAL CELL



a result, the peroxides can be broken down safely within the peroxisomes without harming the cell.

The transport of cargo between individual compartments through the cytoplasm is the job of transport vesicles, tiny membrane-enclosed compartments that contain the cargo and transport it through the cytoplasm. Every cell produces many transport vesicles, and each type is specialized for a distinct shipping route within the cell, for a kind of cargo, or even for the storage of substances (e.g., **neurotransmitters** for communication between cells).

neurotransmitters chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

The energy for all the chemical processes in the cell is generated in compartments called **mitochondria**, which can be considered the cell's powerhouses. Mitochondria produce ATP, the energy source of the cell, using sugars and oxygen in a process called oxidative phosphorylation.

mitochondria organelles in eukaryotic cells that are the site of energy production for the cell

The shape of cells is maintained by a cytoskeleton, or cell skeleton, made of three membrane-free organelles—microtubules, actin filaments, and intermediate filaments. Together these organelles form a network of molecular cables and struts that stabilizes the cell shape.

In contrast to plant cells, which are further stabilized by a cell wall that surrounds the outer cell membrane, animal cells are stabilized by a cytoskeleton and an extracellular matrix made mostly of **glycoproteins**. However, because they are less rigid, animal cells can change their shape more easily and even use these shape changes to move. Animal cells such as the

glycoproteins organic molecules that contain a carbohydrate and a protein

infection-fighting white blood cells can be sophisticated "crawlers." In the absence of a rigid cell wall, they assemble and disassemble parts of their cytoskeleton in such a way that specific shape changes leading to cell movement will occur. Microfilaments are also responsible for the movement of specific organelles within the cell, and microfilaments and microtubules together are essential for cell division. While microtubules ensure the distribution of duplicated chromosomes to the two daughter cells, the microfilaments will finish the separation of the original cell by pinching in the outer cell membrane.

Whereas in single-celled organisms all life functions are performed by a single cell, in multicellular organisms, such as animals, division of labor and specialization among cells occurs. For example, humans have about 200 different cell types that differ in structure and in function. In all but the simplest animals, the sponges, specialized cells that have a similar structure and function are arranged together into tissues. Although there are many different types of animal cells, scientists group them all into only four general tissue types—epithelial tissue, muscle tissue, nervous tissue, and **connective tissue**. The cells in a tissue may be held together by the extracellular matrix that makes the cells sticky or ties them together.

connective tissue cells that make up bones, blood, ligaments, and tendon

In all animals except sponges and jellyfishes, different tissue types may form a functioning unit called an organ. Organs may also be part of an organ system, such as the digestive system and reproductive system, where several organs function together. Each organ system has a different function, but just like the organelles within an individual cell, the function of each organ system must be regulated and coordinated to ensure the survival of the whole animal. SEE ALSO Cell Division; Homeostasis.

Kathrin F. Stanger-Hall

Bibliography

Barnes-Svarney, Patricia. *New York Public Library Desk Reference*. New York: Macmillan USA, 1998.

Ingber, D. E. "The Architecture of Life." *Scientific American* 278 (1998):48–57.

Rhoades, Rodney, and Richard Pflanzer. *Human Physiology*, 3rd ed. Fort Worth, TX: Saunders College Publishing, 1996.

Rothman, James E. "Budding Vesicles in Living Cells." *Scientific American* 274 (1996):70–75.

Cephalization

Cephalization is the process in animals by which nervous and sensory tissues become concentrated in the "head." The evolution of a head allows scientists to distinguish between the head end, or **anterior** end of an animal's body, and the opposite end, the **posterior**. Although cephalization is associated primarily with **bilaterally symmetrical** species, even some of the more primitive, **radially symmetrical** animals show some degree of cephalization.

anterior referring to the head end of an organism

posterior behind or the back

bilaterally symmetrical describes an animal that can be separated into two identical mirror image halves

radially symmetrical describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

Cephalization evolved several times within the animal kingdom, suggesting that it offers certain inherent advantages. In particular, with the

evolution of cephalization, the anterior end of the animal became most likely to first encounter food, predators, and other important features of the external environment. Because brain and sense organs are also concentrated in the anterior end, the organism is well prepared to deal with these features.

Cephalization in the Animal Kingdom

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

Even hydras, which are primitive, radially symmetrical **cnidarians**, show some degree of cephalization. They have a "head" where their mouth, photoreceptive cells, and a concentration of neural cells are located.

Flatworms (phylum *Platyhelminthes*) are the most primitive animals with bilateral symmetry. They also have a fairly advanced degree of cephalization, with sense organs (photosensory and chemosensory cells) and a brain concentrated at the anterior end. Consequently, scientists believe that cephalization characterized all bilaterally symmetrical animals from their origins. However, flatworms differ from more advanced animals in that their mouths are in the center of their bodies, not at the anterior end.

In arthropods, cephalization progressed with the incorporation of more and more trunk segments into the head region. Scientists believe this was advantageous because it allowed for the evolution of more effective mouthparts for capturing and processing food.

Cephalization in vertebrates, the group that includes mammals, birds, and fishes, has been studied extensively. The heads of vertebrates are complex structures with many features not found in close relatives such as the cephalochordates. The cephalochordate *Branchiostoma* (formerly called *Amphioxus*), which is the closest relative of vertebrates, is a burrowing marine creature which lacks most of the head structures that are so distinct in vertebrates, such as distinct sense organs; a large, multilobed brain; teeth; and a tongue.

There was a persistent debate during the twentieth century as to whether the vertebrate head is "old" or "new." Scientists who champion the idea of an "old" head suggest that the vertebrate head resulted from the evolution of important modifications to a previously existing head. The idea of a "new" vertebrate head was proposed originally by American vertebrate morphologists Carl Gans and Glenn Northcutt in 1983. They suggested that the vertebrate head is a new structure, which has no corresponding structure in close relatives such as *Branchiostoma*.

Evidence to support a "new" vertebrate head comes from the observation that most important features of the head are derived from neural crest cells, embryonic cells found only in vertebrates. The neural crest cells are of **ectodermal** origin—rather than mesodermal or endodermal—and arise during the process of neurulation, the time at which the dorsal hollow nerve cord forms.

ectodermal relating to the outermost of the three germ layers in animal embryos

Neural crest cells are exceptional in that they are highly mobile, migrating in streams throughout the head region and the rest of the body, and because they give rise to an unusual diversity of features. The neural crest cells are responsible for forming the bones of the face and jaws, the structures of the tongue and larynx, the teeth, and portions of the eye. Experi-

Cephalopods—such as this Sepioidea Squid, native to waters near Bermuda—exhibit an advanced degree of cepahalized development with regard to sense organs and brain location.

ments in which the neural crest was removed from developing animals confirmed that these critical head structures failed to develop without it.

Scientists hypothesize that increased cephalization in vertebrates, including the evolution of many of their novel head features, is related to adaptations for predation. Sensory structures—the jaw and large brain—are all requirements for a successful existence as a predator.

Losses of Cephalization

Cephalization has been lost in some groups. One example comes from the echinoderms, the phylum that includes the starfishes and sea urchins. These species have lost bilateral symmetry and returned to a radially symmetrical body plan. However, only adult starfishes and sea urchins are radially symmetrical. The larval stage remains bilaterally symmetrical and is characterized by cephalization. Other echinoderms, the sea cucumbers, have regained bilateral symmetry in the adult. Thus the phylum has been characterized by multiple instances of the acquisition and loss of bilateral symmetry and cephalization.

Mollusks represent another group in which cephalization has been lost and regained. For example, **bivalves** are not particularly cephalized (although some scientists have argued that they are "all head"). However, as with the echinoderms, certain mollusks regained cephalization. In particular, the appropriately named cephalopods (the group that includes the squid and octopus) are characterized by an advanced degree of cephalization. Their sense organs, including well-developed eyes and a brain, are concentrated in a distinct head region. Interestingly, as with vertebrates, the evolution of an advanced degree of cephalization in cephalopods was associated with the evolution of a predatory lifestyle.

bivalves mollusks that have two shells

The Origin of the Head

Although cephalization appears to have evolved multiple times, in the last ten years molecular biological work implies that the distinction between head and the rest of the body may actually be quite ancient. In particular, certain genes expressed only in the head region appear to determine the

boundary between head and trunk. These genes are present in diverse animal phyla, including arthropods, chordates, and annelids (other groups have yet to be studied). This broad distribution of the multiple genes indicate that they may have been present in the common ancestor of most animals. Studies of the hydra have shown that it too possesses some of these same genes, suggesting that the distinction between head and trunk is rather ancient in the animal kingdom because the hydra is a member of a primitive lineage (the cnidarians). SEE ALSO BODY PLAN.

Jennifer Yeh

Bibliography

Gould, James L., and William T. Keeton, with Carol Grant Gould. *Biological Science*, 6th ed. New York: W. W. Norton & Co., 1996.

Hickman, Cleveland P., Larry S. Roberts, and Allan Larson. *Animal Diversity*. Dubuque, IA: William C. Brown, 1994.

Hildebrand, Milton, and Viola Hildebrand (ill.). *Analysis of Vertebrate Structure*. New York: John Wiley & Sons, 1994.

Cephalochordata

notochord a rod of cartilage that runs down the back of chordates

lancelet a type of primitive vertebrate

brackish a mix of salt water and fresh water

The cephalochordates are the closest living relatives of the vertebrates. The group derives its name from the **notochord** that extends far forward into the head (farther than the brain, in contrast to vertebrates). The most famous representative of the group is *Branchiostoma lanceolatus* (also known as *Amphioxus*, or **lancelet**). There are about twenty-five living species of cephalochordates. All adults are small, fishlike animals that are rarely longer than 5 centimeters (2 inches). Cephalochordates live in shallow marine or **brackish** water all over the world. They can actively swim around, but most of the time are sedentary, buried in sand.

Swimming and burying are accomplished through an interaction between the notochord (stabilizing element and anchor point for muscles) and large blocks of muscle segments along the body wall. Unlike the vertebral column of vertebrates, the notochord is an elastic, flexible rod. It prevents the body from shortening when the muscles contract, causing it to bend sideways instead. This creates an undulating (wavy) body movement much like that of fishes. However, poor fin development makes cephalochordates relatively inept swimmers, and as a consequence they spend most of their time (except when they disperse and reproduce) buried in sand with only their front end exposed.

pharyngeal having to do with the tube that connects the stomach and the esophagus

When they are buried, their head sticks out to filter out food particles from the water. In this process, water is driven through the mouth opening into the mouth cavity and back out into the environment through **pharyngeal** gill slits. In the process, food particles suspended in the water are caught in a sheet of mucus that covers the inside lining of the pharyngeal slits. Cephalochordates may have up to 200 pharyngeal gill slits, making their filter feeding very efficient. The slits are separated from one another by so-called gill bars, which are supported by cartilage rods. During the evolution of vertebrates (about 500 million years ago) from a cephalochordate-like ancestor, these cartilage rods eventually gave rise to the jawbones of vertebrates.

Cephalochordates have a closed circulatory system (the blood is enclosed in blood vessels) but lack a central pump (heart). Instead, the blood is propelled by pulsation (rhythmic contraction and relaxation) of several blood vessels. The blood contains no pigments or cells and is thought to function largely in nutrient distribution rather than in gas exchange and transport. The central nervous system of the cephalochordates is very simple. A dorsal nerve cord extends through the length of the body, giving rise to segmentally arranged nerves. No brain is detectable. The skin is rich in sensory nerve endings that probably help produce a sense of touch and are important for burrowing. A number of cephalochordates have some photosensors near the front and back ends of their body, but in general (unlike vertebrates) they lack any eyes or organs to sense gravity.

Cephalochordates reproduce by releasing their eggs and sperm into the water, where they are fertilized externally. The fertilized eggs develop into free-swimming larvae that drift in the water for up to 200 days, feeding on plankton and other suspended matter, before settling down as adults. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Kathrin F. Stanger-Hall

Bibliography

Alexander, R. McNeill. *The Chordates.* New York: Cambridge University Press, 1975.

Brusca, Richard C., and Gary J. Brusca. *Invertebrates.* Sunderland, MA: Sinauer Associates, 1990.

Kluge, Arnold G. *Chordate Structure and Function*, 2nd ed. New York: Macmillan Publishing, 1977.

Cestoda

The class Cestoda consists of long, flat, ribbonlike worms that are commonly called tapeworms. Tapeworms are **obligatory parasites**, ones that cannot survive independent of a host, that live in the intestines of vertebrate hosts. They form an extremely varied group, and nearly every vertebrate species is associated with a different parasitic cestode. Most cestodes make use of one or more intermediate hosts to bring them into the body of the ultimate host. Some cestodes can achieve impressive lengths—worms of up to 15 meters (50 feet) have been observed.

obligatory parasites an animal that can only exist as a parasite

Characteristics of Cestodes

All tapeworms share a body plan. At the front end is a head region called the scolex. The scolex maintains a hold on the host's digestive tract and has many suckers and hooks for this purpose. The scolex also contains the tapeworm's sense organs, which consist primarily of cells sensitive to touch and chemical stimuli, as well as the modest concentration of nervous tissue that makes up the tapeworm brain.

The scolex is followed by a short neck region and a trunk, which is divided into a series of segments known as proglottids. New proglottids are produced in the neck region. As these form, older proglottids are pushed back toward the rear of the animal. The proglottids house the reproductive organs, which mature gradually as proglottids move to the back.

The scolix, or head region, of an adult pork tapeworm. The scolix is used to hold onto the host's digestive tract; it also contains the tapeworm's sense organs.

Tapeworms are **hermaphroditic**, so that each proglottid includes both male and female **gonads** and generates both sperm and eggs. A tapeworm can reproduce sexually, either through self-fertilization or cross-fertilization with another tapeworm, or asexually, by breaking off proglottid segments at the end of the trunk. These reproductive traits are admirably adapted to reproduction in an environment (in the body of a host) in which worms are not guaranteed to encounter individuals of the same species.

Proglottids and fertilized eggs exit the host's digestive tract along with the host's excrement. In most tapeworm species, eggs or proglottids are first ingested, or taken in, by an intermediate host, often an arthropod or a different vertebrate species. The cestode may develop into a larval form or may become temporarily dormant within the intermediate host. The ultimate host becomes infested with the cestode when it consumes an infested intermediate host.

Because of the cestodes' parasitic lifestyle, certain organ systems are unnecessary. The most obvious of these is the digestive tract, which is absent from the group. Because cestodes live in an environment that is not only rich in nutrients, but one in which the nutrients are already well processed, further digestion is unnecessary. Instead, food absorption occurs over the entire surface of the cestode body, in an ectodermal, or skin, layer known as the integument. The integument is covered with tiny projections called mitotrichia, which increase the surface area available for absorption.

hermaphroditic having both male and female sex organs

gonads the male and female sex organs that produce sex cells

Subclasses of Cestodes

Cestodes are divided into two subclasses, Cestodaria and Eucestoda. Cestodaria is a small subclass of relatively small tapeworms that are parasites to elasmobranch fishes (sharks, rays, and chimeras). The trunks of cestodarians are not segmented into proglottids. The rear of the body includes a small sucker. Eucestoda is a much more diverse group, and includes all other cestodes. Eucestodes are characterized by the presence of proglottids. SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

Bibliography

Brusca, Richard C., and Gary J. Brusca. *Invertebrates.* Sunderland, MA: Sinauer Associates, 1990.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton and Co., 1996.

Hickman, Cleveland P., Larry S. Roberts, and Allan Larson. *Animal Diversity.* Dubuque, IA: Wm. C. Brown, 1994.

Chitin

Chitin is a major constituent of the exoskeleton, or external skeleton, of many arthropods such as insects, spiders, and crustaceans. Exoskeletons made of this durable and firm compound support and protect the delicate soft tissues of these animals, which lack an internal skeleton. Chitin is a **polysaccharide**, a type of carbohydrate that has a basic structure of a repeating chain of sugar molecules. Chitin is analogous in structure to cellu-

polysaccharide a class of carbohydrates that break down into two or more single sugars

The exoskeleton of the Cayman Islands stone crab is made up, in part, of the polysaccharide chitin.

lose, the compound that provides structural support to plant tissues. In addition to being found in arthropod exoskeletons, chitin is also found in the cell walls of some species of fungi.

Chitin does not work alone in forming exoskeletons. It is associated with a number of proteins, including an elastic, rubberlike substance called resilin. The identity and nature of these proteins determines whether the exoskeleton will be rigid, like a beetle's shell, or soft and flexible like the joints of a crab leg. Chitin also associates with nonprotein compounds, such as the calcium carbonate that is part of the shells of crustaceans such as crabs, lobsters, and shrimp.

Animals that wear their skeletons on the outside are relatively inflexible because of their armor rigidity. Arthropods can bend their limbs or the segments of their body only at the joints, where the exoskeleton is thinner. Therefore, it is important that the composition and character of the exoskeleton complement the anatomy it covers and the overall ecology of the organism.

Chitin confers a number of protective benefits to animals with exoskeletons. As well as defining the basic shape of the animal, the tough shell that encases arthropods protects the wearer from **dessication**, or dehydration. This particular function is essential to terrestrial arthropods, which may perish if too much water is lost from their blood and body tissues. Shells also provide effective protection against some predators.

dessication drying out

Chitinous exoskeletons must be molted, or shed, as the animal grows because the rigid shell does not expand with the rest of the body. After the old shell is cast off, a new, larger exoskeleton is secreted by glands in the epidermis. Newly molted individuals are particularly vulnerable to attack because they have little protection while they wait for their new shells to harden.

chitinous made of a complex carbohydrate called chitin

Exoskeletons would be impractical for larger animals because chitin is not strong enough to protect and support them. Land-dwelling invertebrates, who do not benefit from the buoyant support of water, are limited in size because as an exoskeleton gets larger, it becomes thicker and heavier. These animals would not be able to move very well under the weight of this protective armor. SEE ALSO Bone; Keratin.

Judy P. Sheen

Bibliography

Anderson, D. T. *Atlas of Invertebrate Anatomy.* Portland: International. Specialized Bood Service, 1997.

"Chitin." *The New Columbia Encyclopedia.* Eds. William H. Harris and Judith S. Levy. New York: Columbia University Press, 1975.

Pierce, Sidney K., Timothy K. Maugle, and Lois Reid. *Illustrated Invertebrate Anatomy: A Laboratory Guide.* New York: Oxford University Press, 1989.

Chondrichthyes

The class Chondrichthyes consists of the cartilaginous fishes, including sharks, batoids (rays, skates, guitarfish, and sawfishes), and chimaeras, or ratfishes. A diverse group comprising more than 700 species, Chondrichthyans are found throughout the world's oceans and in some freshwater environments. The group as a whole is characterized not by mineralized bone but by a skeleton of soft, flexible **cartilage** lined with hard tissue. Chondrichthyans lack the air-filled swim bladder found in most bony fish, and therefore must swim continuously to stay afloat. Buoyancy is assisted by light oils in the liver, which can comprise up to 25 percent of a shark's total body weight.

cartilage a flexible connective tissue

Chondrichthyan males have a pelvic clasper, a specialized organ used in mating. Unlike most bony fishes, all chondrichthyans have internal fertilization. Reproduction can be **oviparous** (laying eggs, notably the "mermaid's purses" found on beaches), **viviparous** (live-bearing), or **ovoviviparous** (eggs carried within the mother).

oviparous having offspring that hatch from eggs external to the body

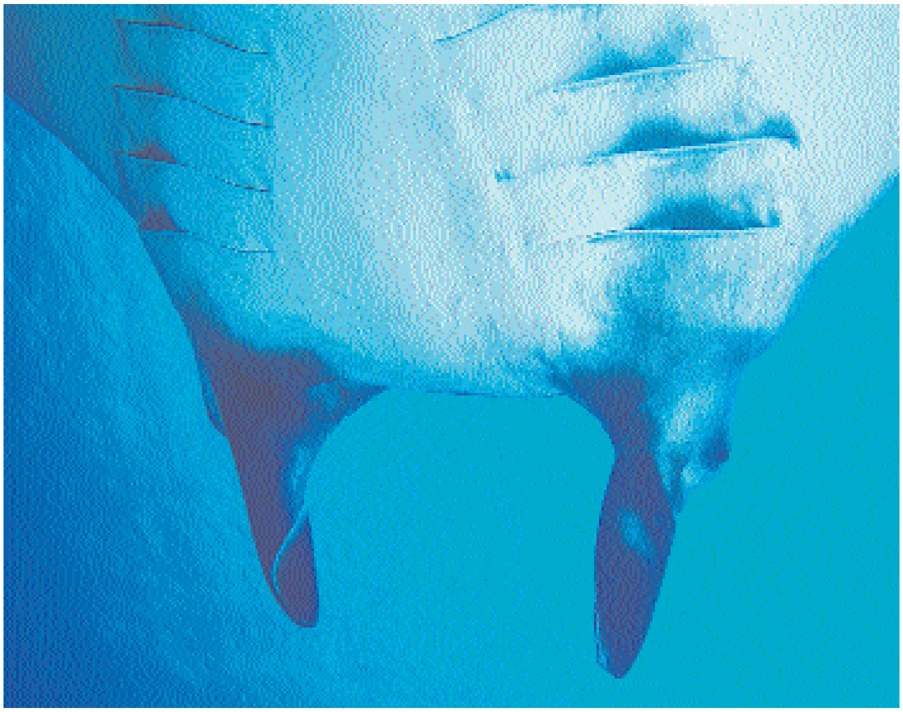
viviparous producing living young (instead of eggs) that were nourished by a placenta between the mother and offspring

ovoviviparous having offspring that hatch from eggs retained in the mother's uterus

placoid scales scales composed of three layers and a pulp cavity

The physiology of Chondrichthyan is of interest to cancer researchers because the cartilage of chondrichthyans contains substances known to inhibit the growth of tumors, and cancer is extremely rare in sharks. The group is characterized by **placoid scales** (also called dermal denticles, or skin teeth), with a structure similar to teeth consisting of an outer enamel layer, dentine, and an inner pulp cavity. As the animal grows, the skin surface is expanded by the addition of more scales rather than by the growth of individual scales. The teeth themselves are simply modified placoid scales; sharks have several rows of teeth, with replacement teeth always developing behind the frontmost rows of functional teeth. In some species, an individual can shed more than 30,000 teeth in its lifetime.

These fishes are often thought of as primitive compared to bony fishes and land-based vertebrates. Many chondrichthyans, however, have evolved sophisticated adaptations that have made them successful predators over a wide range of habitats. The senses of active predators, including many sharks,



The Atlantic manta ray, a member of the Chondrichthyes batoid subgroup. Manta rays are the largest rays, attaining widths of about 7 meters (23 feet).

are especially well developed. A keen sense of hearing allows sharks to locate prey from as far away as 250 meters (800 feet). They are particularly sensitive to low-frequency vibrations such as those emitted by injured animals. Sound is detected through the ears and through the **lateral line**, a series of fluid-filled canals along the head and sides of the body that contain sensory cells sensitive to vibrations. As in many **nocturnal** mammals, the inside of a shark's eye is covered with a **tapetum**, a membrane that reflects light back into the eye, making it easier to see in dim light. Unlike most fishes, sharks can reduce and expand their pupils. In some species, the eyes are protected during feeding by the nictitating membrane, a structure similar to an eyelid. The Elasmobranchi group has external nostrils on the lower side of the body; because of them, sharks can detect tiny concentrations of substances such as blood, which allows them to scent prey from distances of several hundred feet. Finally, sharks can detect electrical signals via the ampullae of Lorenzini, which are specialized organs distributed over a shark's head that detect changes in electrical currents. Sharks use these to sense the electrical fields emitted by the heart and muscles of their prey.

lateral line a row of pressure sensitive sensory cells in a line on both sides of a fish

nocturnal active at night

tapetum a reflective layer in the eye of nocturnal animals

The class Chondrichthyes includes two major groups: the Elasmobranchi (sharks, skates, and rays) and the Holocephali (chimaeras or ratfishes). Elasmobranchs are further divided into selachians (sharks) and batoids (rays and their relatives). The earliest evidence of Chondrichthyes in the fossil record is from the Devonian, the so-called Age of Fishes, from 350 to 400 million years ago.

Selachians (Sharks)

There are approximately 350 species of sharks. They are characterized by a heterocercal tail (the upper half being longer than the lower half), five to seven gill slits for respiration, and a rounded body tapered at both ends.

Sharks are among the most misunderstood of all creatures. Popular culture has exaggerated beyond reason the danger posed by sharks to humans. The California coastline, with a high density of both human and great white shark populations, averages only one shark-related fatality every eight years. There is little evidence that sharks prey on humans for food. A disproportionate number of shark attacks occur near seal and sea lion rookeries, and surfers, whose paddling resembles the behavior of a seal on the surface, are more likely to be attacked than scuba divers. These factors indicate that sharks may be mistaking humans for seals or other large marine prey. Spearfishers carrying wounded fish are also at greater risk of shark attack; the vibrations of a thrashing fish may attract sharks, so one's catch should always be immobilized. Over half of total shark attacks appear to be misdirected territorial or courtship displays, with a characteristic motion preceding the attack: the shark shakes its head from side to side and swims back and forth erratically, with its head pointed up. Most sharks that attack humans are mackerel sharks, including the great white sharks (*Lamnidae*) and requiem sharks (*Carcharhinidae*); sharks in these families feed on large fish or marine mammals. Requiem sharks include the tiger shark and the bull shark, which feed primarily on other sharks. Hammerhead sharks (*Sphyrnidae*) specialize in attacking stingrays.

CHIMAERAS, OR RATFISHES

Chimaeras—also knows as ratfishes—possess unusually large heads with deep, well-developed eyes. They also have a mouth that resembles a rabbit's inside which rest grinding, plate-like teeth.

The plankton-feeding whale sharks (*Rhincodontidae*) are the world's largest fishes, with lengths of up to 18 meters (60 feet). Other huge plankton feeders include the aptly named megamouths (*Megachasmidae*) and basking sharks (*Cetorhinidae*). These sharks swim with their mouths open, straining plankton through modified structures associated with the gills.

While the larger sharks are better known to the general public, smaller species are far more diverse and abundant. The *Squalidae* include the spiny dogfish, which feeds mainly on invertebrates; it is a favorite candidate for inclusion in a fish and chips dinner and for classroom dissection. Another member of the *Squalidae*, the diminutive (four-inch) cookie-cutter shark, apparently uses the light-producing organs arrayed around its body to mimic a school of small fish. This attracts large fish, which the cookie-cutter shark then attacks, cutting out a round portion of flesh with specially modified teeth. Saw sharks (Pristiophoridae) use a long snout lined with sharp teeth to slash their way through schools of fish; they then return to feed on wounded fish and any detached pieces they may find. The angel shark (*Squatinidae*) resembles a ray but can be distinguished by gill openings on the side of the head rather than on its bottom and by the fact that the pectoral fins are not attached to the side of the head as they are in batoids.

Batoids (Rays, Skates, Guitarfishes, and Sawfishes)

The 470 species of this diverse group of fishes have in common a flattened body with expanded pectoral fins fused to the head (the "wings" in rays). Batoids are distributed throughout the world's oceans and in some tropical freshwater environments.

Sawfish (*Pristidiformes*) can exceed 7 meters (23 feet) in length; they have a long snout lined with sawlike teeth and capture prey like the saw sharks described above. Guitarfish or shovelnose rays (*Rhinobatiformes*) are characterized by a long, thick body and relatively narrow pectoral fins; they feed mainly on invertebrates on the sandy bottom. Skates (*Rajiformes*) are found mostly in deep water; they, too, feed on invertebrates and are distinguished by a series of thorns on the tail.

The order Myliobatidiformes contains several types of ray. The large eagle rays (*Myliobatidae*) have strong, muscular pectoral fins for rapid swimming. Manta rays (*Mobulidae*) are the largest rays, attaining widths of about 7 meters (23 feet); like the largest sharks, they bear specialized mouthparts for feeding on plankton. Stingrays (*Dasyatididae*) have a tail ending in a flexible, whiplike section that is equipped with one or more poisonous spines. Persons wading on a sandy bottom, particularly in calm water, often run the risk of stepping on a stingray and being stung as a result; one should always shuffle one's feet while walking on a sandy substrate. These animals almost never sting unless provoked; attack is often preceded by a warning stance where the tail is brought forward over the body.

Torpedo rays (*Torpediniformes*), also known as electric rays or numbfishes, have evolved modified muscles that function as electric organs. The largest electric rays can produce up to 200 volts of electricity in a single discharge. Several species are found exclusively in fresh water.

This bottom dweller ratfish surveys pieces of the Titanic wreckage, most likely looking for its next meal of mollusks.

Holocephalans (Chimaeras, or Ratfishes)

The approximately twenty-five species of ratfishes are mostly bottom dwellers in some of the deeper marine habitats. They feed primarily on mollusks and other invertebrates in the substrate, crushing hard shells with their flat teeth. Ratfishes are characterized by a large head and eyes and by a long, slender tail. They have an **operculum**, a hard, bony layer of tissue covering the gills, found in many bony fishes but absent in all other chondrichthyans. SEE ALSO Phylogenetic Relationships of Major Groups.

operculum a flap covering an opening

Gil G. Rosenthal

Bibliography

Allen, Thomas B. *Shadows in the Sea: The Sharks, Skates, and Rays.* New York: Lyons and Burford Publishing, 1996.

Hamlett, William C., ed. *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes.* Baltimore, MD: Johns Hopkins University Press, 1999.

Moyle, Peter B. *Fish: An Enthusiast's Guide.* Berkeley: University of California Press, 1993.

Moyle, Peter B., and Joseph J. Cech Jr. *Fishes: An Introduction to Ichthyology*, 3rd ed. Upper Saddle River, NJ: Prentice-Hall, 1996.

Parker, Steve, and Jane Parker. *The Encyclopedia of Sharks.* Willowdale, Ontario, Canada: Firefly Books, 1999.

Perrine, Doug. *Sharks and Rays of the World.* Stillwater, MN: Voyageur Press, 1999.

Chordata

Human beings are chordates—of the phylum chordata—and so are all other vertebrates, or animals with a spinal column. In addition, there are two invertebrate groups of chordates: the urochordates and the cephalochordates.

The Urochordata (e.g., tunicates) and Cephalochordata (e.g., lancelets) were the earliest chordates to evolve, and they provide a link between invertebrate and vertebrate animals. However, as different as these organisms are from each other and from vertebrate chordates, they all share the following characteristics that identify them as chordates (and distinguish them from all other invertebrate animals): a notochord, a dorsal hollow nerve cord, and pharyngeal gill slits. Many adult vertebrates have no notochord or pharyngeal gill slits, but these structures can nevertheless be found in their embryos.

The notochord is a long, elastic rod that provides structural support to the chordate body. In cephalochordates it prevents the body from shortening when muscle fibers in the body wall draw together, causing a bending from side to side and propulsion of the animal. In most vertebrates (except some fishes), bony vertebrae develop around the nerve cord and the notochord, and the vertebral structures largely replace the notochord in most adult vertebrates. However, some adult vertebrates may retain remnants of the notochord (e.g., the gelatinous disks between the vertebrae of humans). The dorsal hollow nerve cord is a key element of the chordate nervous system and is present in all chordates. In vertebrate embryos it develops into the **spinal cord** and the brain.

spinal cord thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

The pharyngeal pouches with gill slits originally evolved as filter-feeding devices and can still be found as such in invertebrate chordates. During some point in their development all chordates still exhibit them. However, among the vertebrates only fish retain pharyngeal gill slits as adults. The cartilage-based rods that support the gill bars (the solid areas between the gill slits) in invertebrate chordates gave rise to the vertebrate jaw during vertebrate evolution, completely changing the feeding method in this group of animals. Subsequently, some of the bones in the vertebrate jaw evolved into middle-ear bones in amphibians, reptiles, birds, and mammals; these bones assisted in the transmission of sound and hearing when early vertebrates moved from life in the water onto land.

The first chordates appear as fossils in rocks from the Cambrian period. These rocks are approximately 570 million years old.

Vertebrates differ greatly from other chordates in size and activity level, and the evolution of their distinctive characteristics is largely correlated with this difference. Vertebrates actively move around looking for food. This led to the concentration of sense organs at the front end of the body and an accumulation of nerve cells (i.e., a brain) to process all the sensory information. The need for more efficient movement led to the evolution of a stronger support system (vertebral column), a bony skeleton, and four limbs to support the body on land.

Today the vertebrates, with nearly 43,000 living species, are the most diverse group of all chordates. All vertebrate species can be grouped into seven different classes: Agnatha (jawless fishes), Chondrichthyes (cartilaginous fishes), Osteichthyes (bony fishes), Amphibia (amphibians), Reptilia (reptiles), Aves (birds), and Mammalia (mammals). SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Kathrin F. Stanger-Hall

Bibliography

Alexander, R. McNeill. *The Chordates.* New York: Cambridge University Press, 1975.

Brusca, Richard C., and Gary J. Brusca. *Invertebrates.* Sunderland, MA: Sinauer Associates, Inc., 1990.

Kluge, Arnold G. *Chordate Structure and Function*, 2nd ed. New York: Macmillan Publishing, 1977.

Walker, Warren F. *Functional Anatomy of the Vertebrates: An Evolutionary Perspective.* Philadelphia: Saunders College Publishing, 1987.

Circadian Rhythm

The circadian rhythm describes the internal biological clock that controls an organism's daily activity cycles. It is well-known that in many species, activity does in fact follow daily patterns. This applies to activities such as feeding or sleeping, as well as to physiological attributes such as metabolic rate, body temperature, blood pressure, and **hormone** levels. Most animal and plant species have daily rhythms and even fairly simple creatures like bacteria have been known to have natural daily cycles.

hormone a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

Experiments in which organisms are placed in constantly light or constantly dark environments frequently indicate that daily periodicity in activity patterns persists even when the normal day-night cues from sunlight are removed. These circadian rhythms are important in allowing for the timing of important daily activities.

Circadian Cycles

Circadian rhythms typically describe a twenty-four-hour cycle that corresponds to the length of the day on Earth. However, for almost all species, the "natural" cycle is either a little shorter or a little longer than twenty-four hours. This explains the origin of the term "circadian" rhythm: *circa* means "about" and *diem* refers to "day." Thus, circadian means "about a day."

Changing light cues from the external environment allow organisms to adjust their natural body clocks and conform to a twenty-four-hour day. Research on circadian rhythms in humans has shown that the human body naturally drifts toward a twenty-five-hour cycle in constant-light conditions.

The ways in which circadian rhythms are controlled vary among biological organisms. In many vertebrate species, circadian rhythms are controlled by the hormone melatonin. Melatonin production follows a daily cycle, high during the night hours and low during daylight hours. (Because increased levels of melatonin production cause sleepiness, it is sometimes used as a sleeping aid.) Melatonin is produced by endocrine cells in the pineal gland, which is located in the central part of the brain. Ultimately, melatonin cycling responds to light cues from the environment.

In some species, such as certain fishes and lizards, a minute hole in the otherwise bony skull allows light to pass directly to the pineal gland. In this way, the pineal gland receives direct information from the external environment on day-night cycles. However, direct exposure of light to the pineal gland is not necessary. In birds, photoreceptors in the eyes as well as in the brain are responsible for transmitting signals to the part of the brain that controls circadian rhythms.

In mammals, the eyes alone appear to be responsible for photoreception related to circadian cycles. This involves a special pigment (a light-absorbing molecule) called crytochrome that is present in mammalian eyes. Crytochrome is distinct from the pigments that are responsible for vision, and is also found in a different part of the retina. In certain cases of blindness, the circadian rhythm is not disrupted because the parts of the retina that contain crytochrome are intact.

Patterns of long- and short-term hibernation—exhibited here by a nesting dormouse—are often the product of circadian rhythm, an internal "biological clock" that controls many organisms' activity cycles.

Problems Linked to Circadian Rhythm

Circadian rhythms impact everyday human life in many ways.

Jet lag. Jet lag, which can be the result of travel across several time zones, is caused by discrepancies between an individual's internal clock and signals provided by the external environment. The body generally adjusts to jet lag over the course of a few days as it is exposed to daylight patterns in the new time zone. Working the night shift can also be problematic for humans, because humans are naturally **diurnal**, that is, active during the day and asleep at night. Data indicate that the majority of industrial accidents occur at night, when the body is programmed to slow down in preparation for sleep.

diurnal active in the daytime

Seasonal affective disorder (SAD). Seasonal affective disorder (SAD), which can result in extreme depression during the winter months, may also be related to the operation of circadian clocks. SAD strikes when the days are short and light is scarce. SAD is particularly common at high latitudes, where the days are particularly short during the winter. Short light cycles are likely to disrupt the circadian clock, although the link to depression has not been demonstrated. Regular exposure to artificial bright lights is often effective in treating SAD.

Sleep disorders. Certain sleep disorders, not surprisingly, are related to problems with circadian rhythms. Older people, for example, produce less melatonin. This may be linked to the sleeping patterns associated with age, such as insomnia, early rising, and sleepiness during the day. Delayed sleep phase syndrome (DSPS), which has also been linked to old age, is a more serious problem that causes people to want to sleep from early morning to noon, instead of during more typical night hours.

Circadian rhythms are only one example of the broader category of biological rhythms. Biological rhythms range widely in duration, with circadian rhythms being among the shortest. Other biological activities follow longer cycles, such as lunar cycles, or even periods of several months or a year. The menstrual cycle and seasonal mating activity are examples of processes that occur cyclicly, but over a longer time period. SEE ALSO DIURNAL; NOCTURNAL.

Jennifer Yeh

Bibliography

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Withers, Philip C. *Comparative Animal Physiology*. Fort Worth, TX: Saunders College Publishing, 1992.

Circulatory System

Every living organism on Earth, from amoebas to redwoods to whales, has a circulatory system—a means of gathering and transporting nutrients and collecting and removing waste products.

Plants have an elegant system of strawlike tubes called phloem and xylem, which stretch from the roots to the topmost leaves. Stomata, tiny evaporative holes in the leaves, create suction that steadily draws water up the xylem from the roots, allowing plants hundreds of feet tall to circulate nutrients without a pump.

All cells of the simplest animals, such as single-celled amoebas and multicellular flatworms, are close to the surface. In these cells, nutrients wash through the cell fluid, and wastes pass out through a porous outer membrane between the cell and its environment. The cells of larger animals are buried many layers deep, so these animals require a system that connects each cell to the outer world. This system, which consists of the fluid that carries nutrients through vessels that reach every part of the body and the mechanism that powers the flow of nutrients, is called the circulatory system.

The simplest form of circulatory system is an open circulatory system. In an open circulatory system, blood flows through a network of open tubes and hollow spaces, and the movement of the animal itself keeps the blood flowing. In more complex systems, blood is pumped through the body by contractions of the blood vessels. Invertebrates, such as insects and other **arthropods**, have a central blood vessel that runs down the length of the back. A series of bulbous pumping centers slowly squeeze the blood through a maze of hollow spaces around the body past all the organs.

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

Vertebrates, including amphibians, reptiles, birds, and mammals, have increasingly complex, closed circulatory systems. Closed circulatory systems consist of an intricate network of vessels filled with blood that delivers nutrients, regulates internal temperature, and takes away waste products. The system is powered by the heart, a muscular pump that never stops working, which continually circulates the blood through the body.

A radiograph of a normal coronary artery. The elastic walls of the arteries stretch open to allow the blood to flow in, then squeeze back together to force it along.

lungs sac-like, spongy organs where gas exchange takes place

hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

antibodies proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

In all vertebrates, the heart is made of involuntary muscle tissue, but the structure is very different in each group. Fish have a two-chambered, single-pump heart. Amphibians have a three-chambered heart that also acts as a single pump. Birds and mammals have a more sophisticated four-chambered, double-pump heart design. One chamber sends blood to the **lungs** to be purified and reoxygenated, the other sends the enriched blood out into the body. Interestingly, the human embryo goes through every stage of circulatory development, from a passive single-celled heart to a two-, three-, and four-chambered heart.

In adult humans, the circulatory system consists of blood, the heart, and a network of vessels through which the blood travels. Blood is plasma (a watery liquid) that contains billions of molecules of sugars, proteins, **hormones**, **antibodies**, and gases. The heart is a strong, muscular, double pump that pushes the blood continuously and automatically around the body through roughly 100,000 kilometers (62,000 miles) of arteries, veins, and capillaries. It takes the blood about one minute to complete a circuit around the body, and this happens about 1,000 times a day.

The human circulatory system has two loops. The shorter pulmonary circulation goes from the lower-right chamber of the heart (the ventricle) through the pulmonary artery to the lungs and back to the upper-left chamber (the atrium) through the pulmonary vein. From there, the newly oxygenated blood descends into the left ventricle through a one-way valve and is pumped into the longer systemic circulation through the main artery of the body, the aorta. The spent blood travels back to the right atrium in two main veins. The superior vena cava drains the upper body, the head, neck, and arms. The inferior vena cava handles the lower body. From the right atrium, the blood flows through the relaxed one-way valve into the right ventricle. Then another pulse of the powerful heart muscle closes the valve and spurts the blood into the pulmonary artery, beginning the cycle again. The sound known as the heart "beat" is the sound of the valves between the atria and ventricles and between the ventricles and arteries as they snap shut to keep the blood from flowing backward.

A healthy, relaxed, adult heart beats about seventy times a minute, pumping blood under high pressure into the thick-walled arteries. The elastic walls of the arteries stretch open to allow the blood to flow in, then squeeze back together to force it along. Arteries branch into narrower and more muscular arterioles. Arterioles branch into finer and finer capillaries, thin-walled, hairlike vessels that interact with surrounding body cells to exchange nutrients and wastes. Capillaries then enlarge into venules, which merge into veins, and carry the spent blood back to the heart. After the blood has traveled through the capillary network the pressure is greatly reduced, and the veins can afford to be much thinner than arteries with weaker muscle fiber. Small, one-way valves inside the veins keep the blood moving against gravity toward the heart.

As well as delivering the supplies that keep cells functioning, the bloodstream regulates body temperature by dissipating heat that builds up in the organs. The contraction or dilation of surface capillaries allows more or less heat to escape the system, depending on whether the body is too hot or too cold. The bloodstream also contains disease- and infection-fighting antibodies.

The lymphatic system is a one-way independent drainage network of fine capillaries primarily involved in fighting disease and infection. White blood cells used in neutralizing bacteria collect in lymph glands. Then normal muscle movement and one-way valves keep the lymph flowing toward the chest, where it drains into two large veins and reenters the blood stream. SEE ALSO Blood.

Nancy Weaver

Bibliography

Ballard, Carol. *Heart and Circulatory System.* Austin, TX: Steck Vaughn, 1997.

Silverstein, Alvin, Virginia, and Robert Alvin. *The Circulatory System.* New York: Henry Holt & Co., 1994.

Unschuld, Paul U., trans. *Nan Ching (Chinese Medicine).* Berkeley: University of California Press, 1985.

Classification Systems

There are more than five million different species on Earth. While each species represents the end point of a unique evolutionary path, biologists do not treat each one as completely unrelated to the others. Instead, they have created biological classification systems, or taxonomies, to reflect similarities and differences among species. A taxonomy is hierarchical, meaning that groups, or **taxa**, are themselves members of larger groups. For example, birds and mammals are grouped together as vertebrates because they both have backbones. Jellyfish do not belong to the vertebrate taxon because they lack backbones. However, birds, mammals, and jellyfish all belong to the taxon Animalia.

taxa named taxonomic units at any given level

The fundamental group in a biological **taxonomy** is the species. The most widely accepted definition of a species is "a group of actually or potentially interbreeding natural populations that are reproductively isolated from (unable to mate with) other such groups." In the eighteenth century, a Swedish naturalist named Linnaeus developed a biological taxonomy called "binomial nomenclature." Linnaeus grouped very similar species together into genera (singular, genus). Thus, every species is known by two labels: the name of the genus to which it belongs, and a specific modifier to distinguish it from other species in the genus (e.g., *Homo sapiens*).

taxonomy the science of classifying living organisms

Today, species are organized into groups at many levels higher than genus, including family, order, class, phylum, and kingdom. Systematists, who are biologists specializing in taxonomy, have developed two different methods to organize these groups: cladistics, which considers **phylogeny** (evolutionary history), and numerical phenetics, which considers phenotypic (outwardly observable) similarity. Cladists group taxa according to how long ago they diverged from a common ancestor, using only characteristics that provide information about phylogeny. They group together taxa that are closely related. Pheneticists group taxa according to their overall similarity in appearance, using as many characteristics as possible, regardless of phylogeny. These methods contradict one another when closely related groups appear to be very different. For example, crocodiles are more closely related

phylogeny the evolutionary history of a species or group of related species to birds than to turtles, snakes, or lizards, but look more like turtles, snakes, or lizards than like birds.

Systematists now use molecular techniques to analyze protein and DNA sequences for information on relatedness and similarity. Data at the level of molecules have the advantage of being more easily quantifiable, or reducible to numbers, than much phenotypic data. Furthermore, certain types of DNA and protein are thought to evolve at constant rates over long periods of time, providing "**molecular clocks**" for establishing phylogenetic relatedness. However, the accuracy of these "clocks" is difficult to determine without independent knowledge of phylogeny, such as a detailed fossil record.

molecular clocks using the rate of mutation in DNA to determine when two genetic groups spilt off

While there remains considerable debate over the merits of the various taxonomic methods, there is no doubt about the scientific importance of biological classification. Suppose we want to know how flight evolved. Taxonomic methods tell us that bats, birds, and insects each evolved flight independently. Thus, any other characteristics that bats, birds, and insects share can tell us something about the evolution of flight in general. Without a taxonomy, we might assume that flight evolved just once, making it difficult to draw any conclusions. A more pressing reason to develop taxonomies is the rapid loss of biological diversity, since conservationists may prefer to focus their efforts on unique species with few close relatives, rather than on species that are more similar to others. Taxonomies can help them prioritize the species that are least replaceable. SEE ALSO KINGDOMS OF LIFE; LINNAEUS, CAROLUS; PHYLOGENETIC RELATIONSHIPS OF THE MAJOR GROUPS.

Brian R. West

Bibliography

Campbell, Neil A. *Biology*, 2nd ed. Redwood City, CA: Benjamin Cummings Publishing Company, Inc., 1990.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishers, 1989.

Cnidaria

Cnidaria is one of the more primitive animal phyla. It includes aquatic organisms such as jellyfish, sea anemones, corals, and hydras. Most cnidarians are marine, although a few, such as the well-known hydra, are freshwater species.

Characteristics of Cnidarians

All cnidarians are characterized by **radially symmetric** body plans, rather than the bilaterally symmetric body plans that are found in most other animal phyla. Although cnidarians are more advanced than sponges (phylum Porifera) in that they possess distinct tissue layers, they lack many of the features of more advanced animal phyla, such as internal organs and central nervous systems. Most cnidarians possess tentacles, and many also have nematocysts (specialized stinging cells). Both are involved in feeding.

radially symmetric wheel-like symmetry in which body parts radiate out from a central point

Cnidarians are characterized by the presence of three tissue layers, an outer protective epidermis, a middle layer called the mesoglea, and an inner layer called the gastrodermis, whose function is primarily digestive. The mesoglea of cnidarians is not as highly developed as the **mesoderm** of other animal groups, being primarily gelatinous with only a few fibrous or amoeba-like cells.

Cnidarians possess only one digestive opening, which serves as both the mouth and the anus. This opening is surrounded by tentacles and leads to an internal digestive cavity called the **gastrovascular cavity**.

Cnidarians feed using tentacles that are embedded with stinging nematocysts. The nematocysts are springing barbs with small hairlike triggers that are activated by contact with prey. Most nematocysts require stimulation in more than one sensory mode before they will fire. For example, a nematocyst may respond only if there is mechanical stimulation from physical contact with the prey as well as chemical stimulation signaling the presence of suitable prey. As nematocysts fire, barbs unfold and become embedded in the tissue of the prey. At the same time, the nematocysts inject the prey with an immobilizing toxin through a long hollow thread within the barb. Once the prey item has been captured and subdued, tentacles are used by the cnidarians to bring the prey item into the gastrovascular cavity. Within the gastrovascular cavity, the food item is broken into small particles by digestive enzymes secreted by gastrodermal cells lining the cavity. The minute particles are then taken in by the gastrodermal cells, and digestion is completed in digestive vacuoles (small cavities) within these cells. The indigestible remnants of the prey are expelled from the mouth of the gastrovascular cavity.

One hypothesis about the origin of nematocysts suggests that they were **prokaryotic endosymbionts** which lived within **eukaryotic cells** as **mutualists** (mutualisms are **symbiotic relationships** between individuals of two different species, in which members of both species derive benefits from the relationship), the same way organelles (specialized parts of cells) such as **mitochondria** and chloroplasts are believed to originate.

Unlike more advanced animal phyla, cnidarians lack a central nervous system. Instead, their nerves are organized in nerve nets that cover the entire body. Impulses spread slowly out from the point of stimulation along the nerve net. Some cnidarians, such as jellyfish, have more complicated arrangements of nerves that allow for more complex responses to stimuli as well as more effective patterns of movement.

Cnidarians also lack certain tissue types found in other animal phyla, such as true muscle cells. However, they do have fibers that can contract and therefore can be used in capturing prey and in moving about.

Major Groups of Cnidarians

Cnidarians are divided into three major classes. These are the Hydrozoa (hydras and other colony-forming species), the Scyphozoa (jellyfish), and the Anthozoa (sea anemones and corals).

Hydrozoa. The best-known member of the Hydrozoa is the hydra, a freshwater species. However, the hydra is not a typical hydrozoan. For example,

Like other cnidarians, this sea anemone features a radially symmetric body plan and tentacles used in the feeding process. Sea anemones are anthozoans, existing only in the polyp form.

mesoderm the middle layer of cells in embryonic cells

gastrovascular cavity a single cavity where digestion occurs

prokaryotic endosymbionts single-celled organisms that lack a true cell nucleus that live inside of other cells

eukaryotic cells cells containing a membrane-bound nucleus and membrane-bound organelles

mutualists a symbiotic relationship where both organisms benefit

symbiotic relationships close, long-term relationships where two species live together in direct contact

mitochondria organelles in eukaryotic cells that are the site of energy production for the cell the hydra has only a polyp stage, for example, whereas most hydrozoans have a biphasic (two-stage) life cycle that alternates between a sedentary polyp stage and a mobile, bell-shaped medusa stage. The hydra is not strictly sedentary; it moves in a very unusual way, by turning somersaults. In addition, most hydrozoans are colonial, with each colony arising from the asexual budding of a single individual. Members of a hydrozoan colony have interconnected gastrovascular cavities, and the fluid in this cavity is circulated by cells with long, beating **flagella**. There is typically some degree of division of labor within the colony. Usually, there are feeding polyps, which possess tentacles and nematocysts (stinging cells), and reproductive polyps, which continually bud off tiny mobile medusas. The medusas swim by tightening and relaxing cells within the bell, and are also scattered by prevailing water currents. Medusas release sperm and eggs directly into the water, where fertilization occurs. The **zygote** (fertilized egg) develops into what is called a planula larva—the larvae of cnidarians. The larva ultimately settles to the substrate (rocky bottom of the ocean), finds something to anchor to, develops a mouth and tentacles, and becomes a polyp that subsequently buds to form a new colony.

flagella cellular tails that allow the cell to move

zygote a fertilized egg

Scyphozoa. The Scyphozoa includes the well-known jellyfish. In this group, the polyp stage is far less significant than among the Hydrozoa, since the medusa stage is dominant. Scyphozoan medusas grow to sizes considerably larger than those found among the Hydrozoa. They range in size from a few centimeters to over 2 meters across. The nervous systems of jellyfish are also more developed than those of other cnidarians. Instead of a simple nerve net, they have a nerve ring around the edge of the bell portion of the medusa. **Neurons** throughout the rest of the body connect to this ring. This organization allows for faster conduction of impulses from one side of the body to the other, which in turn allows the jellyfish to swim with coordinated contractions of the entire bell.

neurons nerve cells

Anthozoa. The Anthozoa includes the sea anemones and the corals. These species lack the medusa stage altogether, and exist exclusively in the polyp form. Anthozoans tend to have more highly developed contractile cells (cells capable of contracting) than other cnidarians, as well as a more highly developed, thicker mesoglea, which often forms a fibrous connective tissue. Corals secrete a hard, limy skeleton and can form huge reefs, such as the Great Barrier Reef off the coast of Australia. Coral reefs are an impressive ecosystem, one of the most diverse and productive on Earth. SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

Bibliography

Anderson, Donald Thomas. *Atlas of Invertebrate Anatomy.* Sydney, Australia: UNSW Press, 1996.

Barrington, Ernest James William. *Invertebrate Structure and Function.* New York: Wiley, 1979.

Chesher, Richard H. *Living Corals.* New York: C. N. Potter, 1979.

Clarkson, Euan Neilson Kerr. *Invertebrate Paleontology and Evolution.* Boston: G. Allen and Unwin, 1979.

Mayer, Alfred Goldsborough. *Medusae of the World.* Washington, D.C.: Carnegie Institution of Washington, 1910.

Coevolution

As organisms evolve to take better advantage of their surroundings, they may come into competition. A predator may compete with its prey, or two species eating the same plant may compete with one another to find it. With only a limited amount of resources to go around, living things have to adapt not only to climate, geography, and other slow-changing variables but also to the more rapid evolutionary changes undertaken by their competitors. Although change in climate can be seen as a comparatively slow change, one's living competitors are constantly evolving, and this requires that both parties keep on their respective toes: Fighting for resources can be a never-ending battle, and evolution ensures that the playing field is rarely level. However, evolution does not necessary breed outright competition, as it is also possible for two species to enter a mutually beneficial relationship whereby they help each other. No species lives in a vacuum, and potential interactions with one's neighbors can be beneficial, costly, or both. The chart below details the possible outcome of species interactions.

Note that predation does not differentiate lions eating antelopes from antelopes eating grass—both are predators eating prey, and prey does not have to possess a backbone or sturdy legs. In each case, both predator and prey can respond evolutionary to one another, and those changes may be physiological or behavioral. The antelopes can evolve to run faster. The lions might respond by evolving to run faster too. The grass, although it cannot run away, can evolve to taste bad to discourage antelopes from eating it. This might force the antelopes to find another type of grass, or their taste buds might change. When two (or more) species begin to respond evolutionarily to one another, this is called "coevolution."

Nature offers countless examples of coevolution. Many of these result from predator-prey interactions. Prey may evolve camouflage defenses, which require that predators become progressively better at detecting them. Walking sticks, for example, are insects that closely resemble twigs and are therefore frequently overlooked by predators. Because walking sticks are difficult to detect, their predators must have more acute vision and a greater ability to discern them from the inedible wood they mimic.

Predators, too, may employ camouflage to position themselves closer to prey. Yellow crab spiders reside in yellow flowers, patiently waiting for tasty insects to land on the flower looking for nectar. Such prey finds a nasty surprise instead. Scorpion fish, an extremely toxic species of fish found in temperate and tropical oceans, closely resemble the rock-covered sea floor.

Species A	Species B	Result
0	0	"Neutralism." The species do not interact.
+	0	"Commensalism." One species benefits from, but does not harm the other.
+	-	"Predation" or "parasitism." One species benefits at the cost of the other.
-	-	"Competition." Both species compete for the same resource.
+	+	"Mutualism." Both species derive benefits from the relationship.

Possible outcome of species interaction.

When inattentive prey drifts too close to the lurking scorpion fish, it swiftly gets eaten.

As one species in such a relationship grows more and more camouflaged, the other must get better at detection. More complex camouflage structures result for one, and a more refined nervous system and perhaps keener vision, smell, or hearing develop for the other. The driving forces for these adaptations are the other species, not temperature, geography, or any other variables.

polymorphisms having two or more distinct forms in the same population

Experiments suggest that camouflage is an effective tactic prey can use to confound predators. Theodore D. Sargent and the team of Alexandra T. Pietrewicz and Alan C. Kamil showed in 1981 that blue jays had a difficult time detecting underwing moths (*Catocala*) resting on certain backgrounds. The moths have wing patterns that blend in with tree bark, provided that they are oriented on the bark properly. Slight variations in the moths' wing patterns are called **polymorphisms**. If consistently shown just one polymorphism, blue jays became quite effective at detecting it even when a moth was on tree bark and oriented correctly. But if the blue jays saw different polymorphisms in random order, they never learned. Thus, in this evolutionary arms race, the blue jays have evolved the ability to detect subtle camouflage, but only one type at a time. Adapting to this ability by introducing a polymorphism enables the moths to defeat the blue jays' learning and detection abilities.

The ability of predators to detect hidden, or cryptic, prey can be found elsewhere. For example, John L. Gittleman and P. H. Harvey showed in 1980 that chicks were able to learn to discern camouflaged prey in a comparatively small number of trials. Predators may get better at identifying prey through a variety of mechanisms. They may get better at detecting camouflaged prey against a specific background or they may restrict their searches to more limited areas. In response, prey become more and more devious in their disguises, and each species can exhibit enormous evolutionary pressure on the other as they interact more frequently and grow increasingly adept at duping the other.

Relationships among Species

How do such relationships start? Imagine a worm that can partially conceal itself from its predator, a blue jay. Given that a blue jay has to look for any worm it eats, extra time spent looking for that hidden worm may well be wasted. In a limitless universe of worms, with half being concealed and the other half being unconcealed, the blue jays will never bother to identify the concealed ones, because it will be far easier to just pluck up the easily visible ones. As such, the concealed worms gain a selective advantage over the obvious ones.

But suppose the obvious worms all get eaten up. Then the blue jays have to start eating concealed worms, which they cannot find nearly as fast. So blue jays with better sensing abilities will tend to eat more, grow healthier, and reproduce more. Before long, with an abundance of blue jays with keen vision, the partially concealed worms will start to become scarce, unless they can better conceal themselves.

Two species may sometimes enter into a mutually beneficial relationship whereby they help each other, a situation illustrated by this yucca moth pollinating a yucca flower.

With a small advantage, that of partial concealment on the part of the worms, an evolutionary arms race has been created. The worms get better and better at hiding, and the blue jays get better and better at finding them. In a competitive world, this arms race can be seen everywhere. For example, trees grow taller to get more sunlight than their neighbors. Their neighbors, in response, grow taller too. For all this growing, however, the amount of sunlight reaching the trees does not change: They are expending increasing amounts of energy competing for the same, unchanging supply of a resource.

Competition of such intensity can be costly. To describe this phenomenon, Leigh van Valen coined the term "Red Queen Principle" in 1973. This term comes from an observation made by the Red Queen in Lewis Carroll's *Alice in Wonderland*. Alice and the Queen had been running furiously but could not go anywhere. The Queen told Alice, "Here, you see, it takes all the running you can do to keep in the same place. If you want to go somewhere else, you must run at least twice as fast as that!"

The Red Queen principle suggests that competing species may have to allocate more and more resources into fighting one another for a modest or negligible increase in benefit. As each side grows leaner and faster and better able to fight the other, the balance between competitors can be maintained. However, what is to be said of uneven matches? The struggle between bacteria or viruses and mammals is seriously lopsided. Bacteria, as parasites, can infect mammals and live off of them. A long-lived mammal, such as a human, may take twenty years or longer to go from birth to reproducing age, whereas the infecting bacteria may be able to reproduce within a matter of hours. With a faster generation time and many more **mutations** when they reproduce, bacteria can adapt to different environments and evolve much more quickly. Given this discrepancy, one might be tempted to think that competition between organisms with disparate generation times might always go to the ones that can evolve more quickly. In scenarios like that of lions and antelopes, it seems like an even match. But when bacteria tussle with humans, one might initially think the bacteria should always win.

mutations abrupt changes in the genes of an organism

The Evolutionary Struggle

Fortunately for humans, this is not always so. While the evolutionary arms race gives rise to new structures with which one fights the enemy, it can also give rise to structures that get around the problem of slower generation times. An internal simulation of evolution is an incredibly intricate structure, and it helps illustrate the heights of complexity that an evolutionary arms race can produce. The mammalian immune system has devised a number of strategies that closely resemble a tightly controlled simulation of evolution: The mechanism that generates antibodies (and T-cell receptors) recombines genes far more quickly than does the conventional method of mammalian reproduction. These genes, designed to recognize fast-changing bacterial and viral invaders, can change as fast as their competition.

Like all evolution, bacterial mutations must be beneficial for the bacteria to survive. The genes encoding antibodies do not particularly affect the survival of antibody-generating cells (B cells). But for the system to be effective, the body wants only the cells possessing the genes that can catch up with the bacteria. Thus, after creating an isolated scheme to accelerate mutation of specific genes, the body must create selective pressures to guarantee that it gets only the ones it wants. It does this, too, in the lymph nodes. By keeping little pieces of the bacteria around, the body can select only the B cells that best recognize the invader and discard the rest. Thus, even with lengthy generation times and low mutational rates for the rest of their **genomes**, mammals are able to simulate the conditions of rapid turnover and high mutational rates inside their own bodies to combat invaders with the same characteristics. Stronger and faster muscles are different manifestations of the arms in question, as is the antibody system. One set makes the organism go faster, and the other makes it selectively evolve faster.

genomes the sum of all genes in a set of chromosomes

Selectively speeding up evolution is not necessarily restricted to organisms that need to catch up to their competitors. The butterfly genus *Heliconius* boasts brightly colored wings and produces foul-tasting chemicals to discourage predators. Once a predator eats a *Heliconius* butterfly, it quickly learns to avoid butterflies with similarly idiosyncratic markings. But what if a butterfly that is not *Heliconius* can mimic the colors on *Heliconius* wings? This mimic can enjoy the reputation of being poor prey without actually having to manufacture the foul-tasting components itself.

Of course, this mimicry does not help *Heliconius*. If a predator comes upon a mimic and finds it tasty, it becomes more likely that a *Heliconius* might be eaten later, foul taste or not. This is another form of an evolutionary arms race: The mimic gets an advantage at *Heliconius*' loss. Such mimicry, when a nontoxic species tries to look like a toxic one, is called Batesian mimicry. It is fairly common in the insect world: For example, the hornet moth (*Sesia apiformis*), the wasp beetle (*Clytus arietis*), and the hoverfly (*Syrphus ribesii*) all have the same characteristic stripes as the common wasp (*Vespula vulgaris*), but only the common wasp has that painful stinger. Each one of the stingerless species usurps an ornery reputation from the common wasp, and as predators learn to eat them, the common wasp suffers more predation.

There are a few potential responses to these Batesian mimics. The predator could get better at discerning mimics from the real thing. As the predator gets better, the mimics too will get closer and closer to the real thing to fool the predator. Alternately, the original, toxic species could change its markings, forcing the mimics to change as well. If the mimics and the toxic species have roughly the same mutation rates and generation times, these changes might proceed at the same rate.

Heliconius has come up with a different strategy. It has evolved a select toolbox of wing patterns from which to choose during development. This pattern tactic resembles the rapid evolution enjoyed by the mammalian immune system—*Heliconius* can quickly change its wing pattern over a few short generations rather than taking a long time. Its mimics, on the other hand, must slowly evolve to get that precious wing pattern and thus avoid their predators without having to taste toxic.

Mutualism

Not all coevolution needs to be adversarial. Flowers are a coevolutionary adaptation for pollination. Many plants have flowers that are tailored to the needs of a specific insect or bird or bat. Flowers are designed to catch the eyes of certain animals, and the nectar inside is meant to appeal to particular tastes. Bees cannot see red but readily pick up blue, green, yellow, and ultraviolet. Butterflies have decent vision but a poor sense of smell, so they tend to pollinate brightly colored but odorless flowers.

Other structures can keep the relationship between a plant and its pollinator very close. For example, certain flowers have parts designed specifically for the length of a moth's tongue, and only that certain moth species can drink the nectar inside. Common snapdragons are designed so that the flower opens when an object the exact weight of a bumblebee lands on it.

These adaptations are mutually beneficial. The animal provides the plant with pollination, which means the plant can reproduce. The plant provides the animal with nectar, which can feed and sustain the animal. To ensure reliable pollination, the plant evolves to become more and more recognizable by its pollinator, and, conversely, the pollinator gets a steady food source. Each side grows stronger and can reproduce more under the part-

This bumblebee was attracted to the bright yellow of this flower. The nectar the bee takes away from the flower will be used to create honey, and the pollen the bee carries will fertilize the next flower, thereby helping the flowers to reproduce.

nership. In such cases, coevolution is an enormous asset to the species involved.

Coevolution of two organisms, therefore, aptly demonstrates that evolution does not have to respond exclusively to nonliving forces. Slight pressure from a competitor, or an ally, can redirect a species. Some pressures, such as predatory ones, can cause the species to invest more in camouflage, detection, or muscle and speed. Others, such as ones that lead to mutualism, may promote structures that will help a species more closely work with its partner, like a plant with its pollinator. Also, different strategies can lead to the bending of the rules, such as getting around the problem of evolution rates. As organisms come into close contact with another, a coevolutionary strategy is the most efficient path to success. SEE ALSO BEHAVIOR; BEHAVIORAL ECOLOGY.

Ian Quigley

Bibliography

Davies, N. B., and M. Brooke. "Coevolution of the Cuckoo and Its Hosts." *Scientific American* 264 (1991):92–98.

Dawkins, Richard. *The Selfish Gene*. New York: Oxford University Press, 1989.

Gittleman, J. L., and P. H. Harvey. "Why Are Distasteful Prey Not Cryptic?" *Nature* 286 (1980):149–150.

Sargent, T. D. "Antipredator Adaptations of Underwing Moths." In A. C. Kamil and T. D. Sargent eds., *Foraging Behavior: Ecological, Ethological, and Psychological Approaches*, ed. A. C. Kamil and T. D. Sargent. New York: Garland Press, 1981.

van Valen, Leigh M. "Patch Selection Benefactors and a Revitalisation of Ecology." *Evolutionary Theory* 4 (1980):231–233.

Colonization

Colonization occurs when a species enters and spreads into a new geographic area or habitat. This process involves both the initial entry, or invasion, into the new area by the species and its successful establishment there, which includes finding adequate resources for growth and reproduction. Less commonly, the term may be used when a parasite enters into and spreads inside a host or when a gene enters into and spreads within a new population.

The process of colonization is intensively studied along with theories of island biogeography because islands are discrete, measurable areas where colonization occurs. Island biogeography is the study of the dynamics that effect populations of isolated areas, and that encompasses the entire process of colonization. Island biogeography theories can be divided into three types. The first relates to habitat diversity and focuses on the suitability of the new habitat for the invading species. The second pertains to equilibrium, or the balance of colonization of the new habitat and its rate of extinction. The third concerns itself with the balance between colonization of the new habitat and speciation within it, and employs an evolutionary approach to examine it.

Increased habitat diversity is the most basic explanation to support the well-documented fact that as the area of land under study increases the number of species present increases. An organism that arrives to colonize a new area will need to find an appropriate habitat, or environment, in which to live. For example, a bird that uses large trees in which to nest will not be able to colonize a grassland. The proper habitat is of critical importance for the success of a colonizer, and even small differences in environmental factors such as soil type or humidity contribute to the success or failure of a new colonist.

A second theory of island biogeography is equilibrium theory. It explains the balance that is reached between colonization and extinction. The amount of colonization depends on the distance between the source of the colonizers and the new habitat. For example, the diversity of species on islands is greater when the islands are closer to the mainland than when they are farther away. The obvious reason is that the process of invasion, or the initial journey to the island, is more difficult when the distance is greater. The ease of the journey is different for different taxa, as birds may have no problem flying to an island whereas ground mammals would find it nearly impossible. Extinction is also known to occur faster on smaller islands because the available space fills up more quickly and competition drives some species to extinction.

Sometimes a new colonist finds abundant resources and little competition and is therefore highly successful and potentially free to evolve to take advantage of all the newly available untapped resources. In these cases, the evolutionary process impacts the colonizers faster than invasions of new species.

Examples of this situation can be found on remote islands such as the Hawaiian islands, where there are many closely related species of fruit fly that occur nowhere else. In this case, an ancestor was probably blown into the new habitat, where it established itself and had many generations of progeny, each of which ultimately invaded new habitats or neighboring islands that were free from competition. The new habitats were isolated enough from the founder population so that the invaders evolved into new species. SEE ALSO MIGRATION.

Jean K. Krejca

Bibliography

Begon, Michael, John L. Harper, and Colin R. Townsend. *Ecology*, 2nd ed. Cambridge, MA: Blackwell Scientific Publications, 1990.

Shafer, Craig L. *Nature Preserves: Island Theory and Conservation Practice*. Washington, D.C.: Smithsonian Institution, 1990.

Smith, Robert L. *Elements of Ecology*, 2nd ed. New York: Harper & Row, 1986.

Communication

The world is full of sights, sounds, and smells that organisms use to communicate with each other. Because humans are diurnal (active during the day) and have well-developed eyes and ears, we tend to think of communication in terms of vision and **acoustics**. However, other animals, plants, fungi, and even microorganisms can communicate, and do so using a variety of different methods. Communication is defined as any signal from one organism that influences the behavior of another organism. The type of signaling an organism uses depends on the reception abilities of the receiver.

acoustics a science that deals with the production, control, transmission, reception, and effects of sound

Nocturnal animals use sound and smells to communicate with each other, flowers attract pollinators by smell and sight, microorganisms communicate through touch and chemicals, and aquatic organisms can use electricity.

Communication between different individuals enhances the chances of survival by the sender. The sender may successfully defend a territory, thus ensuring a food supply, or successfully attract a mate, thus increasing reproductive success. Parents communicate with offspring, increasing the probability that the offspring will mature and reproduce.

While the sender of a signal usually benefits, predators have learned to exploit these signals. The calls of male Tungara frogs can be received by bats. Fireflies have learned to prey on other fireflies by mimicking mating signals. There are five modes of communication used by animals: visual, acoustic, chemical, tactile, and electrical.

Visual

infrared an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red. Heat is carried on infrared waves

Visual communication is transmitted by light, ranging from **infrared** to ultraviolet, and is detected by photoreceptors. Only vertebrates and arthropods have photoreceptors advanced enough to be useful in communication. In vertebrates, the receptors are located in the retina of the eye, but in arthropods, they are encased in each of the miniature "eyes" that form their compound eyes. The eyes of arthropods and vertebrates are very different, having independent evolutionary origins. In general, vertebrates have sharper vision than arthropods, but this clarity is due to the larger size of vertebrates rather than a more advanced eye.

aposematic coloration a bright coloration in animals with physical or chemical defenses that act as a warning to predators

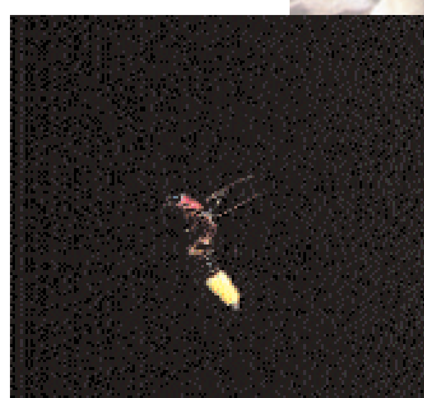
Some visual signals are exhibited simply through color patterns. One example is **aposematic coloration**, in which an animal advertises that it is toxic, distasteful, or otherwise dangerous, through bright colors. Like many signals, aposematic coloration can be deceitful. Coral snakes and scarlet king snakes have yellow, red, and black bands, but only coral snakes are venomous. King snakes mimic coral snakes in order to appear venomous and escape predation. Similarly, a group of harmless flies is marked with yellow and black banding, mimicking the various bees and wasps that actually do pose a danger.

Sometimes visual cues evolve when other forms of communication are ineffective. The semaphore frog in Borneo lives on rocks next to raging waterfalls, so the normal croaks and whistles of frog communication would be ineffective. This species has instead evolved visual signaling, which involves flashing white-spotted feet.

Visual signals, which are most effective in daylight, are usually used by diurnal animals. However, some insects, such as the familiar firefly, have evolved ways to communicate visually in darkness. Male fireflies flash bioluminescent abdomens in a particular pattern, hoping to elicit a similar flash sequence in some female on the ground. After receiving a signal, the male will join the female and mate. One genus of firefly, *Photurus*, has discovered the flash signal of a different genus, *Photinus*. *Photurus* females mimic *Photinus* females, calling in the *Photinus* males. When the male of the wrong species arrives expecting a mate, the female eats him.

Acoustic

Acoustic signals are produced in a variety of ways, from striking objects to vibrating vocal cords. A sound is heard when vibrations in air or water are detected by mechanoreceptors, which vibrate in response. In mammals, reptiles, birds, and amphibians, the receptors are located in the inner ear. Arthropod receptors are variable, and may be found on the legs, thorax, or abdomen. The only fishes that can detect sound are those with modified flexible air sacs.



A meadow firefly flashes a particular bioluminescent pattern in the hope of eliciting a similar flash sequence in some female on the ground.

Since sound is carried farther in water than in air, aquatic mammals can communicate over great distances. Orcas (so-called "killer whales") use an elaborate system of cries to establish dominance, find offspring and mates, and even express contentment. Each pod of orcas develops its own dialect of cries, allowing pod-mates to recognize each other.

Birds use songs to declare territories and enhance their chances of survival by reducing harmful encounters with birds of the same species. When male birds establish territories for the mating season, they often come to physical blows with each other to defend their boundaries. Once the territory has been settled, the birds reinforce their boundaries by singing rather than fighting. If a bird ceases calling, other birds will immediately take over the space.

Chemical

Most organisms can use molecules to communicate. Animals concentrate chemical receptors in the nose, mouth, and antennae. Vertebrates have the most developed senses of smell and taste because the receptors are kept moist and isolated. Plants cannot sense chemical signals in the same way that animals do, but plants do emit them in abundance. For example, pine trees emit terpenes, sharply odoriferous chemicals that communicate distastefulness to herbivorous insects. This signal is an allomone, a term for any chemical used to communicate between members of different species.

Chemicals that communicate between members of the same species are called **pheromones**. Female moths use these powerful signals to attract mates. Male moths, with their fantastically plumed antennae, are able to detect just a few molecules in a square kilometer (approximately 0.4 square miles). Honeybees use pheromones in conjunction with visual cues to communicate to other workers where food sources are located. Mammals rub scent glands on objects to mark their territories, and on each other during the mating season to act as **aphrodisiacs**.

pheromones small, volatile chemicals that act as signals between animals that influence physiology or behavior

aphrodisiacs substances or objects that are thought to arouse sexual desire

Tactile

Touch is detected by **proprioceptors** on pliable body surfaces of the receiver. Proprioceptors respond to temporary changes in the shape of the surface or the movement of sensory structures such as hairs, whiskers, and bristles. Structures that have a large number of receptors are tactile organs. Human fingertips are tactile organs, having about 100 receptors per square centimeter (0.15 square inch). The tentacles of octopuses, antennae of some insects, and bills of sandpiper birds are also tactile organs.

proprioceptors sense organs that receive signals from within the body

Touch is a less informative means of communication than sight, sound, or chemicals, but can be crucial. Male and female crane flies must touch legs before either animal will accept the other as a mate, and human infants must be held and cuddled to develop properly and to recover more quickly from illness.

Electrical

Communication by electrical current has evolved only in fishes, but within this group it has arisen several times independently. The fish generate an electrical charge in specialized cells called electrocytes. Electrocytes are arranged in columns and surrounded by insulating cells. Electric eels can generate charges up to 720 volts, but these strongly electrical fish use their charge to capture prey, rather than for communication.

Weakly electric fish, such as skates and knifefishes, evolved the use of their signals for social communication because they are either active at night or in murky water. Electrical signaling is highly versatile. A single fish can communicate territory boundaries, advertise for a mate, or show aggressiveness just by changing the strength and pattern of pulses. Wave fish use their signals to establish a social hierarchy. Dominant fish reinforce their position by matching their charge frequency to submissive wave fish, forcing the submissive fish to shift their frequencies away. Male Nile fish spend days building a suitable nest and then send out invitations to females by emitting pulses of electricity.

Communication is essential to any form of social interaction, and so all living things have developed some way to transmit and receive information. The few examples provided in this article do not come close to demonstrating the diversity of communication that exists in the natural world. SEE ALSO Acoustic Signals; Aposematism; Courtship; Vocalization.

Jes Marie Creech

Bibliography

Bradbury, Jack W., and Sandra L. Vehrencamp. *Principles of Animal Communication.* Sunderland, MA: Sinauer Associates, 1998.

Kirchner, Wolfgang H., and William F. Towne. "The Sensory Basis of the Honeybee's Dance Language." *Scientific American* 270, no. 6 (1994):52–59.

Moller, Peter. *Electric Fishes: History and Behavior.* New York: Chapman and Hall, 1995.

Morton, Eugene S., and Jake Page. *Animal Talk: Science and the Voices of Nature.* New York: Random House Publishers, 1992.

Narins, Peter M. "Frog Communication." *Scientific American* 273, no. 2 (1995):78–83.

Community Ecology

Community ecology is the study of the organization and functioning of communities of organisms. As populations of species interact with one another, they form biological communities. A community of organisms consists of all the interacting populations of the species living within a particular area or within a particular habitat. Community ecology also studies the relationships of the members of a community to their environment. Community ecology is usually subdivided according to habitat or **biome**. Typical habitats include forest, grassland, desert, and stream or lake environments.

biome a major type of ecological community

The Trophic Pyramid

All biological communities have a similar structure called a trophic pyramid. Each pyramid contains four or five levels. Food energy is passed from one level to the next along a food chain. Since energy is lost to heat at each level in the pyramid, it takes many organisms at a given trophic level to support those in the next level up. The base of the pyramid in every biological community is composed of species called autotrophs, organisms that harvest sunlight (or in rare cases, heat) directly through photosynthesis (or chemosynthesis). All other organisms in the pyramid are called heterotrophs.

A food chain typically contains four or five links, from autotrophs, through grazers and other herbivores, then culminating with a carnivore as top predator. Many animals, however, eat more than one species. Also, animals may eat different foods at different stages of their growth. Many animals eat both plants and other animals and therefore feed at more than one trophic level. Consequently, food chains are usually interconnected into highly complex food webs.

In addition to eating one another, species also compete for resources and interact in other ways within a community. Nontrophic relationships between species are as important as food chains and food webs in shaping the organization of biological communities.

Ecological Succession

Through the process of ecological succession, communities are constantly changing. Disturbances to communities may be local, such as a tree falling and opening the canopy to allow more sunlight, or widespread, such as fires and storms. Whether local or general, each disturbance creates an opportunity for a new species to colonize that region. These new species can alter the biological structure of the community and create an environment that is suitable to other new species. By this process, the community evolves over time.

In some environments, succession eventually produces a stable community dominated by a small number of species. This is called a climax community. The web of biological interactions has become so intricate and interconnected that no other species can successfully compete for food resources. In other environments, small disturbances produce communities that are a diverse mix of species. Some tropical forests contain hundreds of thousands of species within a square kilometer. When a tree dies and falls, the dense canopy is opened and new space is available for different species to take root. Some coral reefs contain thousands of different species, and whichever species is able to rapidly colonize a new disturbance patch will be successful.

Ecological Niches

The way of life of an organism is shaped by its environment and by its interactions with other organisms through the processes of evolution. The role an organism plays in its relation to other species and its environment

Competition plays an important role in community interaction and ecology. This Kirtland's warbler, for example, may be forced to compete with other birds to preserve its nesting site.

is known as its ecological niche. The niche of an organism includes what it eats, how it obtains food, where in the environment it lives, what temperature it prefers, how much light it can tolerate, and many other factors.

Guilds

Some similar species have evolved strategies that allow them to allocate resources in a way that avoids competition. For example, different species of warblers that prey on the same species of insects may forage at different levels in the same trees. A group of organisms that share a common food resource is called a guild. Guild members may have strong interactions with each other but only weak interactions with other members of the community. In the American Southwest, birds, rodents, and ants constitute a guild that competes for the same seeds. Whereas birds exploit temporary patches of seeds, rodents and ants are permanent residents. Ants generally take smaller seeds than rodents. In East Africa, communities of animals form a guild of grazers. First, elephants and buffalo eat the tall, coarse grasses and then move on. They are able to consume large quantities of this low-nutrition food source. Zebras follow along behind the elephants, reducing the plant **biomass** even more. The zebras are followed by a still smaller animal, the wildebeest, which selects among the lower growing plants that remain after the zebras have fed. Finally, the smallest grazers, such as Thompson's gazelles, are able to reach the young, protein-rich sprouts of grass missed by the wildebeest.

biomass the dry weight of organic matter comprising a group of organisms in a particular habitat

Interactive Relationships

The interactive relationships that arise between populations of different species form the interactive web of communities. These interactions range from antagonistic to cooperative and have positive, negative, or neutral effects on the species involved. In antagonistic relationships the interaction is detrimental to individuals of either one or both species; in **commensal** relationships (commensalism) one species benefits while the other remains unaffected; and in **mutualistic relationships** (mutualism) both species benefit.

commensal a symbiotic relationship wherein which one species benefits and the other is neither helped nor harmed

mutualistic relationships symbiotic relationships where both organisms benefit

The organization and stability of biological communities results from the mix of these different kinds of interaction.

There are many different kinds of interspecific interactions within an ecological community. These relationships between species are not static; they evolve as natural selection continually shapes and reshapes them. The complex relationships between prey and predators, for example, are snapshots of one instant during the evolution of interactions. As interactions between species evolve, the nature of relationships may shift. Nineteenth-century British naturalist Charles Darwin called this ever-changing mix of species and their interactions the "entangled bank" and stressed its importance in the evolutionary process. While antagonistic relationships, such as predator-prey or parasite-host, are the most dramatic kinds of relationships, other forms of interaction such as mutualism or commensalism are just as important.

Mutualism. This is a relationship where both participants in the interaction receive benefit. For example, plants are hosts for insects that pollinate them or eat their fruit and for microorganisms that attach themselves to their roots. Mutualistic associations between animals and microorganisms are an important part of the structure of communities. Most animals rely on the microorganisms in their gut to properly digest and metabolize food.

Parasitism. This is possibly the most common way of life in nature. Parasitic organisms may account for half of all living species. The majority of species of wasps are tiny parasites that lay their eggs on a specific host organism. Some wasps are parasitic on plants, some are parasitic on insects, some even parasitize other wasps! The larvae hatch and burrow into the host species. As it is consumed from the inside out, the host species survives long enough to allow the larvae to mature.

Antagonism. Antagonism is a form of relationship where one species benefits and the other is harmed. Grazing, parasitism, and predation are examples of antagonistic relationships. While we generally think of grazers as large herbivores, a grazer is defined as any species that moves from one organism to another, feeding on part of each without actually killing it outright. Grasshoppers are grazers that jump from plant to plant, chewing a portion of the leaves of each one they visit. Some caterpillars are grazers that crawl from one plant to another during development rather than remain as parasites on an individual plant. The grazing lifestyle differs from the parasitic lifestyle in a few important ways. Individuals can vary their diets with different foods. Also, because grazers do not remain attached to a single individual for long periods, their victims do not have time to develop induced specialized defenses, such as an immune response that a host can develop against a parasite.

Predation. This form of relationship differs from both parasitism and grazing. In predation, the victims are killed and often consumed immediately. Predators therefore differ from parasites and grazers in their effects on the dynamics of populations and the organization of communities. As with parasitism and grazing, predation is an interaction that has arisen many times in many taxonomic groups worldwide.

Competition is an important form of interaction in communities in which neither species benefits. In competitive interactions, species evolve either to avoid each other, to tolerate the presence of the other, or to aggressively exclude the other.

Species compete for almost every conceivable kind of resource. Birds compete for nesting sites. Male birds compete for preferred sites to defend as territories for attracting females. While species compete for many resources at the same time, there is often a single resource, called the limiting resource, that is in scarce supply. This resource restricts the growth of each species. In deserts, water is often the limiting resource.

Commensalism. In this kind of interaction, one species benefits and the other is unaffected. For example, cattle egrets (*Bubulcus ibis*) forage around the feet of cattle. The grazing behavior of the cattle stirs up many small insects and other arthropods that the cattle egrets eat. The cattle egrets receive a benefit, but there is no indication that the cattle are affected in any way.

The richness and ubiquity of interactions among populations of organisms demonstrate that the characteristics of all species have been influenced by the interaction with other species. Species have coevolved with each other. Predators have evolved along with their prey. Parasites evolve with their hosts. Rarely is only one interaction responsible for the evolution of a species, however. More common is a sort of diffuse coevolution where the traits of a single species are influenced by interactions with many other species. Such diffuse coevolution may prevent a sort of evolutionary "arms race," where predator and prey become ever faster or stronger. SEE ALSO COEVOLUTION; ECOLOGY; ECOSYSTEM; HABITAT.

Elliot Richmond

Bibliography

Billington, Elizabeth T. *Understanding Ecology.* New York: F. Warne, 1971.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth, 1990.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer, 1987.

Comparative Biology

Under this scientific method, biologists formulate hypotheses, or predictions, from an existing body of knowledge and then test their hypotheses through experiments. Experiments range from simple to complex, and can be performed on a computer, in a laboratory setting, or outdoors. Technological developments during the twentieth century—including high-speed computing, DNA sequencing, and a wide array of visualization techniques—have opened the door to many exciting lines of biological investigation. Biologists are constantly developing new techniques to test increasingly complex questions, and have even designed experiments to re-create natural events such as hurricanes, forest fires, and floods.

The scientific method can be applied to many, but not all, types of scientific inquiry. Experimental methods cannot directly test hypotheses con-

cerning the processes of evolution because these events took place over the course of millions of years, under environmental conditions that are as difficult to define as they would be to recreate. Biologists must therefore rely on a comparative method to deduce how evolutionary events created the patterns of animal diversity that exist today.

One such pattern involves how animals living in similar environments have evolved similarities in particular traits. For centuries, biologists have been interested in how such characteristics adapt the animals to their surroundings and ecological role. A biologist studying the adaptive significance of a morphological trait, such as fur coloration, will look at animals living in similar environments to search for patterns linking this trait with environmental factors such as plant types and density.

A comparative framework can be used while looking at different types of traits, whether they are **genetic**, **morphological**, **behavioral**, or **ecological** in nature. In setting up a comparison, the biologist must be familiar with the evolutionary relationships of the animals in question. For many groups of organisms, these relationships have been described through a branch of biology called phylogenetics. The product of a phylogenetic analysis is called a **phylogeny**, which is a hypothesis about relationships between organisms. Phylogenies can be constructed using a combination of genetic, morphological, and behavioral traits. These phylogenies can describe relationships at various levels: gene, species, genus, and so on.

genetic relating to an organism's genetic make-up

morphological the structure and form of an organism at any stage in its life history

behavioral relating to actions or a series of actions as a response to stimuli

ecological relating to an organism's interaction with its environment

phylogeny the evolutionary history of a species or group of related species

homologous similar but not identical

After the biologist selects the level at which she will make a comparison, she uses a number of criteria, or standards, to decide whether the structure to be examined in each organism is **homologous**. When judging morphological structures to be homologous, criteria may include their position and developmental origin. Function is not a reliable indicator of homology because similar functions may be formed by dissimilar structures (e.g., a bird's wing as opposed to a bat's wing). Such structures would be the result of convergent evolution, and would be called analogous rather than homologous (same function, different structure). The criteria differ for judging homology in other types of traits. For example, judging homology in behavioral traits would require examination of genetic origins and behaviors that may represent a transition between two behaviors that are of interest.

When the biologist maps homologous traits onto the phylogeny and examines the evolutionary relationships between groups sharing similar traits, the patterns revealed may provide clues about how various traits evolved. Biologists may examine, for instance, the correlation, or connection, between the presence of the trait and the environmental or genetic factors that may cause this trait to be expressed. The scientist uses statistical methods to determine whether or not the correlation he has found between the trait of interest and the factors occurred as the result of a random process. If the scientist determines that the patterns were not created randomly, then he concludes that the trait is an adaptation.

A comparative framework is invaluable while studying evolutionary relationships of various animals, and while looking at how traits evolved. However, the comparative method is also useful in cases where the investigator does not need to create a historical, or evolutionary, context. If a biologist

is interested in only the function of a particular structure, and not in how it evolved, she may decide to make comparisons of the same structure in more distantly related animals.

For example, a biologist interested in the functions of morphological traits might be interested in how flight structures differ in birds and bats. He knows that wings evolved independently in birds and bats because a published phylogeny indicates that many bird and bat ancestors did not fly. Rather than assume that wings evolved in the most recent common ancestor of bats and birds, and was subsequently lost later on in many groups of reptiles and mammals (the closest living relatives to birds and bats), it is assumed that wings evolved twice. The functional morphologist uses the knowledge that bird and bat wings evolved independently to help direct future research. SEE ALSO ADAPTATION; BIOLOGICAL EVOLUTION.

Judy P. Sheen

Bibliography

Brooks, Daniel R., and Deborah A. McLennan. *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology.* Chicago: University of Chicago Press, 1991.

Competition

natural selection the process by which organisms best suited to their environment are most likely to survive and reproduce

intraspecific involving members of the same species

Populations of animals are controlled by many factors. **Natural selection** is a broad term that describes one effect of these controls on population. For example, one form of population control that can result in natural selection is competition.

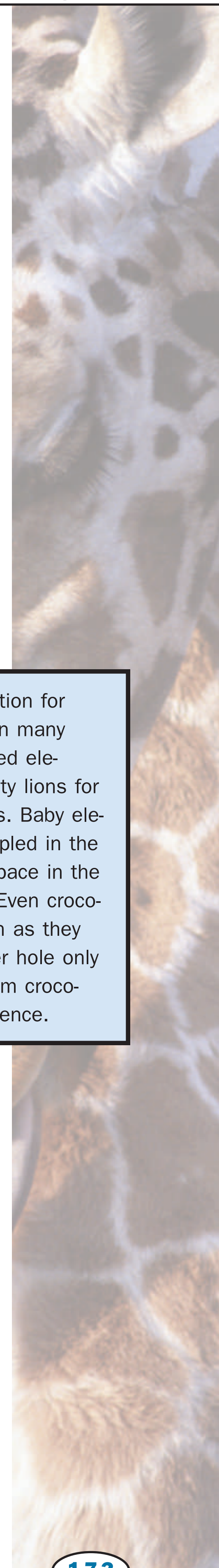
There are a number of essential resources upon which animals' lives depend. Whenever these resources are limited, animals are forced to compete for survival. Competition can be **intraspecific**, between the same species, or interspecific, between different species. Since resources are rarely abundant in any given environment, competition can be fierce. Three resources that animals are likely to complete for are space, water, and food.

Competing for Space

The availability of space is a primary consideration in any habitat. The actual territory in which an animal lives is vitally important since an animal's environment must be able to support the needs of each species. All animals must have enough room for feeding, reproducing, and exercise in order to live comfortably.

Along with the amount of space, some animals require a particular terrain, such as the prairie dog. A prairie dog colony must have enough flat and fairly soft earth in which the animals can build elaborate tunnel systems. If the soil is too rocky, the prairie dogs cannot build their brooding dens and escape tunnels.

Similarly, some birds require lots of open sky in which to perform their courtship flights. Without these elaborate flights the birds do not become stimulated to reproduce. If the terrain does not permit the birds to move in wide-open spaces, the birds' chances of successful reproduction in that habitat are reduced.



Competing for Water

Another important resource that animals compete for is access to water. Most animals require a particular amount of water everyday, which they may use as drinking water, or to contribute to their overall health. In general, animals must maintain a certain moisture balance in order for their tissues to work properly. When animals do not have enough to drink their bodily tissues become dehydrated and cannot function properly. Organs, such as kidneys, stop working, resulting in death.

Using larger bodies of water for bathing purposes is another common use of water as a resource. For instance, overheating in elephants is a problem usually countered by cool baths in rivers or mud. When water becomes scarce in the dry season, competition between individual elephants or between elephants and other species can reach a dangerous peak.

Finally, **aquatic** animals are especially vulnerable when the water level of their environment drops. Fish living in the shrinking rivers and streams are easy prey for birds when the waters become so shallow that they are easily seen. The fish will compete for choice hiding spots from hungry predators, with the unlucky losers being eaten, therefore removing their genetic material from the gene pool.

aquatic living in water

Competing for Food

Food is one of the most basic resources over which individuals compete. In extreme cases where animals have gone for long periods without enough food to sustain them, individuals will compete, sometimes to the death, for mere scraps of food. Animals that practice a high level of parental care have to carefully balance finding enough food for both themselves and their offspring. When food is scarce, the parent may go for months without eating but will rarely risk their own death for the sake of their young. Usually, by the time the parent is in danger of starvation the resources for the young will have already been exhausted and the young will have already died.

Examples of competition for water can be found in many nature videos. Parched elephants threaten thirsty lions for limited water in rivers. Baby elephants may get trampled in the rush for water and space in the limited water pools. Even crocodiles find competition as they march to a new water hole only to find resistance from crocodiles already in residence.

The reason the parent allows its young to die is motivated by the parent's instinct to survive. Once the offspring dies the parent is free to readopt food-finding methods that might lead it farther from the nest or den where its young were kept. The parent is driven to preserve its genetic information by remaining healthy enough so that it can reproduce again, hopefully when there is more food available.

Sometimes species will compete for more than one resource at a time. Competitions for territory and food are easily seen in interactions between ants. On one hand, the social structure of the colony is an amazing example of how the members of a species cooperate and specialize for the benefit of all. The queen lays the eggs and produces the offspring. Workers attend to the maintenance and growth of the colony. Soldier ants defend the colony against invaders. The area around an ant colony, however, is often lacking in food after a few seasons of food gathering and resource use.

Some colony members will forage beyond their usual boundaries and encounter ants from another colony. This will immediately set off a warning throughout both colonies. Soldiers and workers rush out of the two

Competition for food and territory is a highly visible component of ant interaction. For example, if ants from one colony invade the space of another colony, the results often mean war over the disputed area.

colonies to fight each other for the contested territory and food resources. The success of one or both of the colonies may be at risk, and the death toll for each colony can be high. Even colonies of the same species will war against one another. If one species enters the colony area of another, the two colonies may suffer serious battle losses.

Strategies to Avoid Competition

Although competition between animals can be seen in a variety of situations, many species have developed elaborate strategies to avoid competition. It is not the habit of any species to try and obliterate another. Confrontations occur as a last resort. Without this avoidance of direct competition there would be very few stable communities.

More often, the sharing of resources is achieved between species in a habitat. Scientists often refer to the sharing of resources as "**niche** partitioning." In niche partitioning animals tend to use different parts of a resource without coming into direct competition with one another. For instance, grazing animals in parts of Africa come in all sizes. The smaller Thompson's gazelles eat grass that grows close to the ground. Zebras and wildebeests consume the tall grasses and shrub food. The giraffe has a long neck enabling it to browse far above the ground. While all of these animals use plants as a food resource, none come into direct competition with one another. As a result, they **coexist** peacefully and reduce confrontation.

niche how an organism uses the biotic and abiotic resources of its environment

coexist live together

Many species of birds and monkeys in rain forests also partition resources. Some are specialized for feeding on fruit from lower branches of trees nearer the forest floor, while others are able to exploit food items found in the top or canopy region of the forest.

It is only when resources are limited that one observes any actual competition. Even then animals will often find a unique solution to the problem. For example, barnacle colonies exist in competition with other animals for limited space on rocks and hard surfaces in the oceans. While the larvae are free-swimming and float as part of the planktonic community throughout their juvenile stage, the adults need a firm surface to anchor and construct hard permanent shells. From within these shells they extend feathery feeding appendages that sweep food particles from the ocean currents.

Barnacles exploit unique measures in order to avoid the fierce competition from ocean-dwelling **filter feeders** (such as corals, anemones, and limpets) for ocean floor space. Instead of competing, many form colonies on the tough skins of whales. They hitchhike around the sea feeding on food suspended in the water surrounding the whale. It is very common to find whales with large colonies of barnacles on their snouts and jaws. Even ships are suitable landing places for the barnacle larvae. Barnacle colonies can become so large on the bottoms of ships that the ships must be removed from the water and the barnacles scraped off to keep the ship moving smoothly through the water.

filter feeders animals that strain small food particles out of water

Ecological competition is a fascinating and varied topic in biology. Scientists are always discovering new ways in which animals compete with one another. Even more interesting is the way in which they reduce or eliminate competition. Humans can learn a great deal from how animals coexist with one another. SEE ALSO Aggression; Populations.

Brook Ellen Hall

Bibliography

Raven, P., and G. Johnson. *William C. Brown.* Boston: McGraw-Hill, 1999.

Starr, C. *Biology: Concepts and Application.* Belmont, CA: Wadsworth, 1994.

Internet Resources

University of South Carolina, Department of Biology. <http://marine.geol.sc.edu/BIOL/Courses/BIOL>.

University of Tennessee, The Institute for Environmental Modeling. <http://ecology.tiem.utk.edu>.

University of Texas, Department of Biology. <http://www.esb utexas. edu>.

Competitive Exclusion

The competitive exclusion principle states that two species that occupy the same biological niche cannot coexist. Another way of expressing this idea is that "complete competitors" cannot coexist. That is because when two species occupy precisely the same niche, and compete for precisely the same resources, one species will inevitably be better at exploiting those resources than the other. The more effective species will outcompete the other and eliminate it from the habitat. The competitive exclusion principle was first stated in this form in 1934 by G. F. Gause, although other biologists, starting as early as Charles Darwin, appear to have had similar thoughts.

The competitive exclusion principle is actually a µtheoretical result derived from mathematical equations for competition called the Lotka-Volterra equations. However, there appears to be empirical, or factual, support for the idea as well. Studies of coexisting species always show that they differ in at least one important aspect of their niche. In one famous study, Robert MacArthur examined the habitat use of five species of coexisting forest

COMPETITIVE EXCLUSION PRINCIPLE

This principle defines the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently than its competitor. This provides the more efficient species with a reproductive edge, so that the second species will eventually be eliminated.

warblers and found that each species foraged for food on a different part of the tree.

Similar studies of lizards of the genus *Anolis* suggest that in this group, species that are found in the same place tend to be of different sizes, prefer to forage at different branch heights, or use branches of different thicknesses. In certain large lakes of the African Rift Valley, several hundred species of cichlid fish may coexist. Studies of these species suggest that each is specialized to exploit a different food resource.

Competition between species is an interspecific interaction (that is, one that occurs between individuals of different species) that harms both players involved. Consequently, species tend to evolve in such a way as to avoid competition. When two competing species coexist in the same habitat, they tend to shift their niches in such a way as to overlap less. The niche that a species is able to exploit in the absence of any competitors is called its fundamental niche. The resources that are actually exploited by a species in a specific habitat represent its realized niche. The realized niche is always smaller than the fundamental niche and a subset of it.

character displacement a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

If competition occurs over long periods of time, **character displacement** may occur. Character displacement describes a situation where two species are more morphologically different in habitats where they coexist than in habitats where they do not coexist. Character displacement is often interpreted as evidence for past (and perhaps continuing) competition. Character displacement has been observed among species of *Anolis* lizards as well as among the Galapagos finches. SEE ALSO Competition.

Jennifer Yeh

Bibliography

Futuyma, Douglas J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, 1998.

Krebs, Charles J. *Ecology: The Experimental Analysis of Distribution and Abundance.* New York: Harper Collins College Publishers, 1994.

Pianka, Eric R. *Evolutionary Ecology.* New York: Addison Wesley Longman, 2000.

Conservation Biology

Conservation biology is the study of the biological diversity—biodiversity for short—of Earth. Biodiversity is the variety of different living creatures, both plants and animals. Conservation biology is a relatively new field of study, having its start in the 1980s. It applies the principles of many sciences in order to preserve biodiversity throughout the world.

While at the end of the twentieth century the number of described species was about 1.7 million, estimates put the total number of species at 5 to 30 million. Many scientists believe that Earth is experiencing the greatest episode of mass extinction since the extinction of the dinosaurs 65 million years ago. Current rates of species extinctions throughout the world are believed to be 50 to 100 times greater than rates prior to human impact. In tropical forests, the extinction rates are believed to be 1,000 to 10,000 times higher than the expected rate. Given the current rates of extinction, by the year 2020, 30 to 70 percent of the world's

As part of a conservation biology tracking project, a research biologist puts an eartag on a sedated bobcat.

species will be extinct. This crisis is thought to be due largely to human activities. Human population reached 6 billion in September 1999. Every day, this number increases by an estimated 250,000 (an extra 87 million people per year). This huge human population is straining Earth's natural resources in many ways.

The leading factor in the increasing rate of species extinctions has been the human destruction of natural areas where plants and animals live. Since 1950, one-third of the world's forests have been destroyed. Loss of tropical rain forest is estimated at an acre every second. It is estimated that humans consumed one-third of the world's natural resources during the period 1970 to 1995. It has also been estimated that the United States, with only about 5 percent of the world's population, consumes 25 percent of the world's resources and generates 25 to 30 percent of the world's waste.

Other human activities that are increasing species extinctions are the pollution of the environment and the overexploitation of animals, such as whales and tigers, that have commercial value.

There are many reasons to conserve and protect biodiversity. New species could provide new food sources for humans. Genes from wild plants are used to improve food crops. New plants and animals can be used as **biological control** agents to control pests. Nearly all the medicines used today were derived from plants or animals, and other species may provide important new medicines. Plants and animals carry out many functions in the environment that are critical to humans. For example, bees and bats pollinate flowering plants, and green plants provide oxygen.

biological control the introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

There are other less practical reasons to preserve biodiversity. Plants and animals are beautiful and interesting. Humans gain much pleasure and peace of mind interacting with the natural world. In addition, there is the argument that all species have value regardless of their worth to humans.

Denise Prendergast

Bibliography

Meffe, Gary K., C. Ronald Carroll, et al. *Principles of Conservation Biology*, 2nd ed. Sunderland, MA: Sinauer Associates, Inc., 1997.

Internet Resources

Bryant, Peter J. *Biodiversity and Conservation: A Hypertext Book.* <http://darwin.bio.uci.edu/~sustain/bio65/lec01/b65lec01.htm>.

Constraints on Animal Development

Within a given taxon, development generally results in the production of individuals that are recognizable as members of that specific group. Vertebrate embryos can be recognized as such early in development, regardless of whether they will later become fish, birds, or mammals. Humans nearly always have the same number of fingers and toes at birth (rare exceptions do exist, however), and, although there are slight variations in the size and shape of digits and limbs from one individual to the next, they are recognizable as human features (for example, wings, hooves, and fins never appear in humans). Normal development seems to follow the same pathway, and resulting variation is limited. This is because developmental constraints favor certain outcomes and prevent others. Developmental constraints are any aspects of a developmental system that increase the probability of a particular outcome and limit the production of variable **phenotypes**. Just as natural selection favors change to suit environment (adaptation and convergent evolution), developmental constraints limit adaptation and favor conservation of the morphology, or form, of animals. The internal organization of living organisms limits the range of possible phenotypes on which natural selection can operate. Developmental mechanisms are fundamental in generating diversity. At the same time, they impose constraints on the direction of evolutionary change.

phenotypes the physical and physiological traits of an animal

Developmental Mechanisms

Because of the particular pattern of embryonic development characteristic of a given species, some structural patterns are more likely to form than others. The probability that a mutation will result in a potentially functional

Mutations, such as the blue pigment in this green frog's skin, may take place late in the developmental cycle. Late-developing mutations are more likely to benefit an organism's ability to function in its environment.

body form depends on when the mutation is expressed. Mutations that act on early development are likely to have drastic effects on phenotype because normal development of later structures depends on that of earlier structures, a phenomenon known as **epistasis**. Drastic changes early in **ontogeny** are unlikely to result in benefits to the organism and in fact are usually lethal. In contrast, mutations that are expressed late in development are less likely to disrupt the developmental process and more likely to result in functional phenotypes that would benefit the organism.

epistasis a phenomenon in which one gene alters the expression of another gene that is independently inherited

ontogeny the embryonic development of an organism

Morphogenesis includes those processes of development that produce the final form of the organism. Anything that alters the final form through evolutionary time must do so through alterations in development. Yet development is a very tightly integrated process in which it is difficult to change one thing without adversely affecting many other things.

morphogenesis the development of body shape and organization during ontogeny

Constraints on Development

Regardless of the direction and magnitude of external selective pressure, it may be impossible for the organism to change because of internal constraints. Natural selection might not favor even seemingly adaptive changes because of trade-offs among developmental costs because of pleiotropy, the action of genes in multiple tissues that may be otherwise unrelated. Pleiotropy can result in constraints in which no possible genetic change can produce beneficial morphological change without causing other undesirable changes. Groups of characters may also be associated because of pleiotropy, resulting in suites of characters that are inherited together. In this case, change in one character is impossible without change in the others.

Constraints on development can be generally classified as structural or **phylogenetic**. Structural constraints can be physiological, cellular, genetic, metabolic, or mechanical. For example, the respiration rate across cell membranes presents physiological limits to cellular surface-to-volume ratios, and

phylogenetic relating to the evolutionary history of species or group of related species

mechanical constraints limit how long or thin a limb can be and still support the weight of the organism.

Cellular constraints are limits to rates of cell division, secretion of cell products, and cell migration and/or metabolic efficiency. Metabolic constraints such as the maximum rate of respiration limit the abundance of tissues that have high rates of oxygen consumption. Functional constraints arise in embryos as the organ systems responsible for functions such as feeding and respiration become functionally connected.

Limits to the maximum rate of mutation and recombination that reduce the potential rate of evolutionary change are one form of genetic constraint. The other is a form of historical constraint. Some genes are highly conserved, occurring in many species and higher taxonomic units, because they are involved with fundamental aspects of development.

Phylogenetic constraints (also called historical constraints) are reflected in differences among species that result from having different patterns of descent. Phylogenetic constraints are one reason why variation associated with the production of a given baüplan (body plan) is minimal. Therefore, development of the baüplan may be canalized (guided or controlled) by both structural and historical aspects of genetic constraints. SEE ALSO ALLOMETRY; BODY PLAN; MORPHOLOGY; PHYLOGENETICS SYSTEMATICS.

Andrew G. Gluesenkamp

Bibliography

Cockburn, Andrew. *An Introduction to Evolutionary Ecology.* Oxford, U.K.: Blackwell Science, 1991.

Gilbert, Scott F. *Developmental Biology.* Sunderland, MA: Sinauer Associates, 1991.

Gilbert, Scott F., and Anne M. Raunio, eds. *Embryology: Constructing the Organism.* Sunderland, MA: Sinauer Associates, 1997.

McKinney, Michael L., and Kenneth J. McNamara. *Heterochrony: The Evolution of Ontogeny.* New York: Plenum Publishing Corp., 1991.

Raff, Rudolf A. *The Shape of Life.* Chicago: University of Chicago Press, 1996.

Raff, Rudolf A., and Thomas C. Kaufman. *Embryos, Genes, and Evolution: The Developmental-Genetic Basis of Evolutionary Change.* New York: Macmillan, 1983.

Continental Drift

If you have ever looked at a map of the Atlantic Ocean, you have probably noticed that the coastlines of Africa and South America seem to fit together like pieces of a jigsaw puzzle. The fit between the two coastlines is even better when the edges of the continental shelf are compared. For many years, scientists thought this was just a coincidence, because no one could think of a way that the continents could slide around.

Evidence for Continental Drift

Evidence that South America and Africa might once have been joined to each other came from the research of the German geographer, Alexander von Humboldt. Von Humboldt traveled throughout South America, Africa, and other parts of the world, collecting plant and animal specimens and studying geography and geology. He observed many similarities between

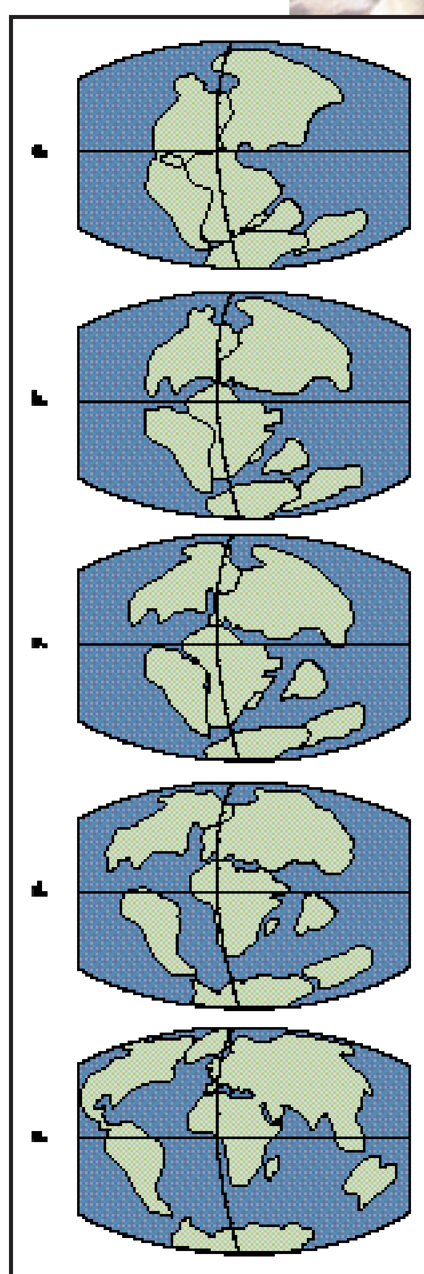
South America and Africa in addition to the apparent fit of continental coastlines. For example, von Humboldt noticed that the mountain ranges near Buenos Aires, Argentina, match mountain ranges in South Africa.

Other mountain ranges in Brazil extend to near the seashore and stop. Similar mountain ranges begin at the corresponding seashore in Ghana in Africa. All of these mountain ranges appear to have the same age and to be formed of the same kinds of rock. The rock strata in these and other mountain ranges would match perfectly if the coastlines of the two continents were lined up. Von Humboldt also observed similar patterns among mountain ranges in Europe and North America.

Von Humboldt and other naturalists also noticed many similarities among fossils of plants and animals on either side of the Atlantic. Although fossil species in eastern South America are somewhat different from fossil species in western Africa, their similarities are often striking. Before long, similarities across other oceanic gaps were observed. Plant and animal fossils found in India, for example, are often remarkably similar to those found in Australia.

Another important piece of evidence was discovered in the early twentieth century. When molten lava freezes, it preserves traces of Earth's magnetic field. Basalt, which freezes deep underground, also records Earth's magnetic field at the time the basalt cooled. Measurements of the direction of Earth's magnetic field from many different rocks of different ages on different continents indicate either that Earth's magnetic poles have moved all over the planet or that the continents themselves have moved.

Continental drift was first proposed in 1908 by American geologist Frank B. Taylor. However, Taylor's paper was mostly ignored and soon forgotten. Then a German meteorologist, Alfred Wegener, began working on a theory of continental drift. By 1912 Wegener had developed a theory suggesting that continental rocks were stronger and lighter than seafloor rocks. He also suggested that the seafloor rocks were like very thick tar. He concluded that the stronger continents were able to drift around on the weaker seafloor rocks.



a) Pangaea at end of Permian; b) Pangaea breaks up at the end of Triassic; c) End of Jurassic; d) End of Cretaceous; e) Today. Redrawn from Matthews, 1981.

Furthermore, Wegener thought the continents had once been part of a single large land mass, which he called Pangaea. Initially, he asserted, the original land mass had broken into two parts, two supercontinents, which he called Gondwanaland and Laurasia. Over millions of years, he suggested, Gondwanaland had broken apart into South America, Africa, India, Australia, and Antarctica, while Laurasia separated into North America and Eurasia.

Unfortunately, Wegener could not suggest any mechanism that would have caused the continents to break apart and move around in this way. In contrast to Taylor's experience, Wegener's theory was met with rejection and open hostility by other scientists, probably because Wegener was a meteorologist, not a geologist.

In the mid 1930s, however, Wegener's ideas were resurrected and rehabilitated. Scientists had discovered a ridge down the middle of the Atlantic seafloor through which hot lava was flowing upward and spreading outward. Stripes of lava on either side of this ridge were progressively older the farther away they were from the ridge. This pattern of stripes of lava strongly suggested to the scientists that the floor of the Atlantic Ocean was getting steadily wider. The discovery of this spreading of the seafloor, along with other discoveries, eventually led to the modern theory of **plate tectonics**.

plate tectonics the theory that Earth's surface is divided into plates that move

Plate Tectonics

Wegener's idea of continental drift had the continents floating around on semisolid oceanic rock. In contrast, plate tectonics suggests that Earth's entire crust is composed of a number of large plates that are in constant motion relative to each other. Some plates are sliding under other plates, some are sliding past each other, others are pulling apart, and still others are colliding. Each of these types of interactions produces unique geological consequences. The Himalayas are formed as two continental plates collide. Along the northwest coast of North America, an oceanic plate is sliding under the North American plate. The resulting geological characteristic is a chain of volcanoes. As one plate is forced under the other, friction causes enormous amounts of heat that builds up until a volcano forms and erupts. Earthquakes are often the result of sudden movement of two adjacent plates. The plates "lock up" until enough force is generated to break them apart, causing the quake. One of the world's most famous earthquake zones, the San Andreas Fault, lies at the boundary of the Pacific and the North American plates.

After being initially rejected and ridiculed, the concept of continental drift (and plate tectonics) is now widely accepted as one of the fundamental unifying ideas of geology. This shift in thinking among geologists depended not only on the discovery of an adequate explanation for continental movement (seafloor spreading, rifts, and trenches) but also on the discovery of more and more similarities between continents.

Evolution and Biological Diversity

Early explorers, mapmakers, and traders were often accompanied on their travels by naturalists (people who studied all the natural sciences). These naturalists made two striking observations. They found that fossils of exactly the same plants and animals were located on continents that are separated by thousands of miles of oceans. For example, the tropical fossil fern, *Glossopteris*, was found in South America, Africa, India, and Australia. Similarly, fossils of the land vertebrate, *Kannemeyrid*, were found in Africa, North and South America, and Asia.

While the ancient fossils on different continents were often similar or identical, the exploring naturalists were finding out that living plants and animals on the different continents were often very different. The naturalists were discovering whole new groups of animals and plants on nearly every island and continent they visited. Most biological species seemed to be unique to the region or continent in which they were found. How could these seemingly contradictory observations be reconciled? Plate tectonics provided the answer. When the different land masses were connected, the same or closely related plants and animals inhabited each. After the land masses were separated, the different populations were geographically isolated from each other by great distances of ocean. Life on the different con-

A marsupial is a member of the mammalian subclass Metatheria, which includes a wide variety of mammals that give birth to undeveloped young. The young complete their development outside the mother's body, attached to a nipple. Most marsupials have a pouch that covers the nipples and protects the young while they are developing.

tinents had apparently evolved into different species, because the populations were isolated from each other by such great distances.

It is possible to correlate, or link, the breakup of the continents with the types of animals found on each. The longer the period of separation, the more differences between species were found. For example, all of the indigenous (native) mammals found in Australia are marsupials. There are no naturally occurring **placental** mammals. This suggests that Australia broke away before placental mammals had evolved. In geographic isolation from the rest of the world, Australia's mammals were able to evolve into many highly sophisticated forms found nowhere else.

placental having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

Has the diversity of life on Earth increased as a result of the breakup of the supercontinents? This idea was first proposed in 1970 by the American geologists James W. Valentine and Eldridge M. Moores. They suggested that the diversity of life increased as continents broke up and moved apart and decreased as land masses moved together and joined.

Since 1970 the study of plate activity as a force in the evolution of life has substantially added to our understanding of evolution. For example, during the Permian period (around 286 million years ago), there was a decrease in the variety of species of animals living in the shallow seas around Pangaea. In contrast, when the Atlantic Ocean began to open during the middle Mesozoic era (144 million years ago), the differences between the species living on opposite shores gradually increased. The greater the distance, the smaller the number of families in common. Differences accumulated more rapidly in the South Atlantic than in the North Atlantic, because a land connection between Europe and North America remained until the Cenozoic era (66 million years ago). The opposite happened when North and South America became connected at the **Isthmus** of Panama. In South America, there were many different marsupials and few large predators. After the isthmus emerged, many large herbivores migrated south. They adapted well to the new environment and were more successful than the local fauna in competing for food. Large predators also moved south and contributed to the extinction of at least four orders of South American land mammals. Only a few species, such as the armadillo and the opossum, migrated in the opposite direction. Many of the invading northerners, such as the llama and tapir, died out in North America and are now found only in the south. SEE ALSO Biogeography.

isthmus a narrow strip of land

Elliot Richmond

Bibliography

Cox, Allan, ed. *Plate Tectonics and Geomagnetic Reversals.* San Francisco: W. H. Freeman, 1973.

Dott, Robert H., Jr., and Roger L. Batten. *Evolution of the Earth*, 3rd ed. New York: McGraw-Hill, 1994.

Faul, Henry, and Carol Faul. *It Began with a Stone: A History of Geology from the Stone Age to the Age of Plate Tectonics.* New York: Wiley, 1983.

Foster, Robert. *Geology*, 3rd ed. Columbus, OH: Charles E. Merrill, 1976.

Hallam, Anthony. *A Revolution in the Earth Sciences: From Continental Drift to Plate Tectonics.* Oxford, U.K.: Clarendon Press, 1973.

Matthews, William H., et al. *Investigating the Earth*, 3rd ed. Boston: Houghton Mifflin, 1981.

Stanley, Stephen. *Earth and Life through Time.* New York: W. H. Freeman, 1989.

Toulmin, Stephen, and June Goodfield. *The Discovery of Time.* New York: Harper and Row, 1965.

Uyeda, Seiya. *The New View of the Earth: Moving Continents and Moving Oceans.* San Francisco: W. H. Freeman, 1978.

Wilson, J. Tuzo, ed. *Continents Adrift and Continents Aground.* San Francisco: W. H. Freeman, 1976.

Wood, Robert Muir. *The Dark Side of the Earth: The Battle for the Earth Sciences, 1800–1980.* London: Allen and Unwin, 1985.

Wyllie, Peter J. *The Way the Earth Works: An Introduction to the New Global Geology and Its Revolutionary Development.* New York: Wiley, 1976.

Convergence

The term "convergence" is used to describe the presence of a similar feature in two or more taxa that are not closely related. Convergent features evolve independently often as a result of natural selection operating on unrelated taxa that occupy similar environments. The recognition of convergence requires an accurate phylogeny. With a **phylogenetic** hypothesis, **homologous** characters can be distinguished from **analogous** traits. Convergent structures are usually derived from different morphological features or by different developmental pathways (although this is not the case in one special class of convergence described below).

phylogenetic relating to the evolutionary history of species or group of related species

homologous similar but not identical

analogous describes a similarity in structures between two species that are not closely related

Convergence can be further broken down into specific phenomena. Analogy describes the convergent modifications of a nonhomologous trait. For example, analogous organs may share a common function but develop from different tissue types in unrelated organisms. The wings of insects and the wings of birds have the same functional role (flight) but they are derived from nonhomologous structures and are structurally very different. Therefore, they are considered analogous structures. The term "parallelism" refers to apomorphic, or derived, traits. Apomorphies are identical traits that are found in different taxa but that do not share a common evolutionary origin. Apomorphies may arise independently (even in closely related taxa) as consequences of similarities in development among species (often due to developmental constraints imposed by similarities in genes that regulate developmental processes). Parallelism differs from other types of convergent evolution in that parallel traits are the product of the same genes and developmental processes operating in different taxa. In this case, convergence is found not only in physical traits but also in the developmental processes that produce them.

A striking example of convergent evolution in animals is the evolution of flight in three different vertebrate taxa: pterosaurs (extinct flying reptiles), birds, and bats. Structural similarities in the wings of each of these groups are indications of common constraints imposed by phylogeny and biomechanics. All vertebrate forelimbs have similar developmental patterns, regardless of whether they will become limbs or wings in the adult. In order to achieve flight, the ratio of the surface area of the wings relative to body mass must be great enough to provide sufficient lift to overcome gravity. Differences among them indicate that in each lineage, unique solutions have evolved under particular historical and functional constraints, resulting in different structural patterns with similar functions. Pterosaurs, like

The Egyptian jerboa is sometimes referred to as a "kangaroo rat" because of its kangaroo-like hind legs, an example of analogous development.

birds, had hollow bones and keeled sterna (breastbones), a short and stout humerus (upper arm bone), and wing fibers that were analogous to bird feathers. The pterosaur wing was supported primarily by an elongated fourth digit. In birds, digits of the forelimb are reduced and the wing is supported primarily by the radius and ulna (bones of the lower arm) and bones of the wrist. Feathers provide rigidity and increased surface area to the wing. In pterosaurs and bats the digits are elongated and provide support for patagia (thin membranes of skin). In birds, feathers provide a unique structural solution to the challenge of flight while elongate digits and patagia have evolved convergently in other groups that lack feathers. SEE ALSO Biological Evolution.

Andrew G. Gluesenkamp

Bibliography

Cockburn, Andrew. *An Introduction to Evolutionary Ecology.* Oxford, U.K.: Blacwell Scientific Publications, 1991.

Futuyma, D. J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, 1986.

McKinney, M. L. *Evolution of Life.* Englewood Cliffs, NJ: Prentice Hall, 1993.

Courtship

Courtship is a collection of instinctive behaviors that result in mating and eventual reproduction. Courtship is important because it helps to ensure that breeding will occur. Organisms within a species must reproduce successfully in order for the species to survive. Courtship has many other functions, including mate selection, regulation of sexual readiness so that the reproductive physiology of a pair may be synchronized, the reduction of hostility between potential sex partners in territorial animals, and species recognition. Courtship may be rather simple, involving a small number of

A male Australian great bowerbird at his bower, a brightly adorned passage or chamber designed to attract female bowerbirds.

visual, chemical, or auditory stimuli, or it may be a highly complex series of acts involving several types of communication. Some of the most complex courtship behaviors are found in birds.

Mating Systems

In addition to complex courtship patterns, birds also have interesting and varied breeding or mating systems. The most common type of mating system is monogamy, which resembles a traditional human marriage. Ninety percent of birds are monogamous. In this type of mating system, two birds come together or form a pair bond for the procreation of young. The length of the pair bond varies greatly between species and between individuals. A mated pair may remain together for life, as in the case of albatrosses, petrels, swans, geese, eagles, and some owls and parrots. They may remain together for several years, as in the case of American robins, tree swallows, and mourning doves. They may remain together for one year, which is the case with most birds; just for one brood, as is the case with house wrens; or for even shorter periods.

The two birds in a pair are usually faithful to each other during the time that they are together. Pair faithfulness appears to depend on the outward appearance of a bird's mate. This might be a simple matter of recognition. Ringed plovers, for example, establish enduring bonds. In one known instance involving two couples, however, one of the mates in each pair had lost a foot and was rejected by its former mate. Fortunately, the two rejected birds were opposite sexes. They met, paired, and successfully raised normal offspring.

It is difficult to determine, however, the exact nature of the physiological bond that holds a pair together. Other factors may be territory, familiarity with one another, or even something similar to human affection. In fact, it is thought that affectionate bonds actually exist between birds. On two separate occasions, it was observed that the partner of a black duck refused to leave its dying mate when the rest of the flock fled from hunters.

Less common than monogamous pair bonding is polygamy, or the practice of having more than one mate at a time. Polygamy occurs in a wide variety of birds, including peacocks, ostriches, and rheas. Polygamy is usually observed as either polygyny or polyandry. In polygyny, one male mates with two or more females, but the females mate with only one male. The inseminated females incubate their eggs in separate nests and rear their young unassisted by the male. This mating system is most likely to happen when males hold territories that vary greatly in the quality of resources. Important resources may include food, water, and shelter. Females will tend to choose superior males, or those with high-quality territories. If a male in a high-quality territory already has a mate, the new female will usually make a choice to either become his second mate or select a male that holds an inferior territory. If she selects a superior male, both will benefit from increased reproduction. Female marsh wrens sometimes mate with already-mated males, even when bachelor males are available. The number of females mated to each male is related to the amount of growing vegetation in the males' territories, which, in turn, appears to be an indicator of the availability of insect food. Studies of red-winged and yellow-headed blackbirds and indigo and lark buntings also show relationships between territory quality and the likelihood that a male holding a given territory will have more than one mate.

In polyandry, one female mates with two or more males. The word polyandry actually means "many males." This mating system is rare and occurs in less than 1 percent of all bird species—mostly in shorebirds. Polyandry is often accompanied by a reversal of sex roles in which males perform all or almost all of the parental duties. Females in this mating system also compete for mates, such as in the case of the northern jacana, Harris' hawk, acorn woodpecker, and spotted sandpiper.

Other unusual mating systems that birds exhibit are promiscuity, cooperative mating, and lekking. In promiscuous pair bonding, males and females mate indiscriminately. In cooperative pair bonding, two females usually rear broods in the same nest simultaneously, or nonbreeding birds serve as helpers in the nest of one or more breeding pairs. The male is usually not involved in caring for the eggs or the young. A remarkable exception is the American rhea, in which several females lay their eggs—on occasion as many as fifty—in one nest, where the male incubates them by himself. He is also responsible for the care of the young.

In lekking, males engage in communal displays at a traditional site known as a lek. In North America, males of certain members of the grouse family, including prairie chickens, sharp-tailed grouse, and sage grouse, compete for mates at leks.

During these elaborate courtship displays, male birds transmit information by special social signals. They call and inflate brightly colored air sacs on their necks while repeatedly carrying out ritualized dances. Females approach the lek, choose and mate with a male from the display group, and then leave to nest and rear the young alone. Male grouse have a hierarchy and often subdivide territories at a lek, with a dominant male usually holding the most central position and mating with the most females. Lekking species of grouse tend to live in open habitats. Not all lekking bird species live in open areas, however. In the tropics, many forest-dwelling birds such as cotingas, manakins, and hermit hummingbirds display at leks on forest floors.

Courtship Displays

While birds have a wide variety of mating systems, they have an equally vast array of courtship behaviors or displays including dancing, singing, sparring with bills, kissing, caressing, entwining necks, nibbling at each other's feathers, and side-by-side body contact. Some male birds even take on a completely different physical appearance during breeding season, when unique features such as specialized combs, wattles, and pouches appear.

Some aspects of nest building have been incorporated into the displays of some birds. Male and female penguins physically look the same—same size, coloration, and feathers, for example. Male penguins, which are unable to determine sex visually, have adopted a trial-and-error method to solve this problem. In a typical courtship, a male may place a pebble at the feet of another bird. If it is a male, it will start a fight. Females typically ignore the gesture or form a pair bond. The stones may be used later in nest building.

The bowerbirds of Australia and New Guinea (relatives of crows and birds of paradise) provide an example of a special category of courtship display. The males construct special display mounds known as bowers. In an attempt to gain the favor of females, less attractive male bowerbirds build the most elaborate bowers while the more attractive males seem to build less elaborate bowers. One common type of bower architecture consists of two parallel hedges of interlaced grasses or twigs stuck in the ground. In the space between the hedges and interlaced grass or twigs is an area where the male may do some of his displaying.

Another type of bower, called the maypole bower because of its height, is formed from a stack of twigs erected around a vertical sapling or arranged in the form of an open-sided, teepee-like hut whose roof center is supported by a sapling. These bowers are often very large, as many as 3 meters (10 feet) high. The floor under or in front of this type of bower is often cleared of all litter and decorated with colorful objects such as leaves, flowers, fruits, sun-bleached bones, snail shells, parrot feathers, seeds, bits of

colored glass, paper, and even jewelry. Some bowerbirds incorporate living orchids into the inner walls of the bower, while others paint the inner walls with mixtures of saliva, grass, or charcoal. One species, the satin bowerbird, paints the mixture onto the walls with a brush of fibers—a rare example of a tool-using animal. This type of bowerbird also has bright blue eyes and favors blue objects. His bower is frequently decorated with blue flowers, blue leaves, and blue-tinted mushrooms. Mating may occur inside the elaborate bowers.

After fertilization, the female builds a nest at a distance and incubates and raises young there. After the young have fledged, she may bring them to the bower where the family engages in a communal display. This may be an imprinting behavior to educate the young in the intricacies of this species' display etiquette. SEE ALSO BEHAVIOR; REPRODUCTION, ASEXUAL AND SEXUAL.

Stephanie A. Lanoue

Bibliography

Andrew, R. J. "The Displays Given by Passerines in Courtship and Reproductive Fighting: A Review." *Ibis* 103A (1961):315–348.

Bednarz, J. C. "Pair and Group Reproductive Success, Polyandry, and Cooperative Breeding in Harris' Hawks." *Auk* 104 (1987):393–404.

Birkhead, T., and A. Moller. "Avian Mating Games." *New Scientist* (1986):34–36.

Ehrlich, Paul R., David Dobkin, and Darryl Wheye. *The Birder's Handbook*. New York: Simon and Schuster, 1988.

Lenington, S., and T. Mace. "Mate Fidelity and Nesting Site Tenacity in the Killdeer." *Auk* 92 (1975):149–151.

Reynolds, J. D. "Mating System and Nest Biology of the Red-Necked Phalarope: What Constrains Polyandry?" *Ibis* 129 (1987):225–242.

Welty, J. C., and L. Baptista. *The Life of Birds*, 4th ed. Orlando, FL: Harcourt, Brace, and Jovanovich, 1990.

Crepuscular

The term "crepuscular" refers to the hours of dawn and dusk. Crepuscular animals include those species that are active at dawn, dusk, or both. Some animals are mistakenly considered to be nocturnal although they are actually crepuscular.

Most crepuscular animals tend to be desert dwellers that remain at rest during the harsh heat of day and the bitter chill of night. Snakes, mice, lizards, and some rabbits use broad daylight and late-night hours for resting in their respective shelters. By mating and foraging for food during the more temperate hours, crepuscular animals are able to conserve precious energy and still pursue those activities that contribute to propagating the species. The saw-scaled adder (*Echis carinatus*) of North Africa, Syria, Iran, and India prospers in arid, sandy regions. During the day, it lies sheltered from the heat under fallen tree trunks or rocks, or flattens its body and digs into the sand by means of its keeled lateral scales.

Not all crepuscular species call the desert their home. Certain deer, snakes, bats, rodents, and opossum tend to be active during early morning

and twilight hours because of rhythms of behavior as opposed to environmental controls. The forest musk deer (*Moschus chrysogaster*) lives in the forests and brushlands from the Himalayas to central China. Active in the morning and evening hours, the animal feeds on grass, moss, shoots, twigs, and buds.

Species that find food, avoid predators, and generally maintain body state more effectively during twilight obviously benefit from responding appropriately to different light levels. They may operate most efficiently if they can predict the changes during any twenty-four-hour period by means of an internal clock.

Ann Guidry

Bibliography

Caduto, Michael J. and Bruchac, Joseph. *Keepers of the Night*. Golden, CO: Fulcrum Publishing, 1994.

Lawlor, Elizabeth P. *Discover Nature at Sundown: Things to Know and Things to Do*. Mechanicsburg, PA: Stackpole Incorporated Book Division, 1995.

Photo and Line Art Credits

The illustrations and tables featured in Animal Sciences were created by GGS Information Services. The photographs appearing in the text were reproduced by permission of the following sources:

Volume One

Acoustic Signals (**4**): Zig Leszczynski/Animals Animals; *Adaptation* (**7**): JLM Visuals, Ken Cole/Animals Animals; *African Cichlid Fish* (**9**): Gerard Lacz/Animals Animals; *Aggression* (**11**): Lynn Stone/Animals Animals; *Agnatha* (**14**): Omikron, National Audobon Society Collection/Photo Researchers, Inc.; *Allometry* (**16**): Redrawn from Scott Gilbert; *Allometry* (**15**): Redrawn from Scott Gilbert; *Altruism* (**18**): Robert J. Huffman/Field Mark Publications; *Amphibia* (**20**): Robert J. Huffman/Field Mark Publications; *Animal Rights* (**25**): AP/Wide World Photos; *Animal Testing* (**29**): Yann Arthus-Bertrand/Corbis; *Annelida* (**31**): E. R. Degginger/Animals Animals; *Antibody* (**34**): Redrawn from Hans and Cassady; *Antlers and Horns* (**35**): Kennan Ward/Corbis; *Apiculture* (**37**): Breck P. Kent/Animals Animals; *Aposematism* (**39**): R. Andrew Odum, Toledo Zoological Society; *Aquaculture* (**42**): David Samuel Robbins/Corbis; *Aristotle* (**45**): UPI/Bettmann Newsphotos/Corbis; *Arthropoda* (**47**): Dr. Dennis Kunkel/Phototake; *Arthropoda* (**50**): JLM Visuals; *Aves* (**53**): Joe McDonald/Animals Animals; *Bailey, Florence Augusta Merriam* (**57**): Courtesy of the Library of Congress; *Bates, Henry Walter* (**58**): Courtesy of the Library of Congress; *Behavior* (**60**): Ross, Edward S., Dr.; *Behavior* (**61**): Carl Purcell/Corbis; *Binomial (Linnaean System)* (**64**): Archive Photos, Inc.; *Biodiversity* (**68**): Joerg Sarback/AP/Wide World Photo; *Bioethics* (**71**): Jacques M. Chenet/Corbis; *Bioethics* (**70**): Robyn Beck/Corbis; *Biological Evolution* (**75**): Sally Morgan/Ecoscene/Corbis; *Biological Evolution* (**76**): P. Parks-OSF/Animals Animals; *Biological Pest Control* (**80**): Bill Beatty/Animals Animals; *Biomechanics* (**84**): Brad Nelson/Phototake; *Biomes* (**88**): W. Wayne Lockwood, M.D./Corbis; *Biomes* (**89**): Robert J. Huffman/Field Mark Publications; *Blood* (**98**): Richard T. Nowitz/Phototake; *Body Cavities* (**100**): Redrawn from Holt, Rinehart and Winston; *Body Cavities* (**101**): Nancy Sefton, National Audubon Society Collection/Photo Researchers, Inc.; *Body Plan* (**108**): JLM Visuals; *Bone* (**111**): CNRI/Phototake; *Burgess Shale and Ediacaran Faunas* (**113**): Lowell Laudon/JLM Visuals; *Cambrian Explosion* (**117**): Robert J. Huffman/Field Mark Publications; *Cambrian Period* (**119**): Mickey Gibson/Earth Scenes; *Camouflage* (**120**): Art Wolfe/The National Audubon Society Collection/Photo Researchers, Inc.; *Cancer* (**123**): Luis M. De La Maza/Phototake; *Carson, Rachel* (**128**): UPI/Bettmann Newsphotos/Corbis; *Cartilage* (**129**): Dr. Mary Notter/Phototake; *Cell Division* (**134**): Redrawn from Gale Research; *Cells* (**136**): Redrawn from New York Public Library Desk Reference; *Cephalization* (**139**): P. Parks-OSF/Animals Animals; *Cestoda* (**142**): Custom Medical Stock Photo, Inc.; *Chitin* (**143**): Chris McLaughlin/Animals Animals; *Chondricthyes* (**145**): Joyce and Frank Burek/Animals Animals; *Chordata* (**147**): Ralph White/Corbis; *Circadian Rhythm* (**150**): George McCarthy/Corbis; *Circulatory system* (**152**): GCA/CNRI/Phototake; *Cnidaria* (**155**): Nancy Rotenberg/Animals Animals; *Coevolution* (**161**): Robert J.

Huffman/Field Mark Publications; *Coevolution* (**159**): Michael and Patricia Fogden/Corbis; *Communication* (**165**): James E. Lloyd/Animals Animals; *Community Ecology* (**168**): Richard Baetson/U.S. Fish and Wildlife Service, Washington D.C.; *Competition* (**174**): Ross, Edward S., Dr.; *Conservation Biology* (**177**): Fred Whitehead/Animals Animals; *Constraints on Animal Development* (**179**): Robert Lubeck/ Animals Animals; *Convergence* (**185**): E. R. Degginger/Animals Animals; *Courtship* (**186**): Michael Fogden/Animals Animals.

Volume Two

Cretaceous (**2**): Richard P. Jacobs/JLM Visuals; *Cultures and Animals* (**6**): Duluth Convention and Visitor's Bureau; *Cultures And Animals* (**8**): Craig Lovell/Corbis; *Darwin, Charles* (**10**): Courtesy of the Library of Congress; *DDT* (**12**): AP/Wide World Photos; *Defense* (**14**): Mark N. Boulton/The National Audubon Society Collection/Photo Researchers, Inc.; *Diamond, Jared* (**18**): AP/Wide World Photos; *Digestive System* (**22**): Roger De La Harpe/ Animals Animals; *Dinosaurs* (**25**): Graves Museum of Archaeology and Natural History/ AP/Wide World Photos; *Domestic Animals* (**29**): Tim Thompson/Corbis; *Dominance Hierarchy* (**32**): Tim Wright/Corbis; *Drosophila* (**34**): UPI/Bettmann Newsphotos/Corbis; *Echinodermata* (**36**): Herb Segars/Animals Animals; *Ecology* (**42**): U.S. National Aeronautics and Space Administration (NASA); *Ecosystem* (**47**): James Watt/Animals Animals; *Elton, Charles Sutherland* (): Animals Animals/©; Scott Johnson; *Embryology* (**52**): Science Pictures Limited/Corbis; *Embryonic Development* (**54**): Redrawn from Scott Gilbert; *Embryonic Development* (**59**): Redrawn from Scott Gilbert; *Endangered Species* (**62**): Vince Streano/The Stock Market; *Entomology* (**72**): Doug Wechsler/Earth Scenes; *Environmental Degradation* (**74**): George H. H. Huey/Earth Scenes; *Environmental Impact* (**78**): David Barron/Earth Scenes; *Excretory and Reproductive Systems* (**88**): Joe McDonald/ Animals Animals; *Exotic Species* (**91**): C. C. Lockwood/Animals Animals; *Extinction* (**100**): Glen Smart/U.S. Fish and Wildlife Service/ Washington, D.C.; *Extremophile* (**103**): TC Nature/Animals Animals; *Farming* (**105**): Tim Page/Corbis; *Feeding* (**111**): Malcolm S. Kirk/Peter Arnold, Inc.; *Feeding Strategies* (**114**): Bruce Davidson/Animals Animals; *Fertilization* (**117**): Hank Morgan/National Audubon Society Collection/Photo Researchers, Inc.; *Flight* (**122**): Zefa Germany/ The Stock Market; *Foraging Strategies* (**130**): Suzanne Danegger/Photo Researchers, Inc.; *Fossey, Dian* (**131**): AP/Wide World Photos; *Fossil Fuels* (**133**): H. David Seawell/Corbis; *Functional Morphology* (**137**): Tim Davis/Photo Researchers; *Genes* (**140**): Biophoto Associates/ National Audubon Society Collection/Photo Researchers, Inc.; *Genetic Engineering* (**149**): Lowell Georgia/Corbis; *Genetic Variation In A Population* (**153**): Eastcott-Momatiuk/Animals Animals; *Genetically Engineered Foods* (**156**): Lowell Georgia/Corbis; *Geneticist* (**157**): Photo Researchers, Inc.; *Genetics* (**160**): AP/ Wide World Photos; *Gills* (**164**): Breck P. Kent/Animals Animals; *Global Warming* (**168**): Bernard Edmaier/Science Photo Library/ Photo Researchers, Inc.; *Goodall, Jane* (**171**): AP/Wide World Photos; *Gould, Steven Jay* (**172**): Wally McNamee/Corbis; *Habitat* (**178**): Johnny Johnson/Animals Animals; *Habitat Loss* (**180**): Ecoscene/Corbis; *Habitat Loss* (**182**): Francois Gohier/National Audubon Society Collection/Photo Researchers, Inc.

Volume Three

Habitat Restoration (**3**): Eastcott-Momatiuk/ Earth Scenes; *Haeckel's Law Of Recapitulation* (**5**): Courtesy of the Library of Congress; *Haldane, J. B. S.* (**6**): Courtesy of the Library of Congress; *Heterochrony* (**9**): Christian Testu/ BIOS; *Home Range* (**11**): Darren Bennet/ Animals Animals; *Hormones* (**17**): Barbra Leigh/Corbis; *Horse Trainer* (**19**): Jerry Cooke/Animals Animals; *Human Commensal and Mutual Organisms* (**31**): LSF OSF/Animals Animals; *Human Evolution* (**35**): John Reader/ Science Photo Library/Photo Researchers, Inc.; *Human Populations* (**41**): AP/Wide World Photos; *Human–Animal Conflicts* (**28**): John Nees/Animals Animals; *HunterGatherers* (**44**): Anthone Bannister/Earth Scenes; *Hunting* (**46**): Raymond Gehman/Corbis; *Imprinting* (**50**): Robert J. Huffman/Field Mark

Publications; *Instinct* (**52**): Anup Shah/Animals Animals; *Interspecies Interactions* (**55**): JLM Visuals; *Iteroparity And Semelparity* (**58**): Kennan Ward/The Stock Market; *Jurassic* (**60**): E. R. Degginger/Earth Scenes; *Keratin* (**63**): L. Lauber-OSF/Animals Animals; *Lamarck* (**69**): Courtesy of the Library of Congress; *Leakey, Louis And Mary* (**70**): UPI/Bettmann Newsphotos/Corbis; *Learning* (**72**): Erwin and Peggy Bauer/Animals Animals; *LeviMontalcini, Rita* (**74**): AP/Wide World Photos; *Linnaeus, Carolus* (**77**): U.S. National Library of Science; *Living Fossils* (**80**): Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc.; *Locomotion* (**88**): Jeffrey L. Rotman/Corbis, Richard Alan Wood/Animals Animals, Ross, Edward S., Dr., Robert Winslow/Animals Animals; *Lorenz, Konrad* (**91**): UPI/Bettmann Newsphotos/Corbis; *Malaria* (**95**): Redrawn from Hans and Cassady; *Malthus, Thomas Robert* (**98**): Archive Photos, Inc.; *Mammalia* (**103**): Leonard Lee Rue III/Animals Animals; *Mayr, Ernst* (**106**): AP/Wide World Photos; *Mendel, Gregor* (**108**): Archive Photos, Inc.; *Mesenchyme* (**110**): Lester V. Bergman/Corbis; *Migration* (**117**): AP/Wide World Photos; *Mimicry* (**122**): Breck P. Kent/Animals Animals; *Molecular Biologist* (**126**): Philippe Plailly/National Audubon Society Collection/Photo Researchers, Inc.; *Molting* (**135**): Ross, Edward S., Dr.; *Morphological Evolution in Whales* (**137**): Bomford/T.Borrill-OSF/Animals Animals; *Mouth, Pharynx, Teeth* (**141**): H. Pooley/OSF/Animals Animals; *Muscular System* (**143**): Custom Medical Stock Photo, Inc.; *Museum Curator* (**145**): Robert J. Huffman/Field Mark Publications; *Natural Resources* (**147**): Richard Hamilton Smith/Corbis; *Nematoda* (**151**): Eric V. Grave/Photo Researchers, Inc.; *Nervous System* (**157**): Redrawn from Neil Campbell.; *Nervous System* (**155**): Secchi-Lecague/Roussel-UCLAF/CNRI/Science Photo Library/National Audubon Society Collection/Photo Researchers, Inc.; *Osteichthyes* (**169**): A. Kuiter/OSF/Animals Animals; *Parasitism* (**179**): Frank Lane Picture Agency/Corbis; *Pasteur, Louis* (**180**): Courtesy of the Library of Congress; *Peppered Moth* (**186**): Breck P. Kent/Animals Animals.

Volume 4

Permian (**2**): Richard P. Jacobs/JLM Visuals; *Pesticide* (**4**): Arthur Gloor/Earth Scenes; *Phylogenetic Relationships of Major Groups* (**6**): Redrawn from Caroline Ladhani.; *Plankton* (**12**): Douglas P. Wilson/Frank Lane Picture Agency/Corbis; *Pleistocene* (**16**): Breck P. Kent/Earth Scenes; *Pollution* (**21**): Wesley Bocxe/National Audubon Society Collection/Photo Researchers, Inc.; *Population Dynamics* (**26**): Wolfgang Kaehler/Corbis; *Populations* (**32**): JLM Visuals; *Predation* (**37**): Johnny Johnson/Animals Animals; *Primates* (**40**): Barbara Vonn Hoffmann/Animals Animals; *Reproduction, Asexual and Sexual* (): Animals Animals/©; Zig Leszczynski; *Reptilia* (**52**): Animals Animals/©; Zig Leszczynski; *Respiration* (**55**): Ron Boardman, Frank Lane Picture Agency/Corbis; *Respiratory System* (**58**): Photo Researchers, Inc.; *Rotifera* (**60**): P. Parks/OSF/Animals Animals; *Scales, Feathers, and Hair* (**62**): Dr. Dennis Kunkel/Phototake; *Selective Breeding* (**65**): George Bernard/Animals Animals; *Sense Organs* (**68**): Robert J. Huffman/Field Mark Publications; *Sexual Dimorphism* (**74**): Gregory G. Dimijian/Photo Researchers, Inc.; *Sexual Selection* (**77**): Animals Animals/©; Darren Bennett; *Shells* (**81**): Spreitzer, A.E., Mr.; *Simpson, George Gaylord* (**85**): Courtesy of the Library of Congress; *Skeletons* (**86**): E. R. Degginger/Animals Animals; *Social Animals* (**91**): G. I. Bernard/OSF/Animals Animals; *Sociality* (**95**): JLM Visuals;*Stevens, Nettie Maria* (**99**): Science Photo Library/Photo Researchers, Inc.; *Sustainable Agriculture* (**101**): Michael Gadomski/Earth Scenes; *Territoriality* (**106**): Jack Wilburn/Animals Animals; *Threatened Species* (**113**): Kenneth W. Fink/Photo Researchers, Inc.; *Tool Use* (**115**): C. Bromhall/OSF/Animals Animals; *Trematoda* (**123**): Photo Researchers, Inc.; *Triassic* (**125**): Robert J. Huffmann/Field Mark Publications; *Urochordata* (**130**): Joyce and Frank Burek/Animals Animals; *Vertebrata* (**132**): Breck P. Kent/JLM Visuals; *Veterinarian* (**134**): Peter Weiman/Animals Animals; *Viruses* (**136**): Scott Camazinr/National Audubon Society Collection/Photo Researchers, Inc.; *Vision* (**139**): J. A. L. Cooke/OSF/Animals Animals;

Vocalization (**142**): Victoria McCormick/ Animals Animals; *Von Baer's Law* (**143**): Courtesy of the Library of Congress; *Water Economy In Desert Organisms* (**147**): Langley, Cory, Mr., (**148**): Maslowski/Photo Researchers, Inc.; *Wild Game Manager* (**150**): Raymond Gehman/Corbis; *Wildlife Biologist* (**152**): Mark Stouffer/Animals Animals; *Wildlife Photographer* (**153**): Johnny Johnson/ Animals Animals; *Wilson, E. O.* (**154**): AP/ Wide World Photos; *Xenopus* (**156**): Zig Leszczynski/Animals Animals, Dr. Dennis Kunkel/Phototake; *Zoological Parks* (**159**): Alfred B. Thomas/Animals Animals; *Zoologist* (**162**): N. Rosing/OSF/Animals Animals; *Zooplankton* (**164**): M. I. Walker/Science Photo Library/National Audubon Society Collection/Photo Researchers, Inc.

Glossary

abiogenic: pertaining to a nonliving origin

abiotic: nonliving parts of the environment

abiotic factors: pertaining to nonliving environmental factors such as temperature, water, and nutrients

absorption: the movement of water and nutrients

acid rain: acidic precipitation in the form of rain

acidic: having the properties of an acid

acoelomate: an animal without a body cavity

acoelomates: animals without a body cavity

acoustics: a science that deals with the production, control, transmission, reception, and effects of sound

actin: a protein in muscle cells that works with myosin in muscle contractions

action potential: a rapid change in the electric charge of the cell membrane

active transport: a process requiring energy where materials are moved from an area of lower to an area of higher concentration

adaptive radiation: a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

adenosine triphoshate: an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

aestivate: a state of lowered metabolism and activity that permits survival during hot and dry conditions

agnostic behavior: a type of behavior involving a contest of some kind that determines which competitor gains access to some resource such as food or mates

alkaline: having the properties of a base

allele: one of two or more alternate forms of a gene

alleles: two or more alternate forms of a gene

allometry: relative growth of one part of an organism with reference to another part

allopatry: populations separated by a barrier

alluvial: sediments from flowing water such as silt, sand, mud, and gravel

alpha: the dominant member of a group

altruistic behavior: the aiding of another individual at one's own risk or expense

alveoli: thin-walled sacs in the lungs where blood in capillaries and air in the lungs exchange gases

ameloblasts: cells that form dental enamel

amiote: embryo of a vertebrate that is surrounded by a fluid-filled sac

ammonites: an extinct group of cephalopods with a curled shell

amnion: the membrane that forms a sac around an embryo

amniote: a vertebrate which has a fluid-filled sac that surrounds the embryo

amniotes: vertebrates which have a fluid-filled sac that surrounds the embryo

anadromous: moving from the ocean up a river to spawn

analogous: a similarity in structures between two species that are not closely related

anemia: a condition that results from a decreased number of red blood cells

angiosperms: a flowering plant that produces seeds within an ovary

annelids: segmented worms

anoxic: an environment that lacks oxygen

anterior: referring to the head end of an organism

anterior pituitary: the front part of the pituitary gland that produces hormones that stimulate the production of sperm and testosterone in the testes

antibodies: proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

antigen: foreign substances that stimulate the production of antibodies in the blood

anurans: the order of amphibians that contains frogs and toads

aphrodisiac: a substance or object that is thought to arouse sexual desire

aphrodisiacs: substances or objects that are thought to arouse sexual desire

aposematic: a feature or signal that serves to warn

aposematic coloration: a bright coloration in animals with physical or chemical defenses that act as a warning to predators

appendicular: having to do with arms and legs

appendicular skeleton: part of the skeleton with the arms and legs

aquatic: living in water

aragonite: a mineral form of calcium carbonate

arboreal: living in trees

Archae: an ancient lineage of prokaryotes that live in extreme environments

arthropod: a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

arthropods: members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

artificial pollination: manual pollination methods

asexual reproduction: a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

asymmetrical: lacking symmetry, having an irregular shape

aural: related to hearing

autonomic nervous system: division of the nervous system that carries nerve impulses to muscles and glands

autotroph: an organism that makes its own food

autotrophs: organisms that make their own food

axial skeleton: the skeleton that makes up the head and trunk

axon: cytoplasmic extension of a neuron that transmits impulses away from the cell body

axons: cytoplasmic extensions of a neuron that transmit impulses away from the cell body

B-lymphocytes: specialized cells produced from stem cells in the bone marrow that secrete antibodies that bind with antigens to form a pathogen fighting complex

bacterium: a member of a large group of single-celled prokaryotes

baleen: fringed filter plates that hang from the roof of a whale's mouth

Batesian mimicry: a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

behavioral: relating to actions or a series of actions as a response to stimuli

benthic: living at the bottom of a water environment

bilateral symmetry: characteristic of an animal that can be separated into two identical mirror image halves

bilaterally symmetrical: describes an animal that can be separated into two identical mirror image halves

bilateria: animals with bilateral symmetry

bilipid membrane: a cell membrane that is made up of two layers of lipid or fat molecules

bio-accumulation: the build up of toxic chemicals in an organism

bioactive protein: a protein that takes part in a biological process

bioactive proteins: proteins that take part in biological processes

biodiversity: the variety of organisms found in an ecosystem

biogeography: the study of the distribution of animals over an area

biological control: the introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

biological controls: introduction of natural enemies such as parasites, predators, or pathogens as a method of controlling pests instead of using chemicals

biomagnification: increasing levels of toxic chemicals through each trophic level of a food chain

biomass: the dry weight of organic matter comprising a group of organisms in a particular habitat

biome: a major type of ecological community

biometry: the biological application of statistics to biology

biotic: pertaining to living organisms in an environment

biotic factors: biological or living aspects of an environment

bipedal: walking on two legs

bipedalism: describes the ability to walk on two legs

birthrate: a ratio of the number of births in an area in a year to the total population of the area

birthrates: ratios of the numbers of births in an area in a year to the total population of the area

bivalve mollusk: a mollusk with two shells such as a clam

bivalve mollusks: mollusks with two shells such as clams

bivalves: mollusks that have two shells

body plan: the overall organization of an animal's body

bone tissue: dense, hardened cells that makes up bones

botany: the scientific study of plants

bovid: a member of the family bovidae which is hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

bovids: members of the family bovidae which are hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

brachiopods: a phylum of marine bivalve mollusks

brackish: a mix of salt water and fresh water

brood parasites: birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

buccal: mouth

budding: a type of asexual reproduction where the offspring grow off the parent

buoyancy: the tendency of a body to float when submerged in a liquid

Burgess Shale: a 550 million year old geological formation found in Canada that is known for well preserved fossils

calcified: made hard through the deposition of calcium salts

calcite: a mineral form of calcium carbonate

calcium: a soft, silvery white metal with a chemical symbol of Ca

capture-recapture method: a method of estimating populations by capturing a number of individuals, marking them, and then seeing what percentage of newly captured individuals are captured again

cardiac: relating to the heart

cardiac muscle: type of muscle found in the heart

cardiopulmonary: of or relating to the heart and lungs

carnivorous: describes animals that eat other animals

carrying capacity: the maximum population that can be supported by the resources

cartilage: a flexible connective tissue

cartilaginous: made of cartilage

catadromous: living in freshwater but moving to saltwater to spawn

character displacement: a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

chelicerae: the biting appendages of arachnids

chemoreceptors: a receptor that responds to a specific type of chemical molecule

chemosynthesis: obtaining energy and making food from inorganic molecules

chemosynthetic autotrophs: an organism that uses carbon dioxide as a carbon source but obtains energy by oxidizing inorganic substances

chemotrophs: animals that make energy and produce food by breaking down inorganic molecules

chitin: a complex carbohydrate found in the exoskeleton of some animals

chitinous: made of a complex carbohydrate called chitin

chloroquine: a drug commonly used to treat malaria

chromosomes: structures in the cell that carry genetic information

cilia: hair-like projections used for moving

circadian rhythm: daily, 24-hour cycle of behavior in response to internal biological cues

clades: a branching diagram that shows evolutionary relationships of organisms

Class Branchiopoda: a group of marine bivalve mollusks

Class Malacostraca: crustaceans such as lobsters, crabs, and shrimp

Class Maxillopoda: crustaceans such as barnacles, ostracods, and copepods

Class Merostomata: crustaceans such as horseshoe crabs and eurypterids

Class Pycnogonida: crustaceans such as sea spiders

cleavage: the process of cytokinesis in animal cells; as cells multiply, the plasma membrane pinches off to make two cells from one

climate: long-term weather patterns for a particular region

cnidaria: a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

cnidarians: aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

codominance: an equal expression of two alleles in a heterozygous organism

codon: the genetic code for an amino acid that is represented by three nitrogen bases

codons: the genetic code for an amino acid that is represented by three nitrogen bases

coelom: a body cavity

coevolution: a situation in which two or more species evolve in response to each other

coexist: live together

commensal: a symbiotic relationship wherein which one species benefits and the other is neither helped nor harmed

competitive exclusion principle: the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

compound eye: a multifaceted eye that is made up of thousands of simple eyes

compound eyes: multifaceted eyes that are made up of thousands of simple eyes

concentric: having the same center

conchiolin: a protein that is the organic basis of mollusk shells

coniferous, conifers: having pine trees and other conifers

connective tissue: cells that make up bones, blood, ligaments, and tendons

consumers: animals that do not make their own food but instead eat other organisms

continental drift: the movement of the continents over geologic time

contour feather: a feather that covers a bird's body and gives shape to the wings or tail

contour feathers: feathers that cover a bird's body and give shape to the wings or tail

controversy: a discussion marked by the expression of opposing views

convergence: animals that are not closely related but they evolve similar structures

copulation: the act of sexual reproduction

crinoids: an echinoderm with radial symmetry that resembles a flower

critical period: a limited time in which learning can occur

critical periods: a limited time in which learning can occur

crustaceans: arthropods with hard shells, jointed bodies, and appendages that mainly live in the water

ctenoid scale: a scale with projections on the edge like the teeth on a comb

cumbersome: awkward

cytoplasm: fluid in eukaryotes that surrounds the nucleus and organelles

cytosolic: the semifluid portions of the cytoplasm

death rate: a ratio of the number of deaths in an area in a year to the total population of the area

deciduous: having leaves that fall off at the end of the growing season

denaturing: break down into small parts

dendrites: branched extensions of a nerve cell that transmit impulses to the cell body

described: a detailed description of a species that scientists can refer to identify that species from other similar species

dessication: drying out

detritus: dead organic matter

deuterostome: animal in which the first opening does not form the mouth, but becomes the anus

deuterostomes: animals in which the first opening does not form the mouth, but becomes the anus

diadromous: animals that migrate between freshwater and saltwater

differentiation: differences in structure and function of cells in multicellular organisms as the cells become specialized

diffusion: the movement of molecules from a region of higher concentration to a region of lower concentration

dioecious: having members of the species that are either male or female

diploblastic: having two germ layers; ectoderm and endoderm

diploid cells: cells with two sets of chromosomes

direct fitness: fitness gained through personal reproduction

diurnal: active in the daytime

DNA replication: the process by which two strands of a double helix separate and form two identical DNA molecules

dominance hierarchies: the structure of the pecking order of a group of individuals of a group where the multiple levels of dominance and submission occur

dominant: an allele that is always an expressed trait

dorsal: the back surface of an animal with bilateral symmetry

dorsal root ganglia: nervous tissue located near the backbone

dorsoventrally: flattened from the top and bottom

dysentery: inflammation of the intestines that is characterized by pain, diarrhea, and the passage of mucous and blood

ecdysis: shedding the outer layer of skin or exoskeleton

ecdysone: hormone that triggers molting in arthropods

echinoderms: sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

ecological: relating to an organism's interaction with its environment

ecology: study of how organisms interact with their environment

ecosystem: a self-sustaining collection of organisms and their environment

ecosystems: self-sustaining collections of organisms and their environments

ecotourism: tourism that involves travel to areas of ecological or natural interest usually with a naturalist guide

ectodermal: relating to the outermost of the three germ layers in animal embryos

ectoparasite: an organism that lives on the surface of another organism and derives its nutrients directly from that organism

ectoparasites: organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

edentates: lacking teeth

El Niño: a periodic condition characterized by a warming of the central Pacific Ocean and the changes in global weather patterns that are brought about

emit: to send out or give off

endocrine system: the grouping of organs or glands that secrete hormones into the bloodstream

endoparasite: an organism that lives inside another organism and derives its nutrients directly from that organism

endoparasites: organisms that live inside other organisms and derive their nutrients directly from those organisms

endoskeleton: a skeleton that is surrounded by muscle tissue

endosymbionts: the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

endotrophic: deriving nourishment from within

enterocoelous: a cavity formed by the in-folding of the wall of the intestinal cavity in a gastrula

enzyme: a protein that acts as a catalyst to start a biochemical reaction

enzymes: proteins that act as catalysts to start biochemical reactions

epidermis: the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

epistasis: a phenomenon in which one gene alters the expression of another gene that is independently inherited

epithelial cells: cells that occur in tightly packed sheets that line organs and body cavities

epithelial lining: sheets of tightly packed cells that cover organs and body cavities

epitope: a localized region on an antigen that is recognized chemically by antibodies

equilibrium: a state of balance

erythrocytes: red blood cells, cells containing hemoglobin that carry oxygen throughout the body

estuaries: an area of brackish water where a river meets the ocean

ethology: animal behavior

eucoelomates: animals that have a true body cavity that is completely surrounded by mesoderm

eukaryota: a group of organisms containing a membrane bound-nucleus and membrane-bound organelles

eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles

eukaryotic cells: contains a membrane-bound nucleus and membrane-bound organelles

euryhaline: animals that can live in a wide range of salt concentrations

eusocial: animals that show a true social organization

evaporites: rocks formed from evaporation of salty and mineral-rich liquid

excrescence: an abnormal growth

excrescences: abnormal growths

exons: the coding region in a eukaryotic gene that is expressed

exoskeleton: a hard outer protective covering common in invertebrates such as insects

exoskeletons: hard outer protective coverings common in invertebrates such as insects

exponential growth: a population growing at the fastest possible rate under ideal conditions

extant: still living

facilitated diffusion: the spontaneous passing of molecules attached to a carrier protein across a membrane

facultative parasites: organisms that can survive either as a parasite or free-living

falconry: a sport where falcons are used for hunting

fascicle: a close cluster

fauna: animals

fertilization: the fusion of male and female gametes

fibroblasts: type of cells found in loose connective tissue that secretes the proteins for connective fibers

fight or flight response: an automatic, chemically controlled response to a stimulus that causes increased heart and breathing rates for increased activity

filter feeders: animals that strain small food particles out of water

fission: dividing into two parts

fixed action pattern: behaviors that are common to all members of a species

flagella (flagellum): cellular tail that allows the cell to move

flagellae: cellular tails that allow cells to move

flora: plants

fossil record: a collection of all known fossils

frequency-dependant selection: a decline in the reproductive success of a particular body type due to that body type becoming common in the population

frugivores: fruit-eating animals

functional morphology: studying form and function

fusion: coming together

gametes: reproductive cells that only have one set of chromosomes

gametocyte: cell that produces gametes through division

gametocytes: cells that produce gametes through division

ganoid scale: hard, bony, and enamel covered scales

gastropods: mollusks that are commonly known as snails

gastrovascular cavity: a single cavity where digestion occurs

gastrulation: the formation of a gastrula from a blastula

gene therapy: a process where normal genes are inserted into DNA to correct a genetic disorder

genes: segments of DNA located on chromosomes that direct protein production

genetic trait: trait related to biological inheritance

genetics: the branch of biology that studies heredity

genome: an organism's genetic material

genomes: the sum of all genes in a set of chromosomes

genotype: the genetic makeup of an organism

germ cell: an egg or sperm cell, a gamete

germ cells: egg or sperm cells, gametes

gill arches: arches of cartilage that support the gills of fishes and some amphibians

gill filaments: the site of gas exchange in aquatic animals such as fish and some amphibians

gills: site of gas exchange between the blood of aquatic animals such as fish and the water

gizzard: the muscular part of the stomach of some animals where food is ground

global warming: a slow and steady increase in the global temperature

glycoprotein: an organic molecule that contains a carbohydrate and a protein

gonad: the male and female sex organs that produce sex cells

gonads: the male and female sex organs that produce sex cells

granulocytes: a type of white blood cell where its cytoplasm contains granules

green house effect: a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

habitat: the physical location where organisms live in an ecosystem

habitat loss: the destruction of habitats through natural or artificial means

habitat requirement: necessary conditions or resources needed by an organism in its habitat

habitats: physical locations where organisms live in an ecosystem

Hamilton's Rule: individuals show less agression to closely related kin than to more distantly related kin

haplodiploidy: the sharing of half the chromosomes between a parent and an offspring

haploid cells: cells with only one set of chromosomes

hemocoel: a cavity between organs in arthropods and mollusks through which blood circulates

hemocyanin: respiratory pigment found in some crustaceans, mollusks, and arachnids

hemoglobin: an iron-containing protein found in red blood cells that binds with oxygen

hemolymph: the body fluid found in invertebrates with open circulatory systems

herbivore: an animal that eats plants only

herbivores: animals that eat only plants

herbivorous: animals that eat plants

heredity: the passing on of characteristics from parents to offspring

heritability: the ability to pass characteristics from a parent to the offspring

hermaphodite: an animals with both male and female sex organs

hermaphroditic: having both male and female sex organs

heterodont: teeth differentiated for various uses

heterotrophic eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles and do not make their own food

heterotrophs: organisms that do not make their own food

heteroxenous: a life cycle in which more than one host individual is parasitized

heterozygote: an organism whose chromosomes contain both genes of a contrasting pair

heterozygote advantage: a condition where a heterozygous individual has a reproductive advantage over a homozygous individual

Hippocrates: a central figure in medicine in ancient Greece, he is considered the father of modern medicine

home range: the area where an animal lives and eats

homeostasis: a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

homeothermic: describes animals able to maintain their body temperatures

hominid: belonging to the family of primates

hominids: belonging to the family of primates

homodont: teeth with a uniform size and shape

homologous: similar but not identical

homology: correspondence in the type of structure and its origin

homoplastic: similar but of different origins

homozygote: an animal with two identical alleles for one trait

hormone: a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

hormones: chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

Horseshoe crabs: "living fossils" in the class of arthropods

Hox genes: also known as selector genes because their expression leads embryonic cells through specific morphologic development

Human Genome Project: a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

hunting season: a period of time during which hunting is permited

hunting seasons: periods of time during which hunting is permited

hybrid: offspring resulting from the cross of two different species

hydrostatic skeleton: a pressurized, fluid-filled skeleton

hyperpolarizing potential: any change in membrane potential that makes the inside of the membrane more negatively charged

hypothalamus: part of the upper end of the brain stem that regulates activities in the nervous and endrocrine systems

IgA: imunoglobin A; a class of proteins that make up antibodies

IgD: imunoglobin D; a class of proteins that make up antibodies

IgE: imunoglobin E; a class of proteins that make up antibodies

IgG: imunoglobin G; a class of proteins that make up antibodies

IgM: imunoglobin M; a class of proteins that make up antibodies

inbreeding depression: loss of fitness due to breeding with close relatives

incomplete dominance: a type of inheritance where the offspring have an intermediate appearance of a trait from the parents

incus: one of three small bones in the inner ear

indirect fitness: fitness gained through aiding the survival of non-descendant kin

infrared: an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red; heat is carried on infrared waves

innate behavior: behavior that develops without influence from the environment

innervate: supplied with nerves

inoculation: introduction into surroundings that support growth

insectivore: an animal that eats insects

insectivores: animals that eat insects

instars: the particular stage of an insect's or arthropod growth cycle between moltings

integument: a natural outer covering

intercalation: placing or inserting between

intraspecific: involving members of the same species

introns: a non-coding sequence of base pairs in a chromosome

invagination: a stage in embryonic development where a cell layer buckles inward

invertebrates: animals without a backbone

involuntary muscles: muscles that are not controlled by will

isthmus: a narrow strip of land

iteroparous: animals with several or many reproductive events in their lives

***k*-selected species:** a species that natural selection has favored at the carrying capacity

***k*-selecting habitat:** habitat where there is a high cost of reproduction and is sensitive to the size of the offspring

key innovation: a modification that permits an individual to exploit a resource in a new way

keystone species: a species that controls the environment and thereby determines the other species that can survive in its presence

krill: an order of crustaceans that serves as a food source for many fish, whales, and birds

lancelet: a type of primitive vertebrate

lancelets: primitive vertebrates

lateral inhibition: phenomenon that amplifies the differences between light and dark

lateral line: a row of pressure sensitive sensory cells in a line on both sides of a fish

learned behavior: behavior that develops with influence from the environment

learning: modifications to behavior motivated by experience

leukocytes: a type of white blood cells that are part of the immune system

life history strategies: methods used to overcome pressures for foraging and breeding

life history strategy: methods used to overcome pressures for foraging and breeding

lipids: fats and oils; organic compounds that are insoluble in water

logistic growth: in a population showing exponential growth the individuals are not limited by food or disease

lungs: sac-like, spongy organs where gas exchange takes place

lymphocytes: white blood cell that completes development in bone marrow

macroparsite: a parasite that is large in size

macroparasites: parasites that are large in size

macrophages: white blood cell that attacks anything foreign such as microbes

malleus: the outermost of the inner ear bones

mantle: the tissue in mollusks that drapes over the internal organs and may secrete the shell

mantles: tissues in mollusks that drape over the internal organs and may secrete the shell

matrix: the nonliving component of connective tissue

megachiroptera: fruit bats and flying foxes

meiosis: a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

merozoite: a motile stage in some parastic protozoa

mesenchyme: the part of the mesoderm from which the connective tissues (bone, cartilage, and vascular system) arise

mesenteries: the membrane that suspends many internal organs in the fluid-filled body cavity of vertebrates

mesoderm: the middle layer of cells in embryonic tissue

messenger RNA: a type of RNA that carries protein synthesis information from the DNA in to the nucleus to the ribosomes

metamorphose: to change drastically from a larva to an adult

metamorphoses: changes drastically from its larval form to its adult form

metamorphosing: changing drastically from a larva to an adult

metamorphosis: a drastic change from a larva to an adult

metazoan: a subphylum of animals that have many cells, some of which are organized into tissues

metazoans: a subphylum of animals that have many cells, some of which are organized into tissues

microchiroptera: small bats that use echolocation

microparasite: very small parasite

microparasites: very small parasites

midoceanic ridge: a long chain of mountains found on the ocean floor where tectonic plates are pulling apart

mitochondria: organelles in eukaryotic cells that are the site of energy production for the cell

Mitochondrial DNA: DNA found within the mitochondria that control protein development in the mitochondria

mitosis: a type of cell division that results in two identical daughter cells from a single parent cell

modalities: to conform to a general pattern or belong to a particular group or category

modality: to conform to a general pattern or belong to a particular group or category

molecular clock: using the rate of mutation in DNA to determine when two genetic groups spilt off

molecular clocks: using the rate of mutation in DNA to determine when two genetic groups spilt off

mollusks: large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

molted: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

molting: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

monoculture: cultivation of a single crop over a large area

monocultures: cultivation of single crops over large areas

monocytes: the largest type of white blood cell

monophyletic: a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

monotremes: egg-laying mammals such as the platypus and echidna

monoxenous: a life cycle in which only a single host is used

morphogenesis: the development of body shape and organization during ontogeny

morphological: the structure and form of an organism at any stage in its life history

morphological adaptation: an adaptation in form and function for specific conditions

morphological adaptations: adaptations in form and function for specific conditions

morphologies: the forms and structures of an animal

mutation: an abrupt change in the genes of an organism

mutations: abrupt changes in the genes of an organism

mutualism: ecological relationship beneficial to all involved organisms

mutualisms: ecological relationships beneficial to all involved organisms

mutualistic relationship: symbiotic relationship where both organisms benefit

mutualistic relationships: symbiotic relationships where both organisms benefit

mutualists: a symbiotic relationship where both organisms benefit

myofibril: longitudinal bundles of muscle fibers

myofilament: any of the ultramicroscopic filaments, made up of actin and myosin, that are the structural units of a myofibril

myosin: the most common protein in muscle cells, responsible for the elastic and contractile properties of muscle; it combines with actin to form actomyosin

natural selection: the process by which organisms best suited to their environment are most likely to survive and reproduce

naturalist: a scientist who studies nature and the relationships among the organisms

naturalists: scientists who study nature and the relationships among the organisms

neuromuscular junction: the point where a nerve and muscle connect

neuron: a nerve cell

neurons: nerve cells

neurotransmitters: chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

niche: how an organism uses the biotic and abiotic resources of its environment

nocturnal: active at night

notochord: a rod of cartilage that runs down the back of Chordates

nucleotide: the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

nucleotide chain: a chain composed of five-carbon sugar groups that forms the basis for nucleic acid

nucleotides: building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

obligative mutualism: an animal that must exist as part of a mutually beneficial relationship

obligatory parasites: an animal that can only exist as a parasite

olfactory: relates to the sense of smell

omnivorous: eating both plants and animals

ontogeny: the embryonic development of an organism

oocyst: a cyst in sporozoans that contains developing sporozoites

operculum: a flap covering an opening

operculum chamber: space covered by a flap

organelles: membrane-bound structures found within a cell

ornithology: the study of birds

osmoregulatory functions: controlling the water balance within an animal

osmoregulatory system: system that regulates the water balance between an organism and its environment

osmosis: the diffusion of water across a membrane

ossification: deposition of calcium salts to form hardened tissue such as bone

osteoblasts: potential bone forming cells found in cartilage

oviparous: having offspring that hatch from eggs external to the body

ovoviparity: having offspring that hatch from eggs retained in the mother's uterus

ovoviviparous: having offspring that hatch from eggs retained in the mother's uterus

paleoanthropology: the study of ancient humans

parasitology: the study of parasites

parasympathetic division: part of the nervous system that generally enhances body activities that gain and conserve energy such as digestion and heart rate

parental imprinting: a process by which a gene's expression in a child depends on which parent donated it before development

passive diffusion: the passing of molecules across a membrane from an area of higher concentration to an area of lower concentration without any energy input

pathogens: disease-causing agents such as bacteria, fungi, and viruses

pecking order: the position of individuals of a group wherein multiple levels of dominance and submission occur

pectoral: of, in, or on the chest

pedipapls: one pair of short appendages near the mouth in some arthropods used for feeding and copulation

pericardial cavity: the space within the membrane that surrounds the heart

peripheral nervous system: the sensory and motor nerves that connect to the central nervous system

peritoneum: the thin membrane that lines the abdomen and covers the organs in it

pesticide: any substance that controls the spread of harmful or destructive organisms

pesticides: substances that control the spread of harmful or destructive organisms

pH: a measure of how acidic or basic a substance is by measuring the concentration of hydrogen ions

phalanges: bones of the fingers and toes

pharyngeal: having to do with the tube that connects the stomach and the esophagus

phenotype: physical and physiological traits of an animal

phenotypes: the physical and physiological traits of an animal

phenotypic: describes the physical and physiological traits of an animal

phenotypic trait: physical and physiological variations within a population

phenotypic variation: differences in physical and physiological traits within a population

pheromones: small, volatile chemicals that act as signals between animals that influence physiology or behavior

phlogenetic: relating to the evolutionary history

phospholipid: molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water

photoreceptors: specialized cells that detect the presence or absence of light

photosynthesis: the combination of chemical compounds in the presence of sunlight

photosynthesizing autotrophs: animals that produce their own food by converting sunlight to food

phyla: broad, principle divisions of a kingdom

phylogenetic: relating to the evolutionary history of species or group of related species

phylogeny: the evolutionary history of a species or group of related species

physiological: relating to the basic activities that occur in the cells and tissues of an animal

physiology: the study of the normal function of living things or their parts

placenta: the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placental: having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placoid scale: a scale composed of three layers and a pulp cavity

placoid scales: scales composed of three layers and a pulp cavity

plankton: microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

plate tectonics: the theory that Earth's surface is divided into plates that move

platelet: cell fragment in plasma that aids clotting

platelets: cell fragments in plasma that aid in clotting

pleural cavity: the space where the lungs are found

plumose: having feathers

pluripotent: a cell in bone marrow that gives rise to any other type of cell

poaching: hunting game outside of hunting season or by using illegal means

poikilothermic: an animal that cannot regulate its internal temperature; also called cold blooded

polymer: a compound made up of many identical smaller compounds linked together

polymerase: an enzyme that links together nucleotides to form nucleic acid

polymerases: enzymes that link together nucleotides to form nucleic acid

polymodal: having many different modes or ways

polymorphic: referring to a population with two or more distinct forms present

polymorphism: having two or more distinct forms in the same population

polymorphisms: having two or more distinct forms in the same population

polyploid: having three or more sets of chromosomes

polysaccharide: a class of carbohydrates that break down into two or more single sugars

polysaccharides: carbohydrates that break down into two or more single sugars

population: a group of individuals of one species that live in the same geographic area

population density: the number of individuals of one species that live in a given area

population dynamics: changes in a population brought about by changes in resources or other factors

population parameters: a quantity that is constant for a particular distribution of a population but varies for the other distrubutions

populations: groups of individuals of one species that live in the same geographic area

posterior: behind or the back

precursor: a substance that gives rise to a useful substance

prehensile: adapted for siezing, grasping, or holding on

primer: short preexisting polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase

producers: organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

progeny: offspring

prokaryota: a group of organisms that lack a membrane-bound nucleus and membrane-bound organelles

prokaryotes: single-celled organisms that lack a true cell nucleus

prokaryotic endosymbionts: single-celled organisms that lack a true cell nucleus that live inside of other cells

proprioceptors: sense organs that receive signals from within the body

protostome: animal in which the initial depression that starts during gastrulation becomes the mouth

protostomes: animals in which the initial depression that starts during gastrulation becomes the mouth

protozoa: a phylum of single-celled eukaryotes

protozoan: a member of the phylum of single-celled organisms

pseudocoelom: a body cavity that is not entirely surrounded by mesoderm

pseudocoelomates: animals with a body cavity that is not entirely surrounded by mesoderm

pterylae: feather tracks

quadrupedal: describes an animal with four legs

quadrupeds: animals with four legs

quinine: substance used to treat malaria

***r*-selected species:** a species that shows the following characteristics: short lifespan; early reproduction; low biomass; and the potential to produce large numbers of usually small offspring in a short period of time

***r*-selecting habitat:** the concept where a high reproductive rate is the chief determinant of life history

radially symmetric: wheel-like symmetry in which body parts radiate out from a central point

radially symmetrical: describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

recessive: a hidden trait that is masked by a dominant trait

recombinant DNA: DNA that is formed when a fragment of DNA is incorporated into the DNA of a plasmid or virus

regeneration: regrowing body parts that are lost due to injury

relative abundance: an estimate of population over an area

rennin: an enzyme used in coagulating cheese; is obtained from milk-fed calves

resorbed: absorption of materials already in the body

resorption: absorbing materials that are already in the body

respiratory pigments: any of the various proteins that carry oxygen

restriction enzymes: bacterial proteins that cut DNA at specific points in the nucleotide sequence

retina: a layer of rods and cones that line the inner surface of the eye

riparian: habitats in rivers and streams

ruminants: plant-eating animals with a multicompartment stomach such as cows and sheep

sagital plane: a plane that runs long-ways through the body

salamanders: four-legged amphibians with elongated bodies

sarcomere: one of the segments into which a fibril of striated muscle is divided by thin dark bands

scavengers: animals that feed on the remains of animals it did not kill

schizocoelous: the mesoderm originates from existing cell layers when the cells migrate

scleroblasts: cells that give rise to mineralized connective tissue

sedimentary rock: rock that forms when sediments are compacted and cemented together

semelparous: animals that only breed once and then die

serial homology: a rhythmic repetition

sessile: not mobile, attached

sexual reproduction: a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

sexual selection: selection based on secondary sex characteristics that leads to greater sexual dimorphorphism or differences between the sexes

sexual size dimorphism: a noticeable difference in size between the sexes

shoals: shallow waters

single-lens eyes: an eye that has a single lens for focusing the image

skeletal muscle: muscle attached to the bones and responsible for movement

smooth muscle: muscles of internal organs which is not under conscious control

somatic: having to do with the body

somatic nervous system: part of the nervous system that controls the voluntary movement of skeletal muscles

somatosensory information: sensory information from different parts of the body except for the eyesm tongue, ears, and other primary sense organs

somites: a block of mesoderm along each side of a chordate embryo

sonar: the bouncing of sound off distant objects as a method of navigation or finding food

spinal cord: thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

splicing: spliting

spongocoel: the central cavity in a sponge

sporozoa: a group of parasitic protozoa

sporozoans: parasitic protozoans

sporozoite: an infective stage in the life cycle of sporozoans

stapes: innermost of the three bones found in the inner ear

stimuli: anything that excites the body or part of the body to produce a specific response

stimulus: anything that excites the body or part of the body to produce a specific response

strata: layers of sedimentary rock consisting of approximately the same kinds of material

striated muscle: a type of muscle with fibers of cross bands usually contracted by voluntary action

striated muscles: muscles with fibers of cross bands usually contracted by voluntary actions

superposition: the order in which sedimentary layers are found with the youngest being on top

symbiosis: any prolonged association or living together of two or more organisms of different species

symbiotic relationship: close, long-term relationship where two species live together in direct contact

symbiotic relationships: close, long-term relationships where two species live together in direct contact

symmetrical: a balance in body proportions

synapse: the space between nerve cells across which impulses are chemically transmitted

systematic: study of the diversity of life

tactile: the sense of touch

tapetum: a reflective layer in the eye of nocturnal animals

taxa: named taxonomic units at any given level

taxon: named taxonomic unit at any given level

taxonomy: the science of classifying living organisms

terraria: a small enclosure or closed container in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrariums: small enclosures or closed containers in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrestrial: living on land

thoracic: the chest area

thromboplastin: a protein found in blood and tissues that promotes the conversion of prothrombin to thrombin

torpid: a hibernation strategy where the body temperature drops in relation to the external temperature

trachea: the tube in air-breathing vertebrates that extends from the larynx to the bronchi

transcription: process where enzymes are used to make an RNA copy of a strand of DNA

transgenic: an organism that contains genes from another species

transgenic organism: an organism that contains genes from another species

translation: process where the order of bases in messenger RNA codes for the order of amino acids in a protein

transverse plane: a plane perpendicular to the body

trilobites: an extinct class of arthropods

triploblasts: having three germ layers; ectoderm, mesoderm, and endoderm

trophic level: the division of species in an ecosystem by their main source of nutrition

trophic levels: divisions of species in an ecosystem by their main source of nutrition

ungulates: animals with hooves

urea: soluble form of nitrogenous waste excreted by many different types of animals

urethra: a tube that releases urine from the body

uric acid: insoluble form of nitrogenous waste excreted by many different types of animals

ventral: the belly surface of an animal with bilateral symmetry

vertebrates: animals with a backbone

viviparity: having young born alive after being nourished by a placenta between the mother and offspring

viviparous: having young born alive after being nourished by a placenta between the mother and offspring

vocalization: the sounds used for communications

voluntary muscles: a type of muscle with fibers of cross bands usually contracted by voluntary action

wavelength: distance between the peaks or crests of waves

zooplankton: small animals who float or weakly move through the water

zygote: a fertilized egg

zygotes: fertilized eggs

zymogens: inactive building-block of an enzyme

Topic Outline

ADAPTATIONS

Adaptation
Antlers and Horns
Aposematism
Biological Evolution
Biomechanics
Blood
Camouflage
Catadromous—Diadromous and Anadromous Fishes
Colonization
Communication
Community Ecology
Comparative Biology
Defense
Echolocation
Egg
Extremophile
Locomotion
Mimicry
Peppered Moth
Tool Use
Water Economy in Desert Organisms

AGRICULTURE

Apiculture
Aquaculture
Classification Systems
Dinosaurs
Domestic Animals
Farmer
Farming
Selective Breeding
Sustainable Agriculture

ANIMAL DIVERSITY

Animal
Biodiversity
Biogeography
Biological Evolution
Cambrian Explosion
Camouflage
Cephalization
Coevolution
Colonization
Community Ecology
Constraints on Animal Development
Diversity of Major Groups
Extremophile
Functional Morphology
Kingdoms of Life
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Prokaryota
Sexual Dimorphism
Taxonomy

ANIMAL GROUPS

Agnatha
Amphibia
Annelida
Arthropoda
Aves
Cephalochordata
Cestoda
Chondricthyes
Chordata
Cnidaria
Dinosaurs
Echinodermata

Eukaryota
Mammalia
Metazoan
Molluska
Nematoda
Osteicthyes
Platyhelmithes
Porifera
Primates
Prokaryota
Reptilia
Rotifera
Trematoda
Turbellaria
Urochordata
Vertebrata

ANIMAL HISTORY

African Cichlid Fishes
Animal
Burgess Shale and Ediacaran Faunas
Cambrian Explosion
Coevolution
Colonization
Constraints on Animal Development
Domestic Animals
Eukaryota
Extinction
Fossil Record
Horses
Kingdoms of Life
Living Fossils
Paleontologist
Paleontology
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Tetropods—From Water to Land
Xenopus

ANATOMY

Acoustic Signals
Biomechanics
Body Cavities
Body Plan
Bone
Cartilage
Cells
Cephalization
Comparative Biology
Echolocation
Embryology
Embryonic Development
Feeding
Functional Morphology
Gills
Growth And Differentiation of the Nervous System
Homology
Keratin
Locomotion
Mouth, Pharynx, and Teeth
Muscular System
Neuron
Scales, Feathers, and Hair
Sense Organs
Skeletons
Vision

BEHAVIOR

Acoustic Signals
Aggression
Altruism
Behavior
Behavioral Ecology
Circadian Rhythm
Courtship
Crepuscular
Diurnal
Dominance Hierarchy
Ethology
Homeostasis
Imprinting
Instinct
Learning
Migration
Nocturnal
Social Animals
Sociality
Sociobiology
Territoriality

BIOCHEMISTRY AND PHYSIOLOGY

Absorption
Allometry
Antibody
Blood

Cancer
Cell Division
Cells
Digestion
Egg
Homeostasis
Hormones
Keratin
Molecular Biologist
Molecular Biology
Molecular Systematics
Physiologist
Physiology
Respiration
Transport

BIODIVERSITY

Biodiversity
Biogeography
Biomass
Biomes
Colonization
Community Ecology
Diversity of Major Groups
Eukaryota
Habitat
Habitat Loss
Habitat Restoration
Zooplankton

CAREERS IN ANIMAL SCIENCE

Ecologist
Environmental Lawyer
Farmer
Functional Morphologist
Geneticist
Horse Trainer
Human Evolution
Livestock Manager
Marine Biologist
Medical Doctor
Molecular Biologist
Museum Curator
Paleontologist
Physiologist
Scientific Illustrator
Service Animal Trainer
Systematist
Taxonomist
Veterinarian
Wild Game Manager
Wildlife Biologist
Wildlife Photographer
Zoologist

CELL BIOLOGY

Absorption
Blood
Cell Division
Cells
Viruses

ECOLOGY

African Cichlid Fishes
Behavioral Ecology
Biotic Factors
Camouflage
Community Ecology
Competition
Competitive Exclusion
Conservation Biology
DDT
Ecologist
Ecology
Ecosystem
Evolutionary Stable Strategy
Exotic Species
Expenditure per Progeny
Feeding Strategies
Fitness
Food Web
Foraging Strategies
Growth And Differentiation of the Nervous System
Habitat
Habitat Loss
Habitat Restoration
Home Range
Human Commensals and Mutual Organisms
Interspecies Interactions
Iteroparity and Semelparity
Keystone Species
Life History Strategies
Malthus, Thomas Robert

Parasitism
Plankton
Population Dynamics
Populations
Predation
Territoriality
Trophic Level
Zooplankton

ENVIRONMENT

Biological Pest Control
Biomass
Biomes
Biotic Factors
Carson, Rachel
DDT
Ecosystem
Endangered Species
Environment
Environmental Degradation
Environmental Impact
Environmental Lawyer
Fossil Fuels
Global Warming
Human Populations
Natural Resources
Pesticide
Pollution
Silent Spring
Threatened Species

ETHICS

Animal Rights
Animal Testing
Bioethics

EVOLUTION

Adaptation
African Cichlid Fishes
Aposematism
Biological Evolution
Camouflage
Coevolution
Constraints on Animal Development
Continental Drift
Convergence
Darwin, Charles
Genetic Variation in a Population
Heterochrony
Homology
Human Evolution
Lamarck
Leakey, Louis and Mary
Modern Synthesis
Morphological Evolution in Whales
Morphology
Natural Selection
Peppered Moth
Sexual Dimorphism
Sexual Selection
Spontaneous Generation

FORM AND FUNCTION

Acoustic Signals
Adaptation
African Cichlid Fishes
Antlers and Horns
Aposematism
Biomechanics
Blood
Body Cavities
Body Plan
Bone
Burgess Shale and Ediacaran Faunas
Camouflage
Cell Division
Cells
Cephalization
Chitin
Circulatory System
Communication
Defense
Digestion
Digestive System
Echolocation
Endocrine System
Excretory and Reproductive Systems
Feeding
Flight
Gills
Gliding and Parachuting
Locomotion
Mimicry
Nervous System

Respiratory System
Sexual Selection
Shells
Vision
Vocalization

GENETICS

Drosophila
Genes
Genetic Engineering
Genetic Variation in a Population
Genetically Engineered Foods
Geneticist
Genetics
Mendel, Gregor
Modern Synthesis
PCR
Viruses

GEOLOGIC HISTORY

Cambrian Period
Carboniferous
Continental Drift
Cretaceous
Devonian
Geological Time Scale
Jurassic
K/T Boundary
Oligocene
Ordovician
Permian
Pleistocene
Quaternary
Silurian
Tertiary
Triassic

GROWTH AND DEVELOPMENT

Allometry
Antlers and Horns
Body Cavities
Body Plan
Bone
Cartilage
Cell Division
Cells
Comparative Biology
Constraints on Animal Development
Egg
Embryology
Embryonic Development
Haeckel's Law of Recapitulation
Heterochrony
Mesenchyme
Metamorphosis
Molting
Ontogeny
Serial Homology
Von Baer's Law

HISTORICAL FIGURES IN SCIENCE

Aristotle
Bailey, Florence Augusta Merriam
Bates, Henry Walter
Carson, Rachel
Darwin, Charles
Diamond, Jared
Elton, Charles Sutherland
Fausto–Sterling, Anne
Fossey, Dian
Goodall, Jane
Gould, Steven Jay
Haldane, J. B. S.
Lamarck, Jean-Baptiste
Leakey, Louis and Mary
Linnaeus, Carolus
Lorenz, Konrad
Malthus, Thomas Robert
Mayr, Ernst
McArthur, Robert
Mendel, Gregor
Montalcini, Rita Levi
Pasteur, Louis
Simpson, George Gaylord
Stevens, Nettie Maria
Wallace, Alfred Russel
Wilson, E. O.

HUMANS AND THE ANIMAL WORLD

Cultures and Animals
Human Commensals and Mutual Organisms
Human Populations
Human–Animal Conflicts
Hunter-Gatherers

LIFE CYCLES

REPRODUCTION

SCIENTIFIC FIELDS OF STUDY

animal sciences

animal sciences

VOLUME 2
Cret–Hab

Allan B. Cobb, Editor in Chief

MACMILLAN REFERENCE USA™

THOMSON GALE™

New York • Detroit • San Diego • San Francisco • Cleveland • New Haven, Conn. • Waterville, Maine • London • Munich

Macmillan Reference USA	The Gale Group
1633 Broadway	27500 Drake Rd.
New York, NY 10019	Farmington Hills, 48331-3535

Printed in the United States of America
1 2 3 4 5 6 7 8 9 10

Library of Congress Cataloging-in-Publication Data
Animal Sciences / Allan B. Cobb, editor in chief.
p. cm.
Includes bibliographical references and index.
ISBN: 0-02-865556-7 (set) - ISBN 0-02-865557-5 (vol. 1) - ISBN 0-02-865558-3 (vol. 2) - ISBN 0-02-865559-1 (vol. 3) - ISBN 0-02-865560-5 (vol. 4)
1. Animal Culture. 2. Livestock. I. Title.
SF61.C585 2001
590.3-dc21 2001026627
Rev

Preface

Six hundred million years of animal evolution and adaptation have produced a stunning range and variety of life on Earth. From the oldest, single-celled creatures to the most complex mammalian forms, animal diversity defies easy categorization or explanation. The Macmillan *Animal Sciences* encyclopedia provides a clear and comprehensive resource for better understanding this vast domain. By the nature of its interdisciplinary scope, the subject of animal sciences demands an approach that is both specific and general, detailed and thematic. *Animal Sciences* achieves this end in the course of nearly three hundred well-researched, clearly presented entries that explore the wide ranging diversity that exists within the animal kingdom.

Students will learn how animals develop throughout their lives, how they adapt to their changing environments, and how they develop specialized structures over time. Entries in this category explain how animals develop from fertilized eggs to adults. While some forms of development are straightforward—like a puppy maturing to become a dog—other changes are more dramatic—like a caterpillar changing its body forms over the course of its metamorphosis into a butterfly. Other entries study the various forms of animals and how body parts function.

The encyclopedia gives significant attention to animal ecology and behavior. Entries show how animals are part of the world environment while exhibiting unique behaviors within their own particular environments. Animal ecology addresses how animals are a part of ecosystems and how they interact with plants and other animals, both within and beyond their individual species. Given the close relationship of animal behavior and ecology, a number of entries discuss how animals select mates, whether they live alone or as members of groups, or how they share resources within an ecosystem, to give just a few examples.

Finally, *Animal Sciences* surveys the connection between animals and humans. Humans are unique in the animal kingdom because of their ability to alter environments significantly. Agriculture, which includes the domestication of animals and farming, serves as the chief example of such human-inspired environmental change and its impact on animal life worldwide. In addition, humans are the most social of animals and have developed complex social interactions. As human populations grow, habitat once occupied

by other animals is converted to human use. One consequence of such socialization is the pollution generated from an expanding human population and its deleterious effect on animal environments.

Animal Sciences also presents biographies of selected scientists who have made significant contributions to the many related fields, and introduces readers to the myriad career opportunities in the discipline.

The authors who contributed entries to *Animal Sciences* represent diverse backgrounds, and include members of academic and research institutions, as well as practicing scientists. The editorial board sought informative, up-to-date, and engaging articles, most of which include cross references, photographs or illustrations that prove helpful in understanding challenging concepts. A generous collection of sidebars accent related subjects. Every attempt has been made to avoid overly technical terms or scientific jargon, and whenever necessary such terms are highlighted and defined in the margin. Selected bibliographies guide readers to additional up-to-date resources, including those found on the Internet. Each of the four volumes also includes a geologic time scale, with particular emphasis on animals, as well as a phylogenetic tree and an alternative table of contents that groups articles under more general topic headings.

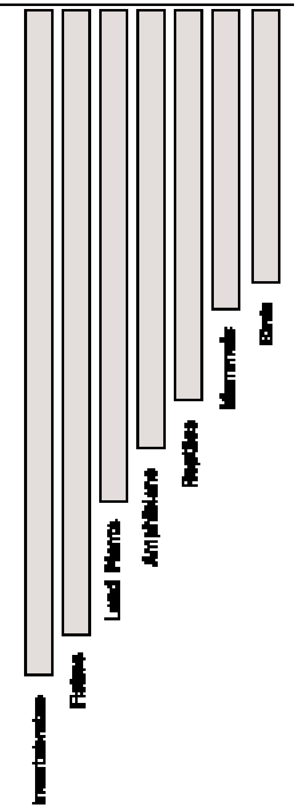
I wish to thank the staff at Macmillan Reference USA and the Gale Group for their hard work and attention to detail. In particular, I would like to thank Hélène Potter, Elly Dickason, Linda Hubbard, and Christa Brelin. I want to offer special thanks to Kate Millson for all her efforts and long hours in helping guide this project to fruition. I wish to thank the editorial board members—Amy Bryan, Andrew Gluesenkamp, and Marvin Elliot Richmond—for their vast knowledge and hard work. Finally, it is my hope that *Animal Sciences* can spark the interest of the next generation of committed scholars, researchers, and laypersons.

Allan B. Cobb
Editor in Chief

Geological Time Scale

Eon	Era	Period	Epoch	Significant Events	Million Years Before Present
Phanerozoic	Cenozoic	Quaternary	Holocene	recorded human history, rise and fall of civilizations, global warming, habitat destruction, pollution mass extinction	0.01
			Pleistocene	Homo sapiens, ice ages	1.6
		Tertiary	Pliocene	global cooling, savannahs, grazing mammals	5.3
			Miocene	global warming, grasslands, Chalicotherium	24
			Oligocene		37
			Eocene	modern mammals flourish, ungulates	58
			Paleocene		66
	Mesozoic	Cretaceous		last of age of dinosaurs, modern mammals appear, flowering plants, insects	144
		Jurassic		large plant-eating dinosaurs, carnivorous dinosaurs, first birds, breakup of Pangea	208
		Triassic		lycophytes, glossopterids, and dicynodonts, and the dinosaurs	245
	Paleozoic	Permian		Permian ends with largest mass extinction in history of Earth, most marine invertebrates extinct	286
		Pennsylvanian		vast coal swamps, evolution of amniote egg allowing exploitation of land	320
		Mississipian		shallow seas cover most of Earth	360
		Devonian		vascular plants, the first tetrapods, wingless insects, arachnids, brachiopods, corals, and ammonite were also common, many new kinds of fish appeared	408
		Silurian		Coral reefs, rapid spread of jawless fish, first freshwater fish, first fish with jaws, first good evidence of life on land, including relatives of spiders and centipedes	438
		Ordovician		most dry land collected into Gondwana, many marine invertebrates, including graptolites, trilobites, brachiopods, and the conodonts (early vertebrates), red and green algae, primitive fish, cephalopods, corals, crinoids, and gastropods, possibly first land plants	505
		Cambrian		most major groups of animals first appear, Cambrian explosion	570
Precambrian	Proterozoic			stable continents first appear, first abundant fossils of living organisms, mostly bacteria and archaeobacteria, first eukaryotes, first evidence of oxygen build-up	2500
	Archean			atmosphere of methane, ammonia, water and continental plates began to form, oldest fossils consist of bacteria microfossils stromatolites, colonies of photosynthetic bacteria	3800
	Hadean			pre-geologic time, Earth in formation	4600

Time Range of Several Groups of Plants & Animals



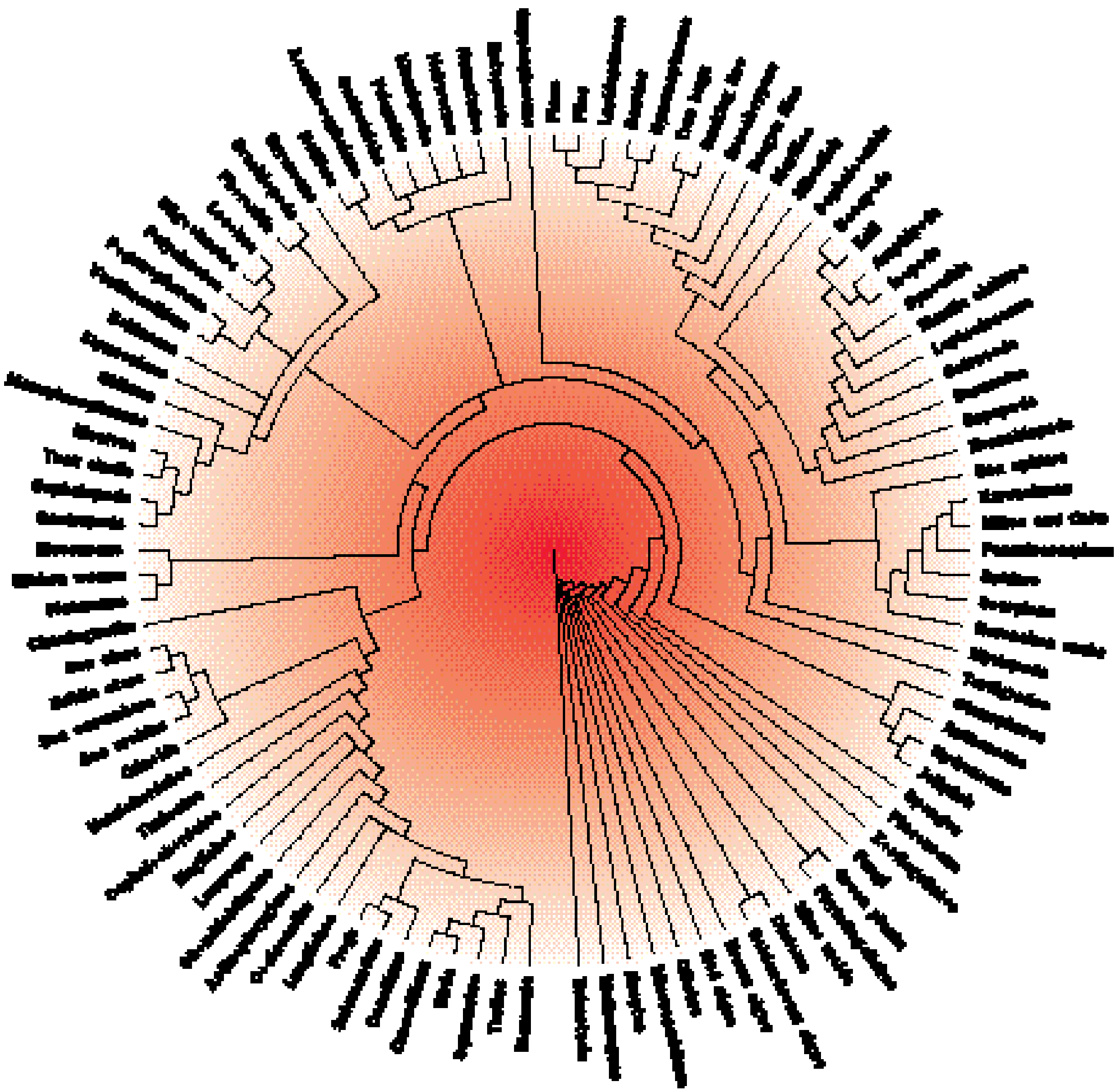
COMPARISON OF THE FIVE-KINGDOM AND SIX-KINGDOM CLASSIFICATION OF ORGANISMS

Five Kingdom	Six Kingdom
Kingdom: Monera Phylum: Bacteria Phylum: Blue-green algae (cyanobacteria)	Kingdom: Archaebacteria Kingdom: Eubacteria

- Kingdom: Protista
  - Phylum: Protozoans
    - Class: Ciliophora
    - Class: Mastigophora
    - Class: Sarcodina
    - Class: Sporozoa
  - Phylum: Euglenas
  - Phylum: Golden algae and diatoms
  - Phylum: Fire or golden brown algae
  - Phylum: Green algae
  - Phylum: Brown algae
  - Phylum: Red algae
  - Phylum: Slime molds
- Kingdom: Fungi
  - Phylum: Zygomycetes
  - Phylum: Ascomycetes
  - Phylum: Basidiomycetes
- Kingdom: Plants
  - Phylum: Mosses and liverworms
  - Phylum: Club mosses
  - Phylum: Horsetails
  - Phylum: Ferns
  - Phylum: Conifers
  - Phylum: Cone-bearing desert plants
  - Phylum: Cycads
  - Phylum: Ginko
  - Phylum: Flowering plants
    - Subphylum: Dicots (two seed leaves)
    - Subphylum: Monocots (single seed leaves)
- Kingdom: Animals
  - Phylum: Porifera
  - Phylum: Cnidaria
  - Phylum: Platyhelminthes
  - Phylum: Nematodes
  - Phylum: Rotifers
  - Phylum: Bryozoa
  - Phylum: Brachiopods
  - Phylum: Phoronida
  - Phylum: Annelids
  - Phylum: Mollusks
    - Class: Chitons
    - Class: Bivalves
    - Class: Scaphopoda
    - Class: Gastropods
    - Class: Cephalopods
  - Phylum: Arthropods
    - Class: Horseshoe crabs
    - Class: Crustaceans
    - Class: Arachnids
    - Class: Insects
    - Class: Millipedes and centipedes
  - Phylum: Echinoderms
  - Phylum: Hemichordata
  - Phylum: Cordates
    - Subphylum: Tunicates
    - Subphylum: Lancelets
    - Subphylum: Vertebrates
      - Class: Agnatha (lampreys)
      - Class: Sharks and rays
      - Class: Bony fishes
      - Class: Amphibians
      - Class: Reptiles
      - Class: Birds
      - Class: Mammals
        - Order: Monotremes
        - Order: Marsupials
        - Subclass: Placentals
          - Order: Insectivores
          - Order: Flying lemurs
          - Order: Bats
          - Order: Primates (including humans)
          - Order: Edentates
          - Order: Pangolins
          - Order: Lagomorphs
          - Order: Rodents
          - Order: Cetaceans
          - Order: Carnivores
          - Order: Seals and walruses
          - Order: Aardvark
          - Order: Elephants
          - Order: Hyraxes
          - Order: Sirenians
          - Order: Odd-toed ungulates
          - Order: Even-toed ungulates

PHYLOGENETIC TREE OF LIFE

This diagram represents the phylogenetic relationship of living organisms, and is sometimes called a “tree of life.” Often, these diagrams are drawn as a traditional “tree” with “branches” that represent significant changes in the development of a line of organisms. This phylogenetic tree, however, is arranged in a circle to conserve space. The center of the circle represents the earliest form of life. The fewer the branches between the organism’s name and the center of the diagram indicate that it is a “lower” or “simpler” organism. Likewise, an organism with more branches between its name and the center of the diagram indicates a “higher” or “more complex” organism. All of the organism names are written on the outside of the circle to reinforce the idea that all organisms are highly evolved forms of life.



SI BASE AND SUPPLEMENTARY UNIT NAMES AND SYMBOLS

Physical Quality	Name	Symbol
Length	meter	m
Mass	kilogram	kg
Time	second	s
Electric current	ampere	A
Thermodynamic temperature	kelvin	K
Amount of substance	mole	mol
Luminous intensity	candela	cd
Plane angle	radian	rad
Solid angle	steradian	sr

Temperature

Scientists commonly use the Celsius system. Although not recommended for scientific and technical use, earth scientists also use the familiar Fahrenheit temperature scale (°F). 1°F = 1.8°C or K. The triple point of H_2O, where gas, liquid, and solid water coexist, is 32°F.

- To change from Fahrenheit (F) to Celsius (C):
  °C = (°F-32)/(1.8)
- To change from Celsius (C) to Fahrenheit (F):
  °F = (°C x 1.8) + 32
- To change from Celsius (C) to Kelvin (K):
  K = °C + 273.15
- To change from Fahrenheit (F) to Kelvin (K):
  K = (°F-32)/(1.8) + 273.15

UNITS DERIVED FROM SI, WITH SPECIAL NAMES AND SYMBOLS

Derived Quantity	Name of SI Unit	Symbol for SI Unit	Expression in Terms of SI Base Units
Frequency	hertz	Hz	s-1
Force	newton	N	m kg s-2
Pressure, stress	Pascal	Pa	N m-2 =m-1 kg s-2
Energy, work, heat	Joule	J	N m =m2 kg s-2
Power, radiant flux	watt	W	J s-1 =m2 kg s-3
Electric charge	coulomb	C	A s
Electric potential, electromotive force	volt	V	J C-1 =m-2 kg s-3 A-1
Electric resistance	ohm	_	V A-1 =m2 kg s-3 A-2
Celsius temperature	degree Celsius	C	K
Luminous flux	lumen	lm	cd sr
Illuminance	lux	lx	cd sr m-2

UNITS USED WITH SI, WITH NAME, SYMBOL, AND VALUES IN SI UNITS

The following units, not part of the SI, will continue to be used in appropriate contexts (e.g., angtsrom):

Physical Quantity	Name of Unit	Symbol for Unit	Value in SI Units
Time	minute	min	60 s
	hour	h	3,600 s
	day	d	86,400 s
Plane angle	degree	°	(π/180) rad
	minute	'	(π/10,800) rad
	second	"	(π/648,000) rad
Length	angstrom	Å	10^{-10} m
Volume	liter	l, L	1 dm^3 = 10^{-3} m^3
Mass	ton	t	1 mg = 10^3 kg
	unified atomic mass unit	u (=m_a(^{12}C)/12)	≈1.66054 x 10^{-27} kg
Pressure	bar	bar	10^5 Pa = 10^5 N m^{-2}
Energy	electronvolt	eV (= e X V)	≈1.60218 x 10^{-19} J

CONVERSIONS FOR STANDARD, DERIVED, AND CUSTOMARY MEASUREMENTS

Length

1 angstrom (Å)	0.1 nanometer (exactly) 0.000000004 inch
1 centimeter (cm)	0.3937 inches
1 foot (ft)	0.3048 meter (exactly)
1 inch (in)	2.54 centimeters (exactly)
1 kilometer (km)	0.621 mile
1 meter (m)	39.37 inches 1.094 yards
1 mile (mi)	5,280 feet (exactly) 1.609 kilometers
1 astronomical unit (AU)	1.495979 x 10^{13} cm
1 parsec (pc)	206,264.806 AU 3.085678 x 10^{18} cm 3.261633 light-years
1 light-year	9.460530 x 10^{17} cm

Area

1 acre	43,560 square feet (exactly) 0.405 hectare
1 hectare	2.471 acres
1 square centimeter (cm^2)	0.155 square inch
1 square foot (ft^2)	929.030 square centimeters
1 square inch (in^2)	6.4516 square centimeters (exactly)
1 square kilometer (km^2)	247.104 acres 0.386 square mile
1 square meter (m^2)	1.196 square yards 10.764 square feet
1 square mile (mi^2)	258.999 hectares

MEASUREMENTS AND ABBREVIATIONS

Volume

1 barrel (bbl)*, liquid	31 to 42 gallons
1 cubic centimeter (cm^3)	0.061 cubic inch
1 cubic foot (ft^3)	7.481 gallons 28.316 cubic decimeters
1 cubic inch (in^3)	0.554 fluid ounce
1 dram, fluid (or liquid)	⅛ fluid ounce (exactly) 0.226 cubic inch 3.697 milliliters
1 gallon (gal) (U.S.)	231 cubic inches (exactly) 3.785 liters 128 U.S. fluid ounces (exactly)
1 gallon (gal) (British imperial)	277.42 cubic inches 1.201 U.S. gallons 4.546 liters
1 liter	1 cubic decimeter (exactly) 1.057 liquid quarts 0.908 dry quart 61.025 cubic inches
1 ounce, fluid (or liquid)	1.805 cubic inches 29.573 milliliters
1 ounce, fluid (fl oz) (British)	0.961 U.S. fluid ounce 1.734 cubic inches 28.412 milliliters
1 quart (qt), dry (U.S.)	67.201 cubic inches 1.101 liters
1 quart (qt), liquid (U.S.)	57.75 cubic inches (exactly) 0.946 liter

* There are a variety of "barrels" established by law or usage. For example, U.S. federal taxes on fermented liquors are based on a barrel of 31 gallons (141 liters); many state laws fix the "barrel for liquids" as 31½ gallons (119.2 liters); one state fixes a 36-gallon (160.5 liters) barrel for cistern measurement; federal law recognizes a 40-gallon (178 liters) barrel for "proof spirits"; by custom, 42 gallons (159 liters) comprise a barrel of crude oil or petroleum products for statistical purposes, and this equivalent is recognized "for liquids" by four states.

Units of mass

1 carat (ct)	200 milligrams (exactly) 3.086 grains
1 grain	64.79891 milligrams (exactly)
1 gram (g)	15.432 grains 0.035 ounce
1 kilogram (kg)	2.205 pounds
1 microgram (μg)	0.000001 gram (exactly)
1 milligram (mg)	0.015 grain
1 ounce (oz)	437.5 grains (exactly) 28.350 grams
1 pound (lb)	7,000 grains (exactly) 453.59237 grams (exactly)
1 ton, gross or long	2,240 pounds (exactly) 1.12 net tons (exactly) 1.016 metric tons
1 ton, metric (t)	2,204.623 pounds 0.984 gross ton 1.102 net tons
1 ton, net or short	2,000 pounds (exactly) 0.893 gross ton 0.907 metric ton

Pressure

1 kilogram/square centimeter (kg/cm^2)	0.96784 atmosphere (atm) 14.22334 pounds/square inch (lb/in^2) 0.98067 bar
1 bar	0.98692 atmosphere (atm) 1.02 kilograms/square centimeter (kg/cm^2)

Contributors

Allan B. Cobb
Austin, Texas
Jes Marie Creech
University of Texas, Austin
Emily H. DuVal
University of California, Berkeley
Andrew G. Gluesenkamp
University of Texas, Austin
Ann Guidry
Austin, Texas
Brook Ellen Hall
California State University, Sacramento
Laura A. Higgins
University of Texas, Austin
Ryan I. Hill
University of Texas, Austin
Alisha K. Holloway
University of Texas, Austin
Leslie Hutchinson
Flagstaff, Arizona
Jean Krejca
University of Texas, Austin
Stephanie A. Lanoue
Panama City Beach, Florida
Denise Prendergast
Austin, Texas
Ian Quigley
University of Texas, Austin
Elliot Richmond
Austin Community College
Karen Rogowski
University of Texas, Austin
Gil G. Rosenthal
University of California, San Diego
Todd A. Schlenke
University of Texas, Austin
Danielle Schnur
Austin, Texas
Judy P. Sheen
University of California, Berkeley
Kathrin F. Stanger-Hall
University of Texas, Austin
Rebecca M. Steinberg
University of Texas, Austin
Nancy Weaver
Driftwood, Texas
Brian R. West
University of Texas, Austin
Jennifer Yeh
University of Texas, Austin

Table of Contents

VOLUME 1:

VOLUME TWO:

H

VOLUME THREE:

I

J

K

L

M

Cretaceous Period

The Cretaceous period is the third of the three divisions of the Mesozoic era of the geologic time scale. The period lasted 79 million years, from 144 million to 65 million years ago. The Cretaceous is named for chalk beds found in England.

Era	Period	Epoch	Million Years Before Present
Mesozoic	Cretaceous		144
	Jurassic		208
	Triassic		245

Cretaceous and surrounding time periods.

Laurasia and Gondwanaland, the northern and southern landmasses that resulted from the initial breakup of the supercontinent Pangea, continued to separate from each other during the Cretaceous period. These landmasses also began to fragment within themselves to form our modern continents. Throughout most of the Cretaceous, North America was divided by a vast inland sea that extended from the Gulf of Mexico to Canada.

Early in the Cretaceous, the **climate** was warm and semitropical, very much like at the end of the Jurassic period (144 million years ago). However, during the second forty million years the climate became colder at the polar regions and warmer at the equator, setting in motion ecological changes that affected the evolution of plants and animals.

climate long-term weather patterns for a particular region

Shallow oceans supported abundant marine life, including new forms of oysters, diatoms, and algae as well as fish and sharks, corals, **echinoderms**, ammonoids, and mollusks. The edges of these shallow seas provided important **habitat** for mammals, turtles, crocodiles, fish, lizards, and many **invertebrates**.

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

habitat the physical location where an organism lives in an ecosystem

invertebrates animals without a backbone

Dramatic changes occurred in plant life during the Cretaceous. Pollinating insects such as bees and butterflies allowed the emerging flowering plants—the **angiosperms**—an advantage over seed-bearing plants that relied on the wind or a chance encounter with an animal to disperse their seeds. Today, nearly 90 percent of plants on Earth are angiosperms, signifying a remarkable evolutionary success story. Forests of oak and willow, cypress, magnolia, palms, and sycamore slowly replaced the cycad forests—palm-like

angiosperms a flowering plant that produces seeds within an ovary

These dinosaur eggs dating from the Cretaceous Period are part of the Smithsonian collection in Washington, D.C.

plants with a barrel shaped trunk and many long leaves growing from the top. These new plant communities provided new sources of food and habitat for many kinds of animals.

During the Cretaceous, the dinosaurs reached the height of their evolutionary success. Fossil bones found in Africa, the Gobi Desert, South America, China, Mongolia, and North America suggest that many new species emerged while earlier dinosaurs went extinct. The **carnivorous** animals such as *Albertasaurus* and *Tyrannosaurus* remained the top predators as they roamed and hunted their prey. Hadrosaurs, (duck-billed dinosaurs), Ankylosaurs (armored dinosaurs), and Ceratopsians (horned dinosaurs) replaced the giant Jurassic sauropods as the main **herbivores**. *Triceratops* fossils by the hundreds have been found, suggesting that these cows of the Cretaceous traveled in huge herds across the plains. Both herbivore and carnivore nests found in Montana, Mongolia, China, and South America suggest that many Cretaceous dinosaurs nested in colonies and possibly even cared for their young after they hatched.

carnivorous describes animals that eat other animals

herbivores animals who eat plants only

Mammals became more abundant during the Cretaceous. One group, the multituberculates, were a successful group of early mammals. By the end of the Cretaceous, when the dinosaurs were becoming extinct, the mammals survived and became a very successful group of animals.

A worldwide mass extinction occurred at the end of the Cretaceous period. This extinction killed off nearly 50 percent of Earth's existing species, including all of the remaining **terrestrial** dinosaurs other than birds, all marine and flying reptiles, and the ammonoids and other invertebrate and microscopic marine organisms. Many groups, however, including most plant species, birds, lizards and snakes, crocodiles and turtles, fish and sharks, many invertebrates, and the mammals survived into modern times.

terrestrial living on land

The causes of this mass extinction are still not completely understood and have led to many lively debates among scientists. One theory suggests that massive volcanic eruptions ejected enormous amounts of ash and harmful gases into the atmosphere, creating dark and cold conditions inhospitable to some plants and animals. One hypothesis suggests that a large asteroid hit the Earth, contributing to devastating climate changes. Still others, however, counter with the argument that the global climate was already in the process of cooling off, perhaps in part because of the drying up of North America's inland sea, and that this slow cooling may have led to more gradual changes in plant and animal life. Another proposition is that multiple factors, rather than one single catastrophic event, was responsible for the mass extinction. SEE ALSO Geological Time Scale; K/T Boundary.

Leslie Hutchinson

Bibliography

Lane, Gary, A., and William Ausich. *Life of the Past.* 4th ed. Englewood, NJ: Prentice Hall, 1999.

Russell, D. A. *An Odyssey in Time: The Dinosaurs of North America.* Chicago: Northwood Press, 1989.

Cultures and Animals

There have been many attempts to determine what it means to be human. At one time, biologists suggested that humans were the only tool users. However, many different animals use tools. Some scientists thought humans were the only animals that had language. But we now know that many animals use sophisticated communication systems similar to language. It would be an ironic twist if the thing that makes us most distinctly human is our relation to other animals, but as far as we know, humans are the only animals that keep other animals as pets.

Humans have had relationships with animals for as long as there have been humans. The human record, from prehistoric through the classical and modern periods and in every culture, is filled with examples of animals helping to shape our understanding of ourselves. Animals figure in our traditions, in our religions, in the stories we tell each other, and in our literature, such as the animal fables and parables of Aesop or Orwell.

hominid belonging to the family of primates

In West African and Caribbean cultures, animals play central roles in the native folklore. Asanti folk literature tells of the clever spider, Anancy, who frequently outwits the other creatures in his animal world. In the Caribbean, Anancy and monkey stories are known and narrated by most Afro-Caribbean children and adults. Throughout the African diaspora, these and other anthropomorphic folk tales frequently convey information about expected human behavior, good or bad.

Animals as a Natural Resource

Current debate on environmental issues is dominated by discussion of the dwindling supply of certain renewable and nonrenewable natural resources. However, one obvious renewable natural resource is often overlooked in this discussion: humans depend heavily on other animals.

As far back as our **hominid** beginnings, humans have exploited other animal species to meet our fundamental requirements for food and shelter. Animals have also served to meet other less tangible needs. The exploitation of animals as natural resources began at least 10,000 years ago as humans made the transition from a hunting and gathering lifestyle to the sedentary lifestyles of agriculture and pastoralism (herding of domestic animals). The domestication of animals brought about a fundamental change in the nature of human-animal relations. Instead of human as hunter and animals as prey, the relation became one of humans as master and animals as servant. Instead of thinking only of the dead animal as a source of food for the present, humans began to consider the living animal as a source of food for the future. With human protection, domesticated animal species have flourished, multiplied, and been transformed in many ways, so that they bear little resemblance to their wild ancestors.

We usually do not think of domesticated animals as a natural resource because they have become so much a part of our industrialized society. We tend to think of domestic animals as a sort of organic machinery for producing food. To some extent this is true. Selective breeding for desired characteristics in domestic animals has substantially reduced the genetic diversity of domestic animals in addition to making them into cultural objects. The size, shape, behavior, color, and fur of domestic animals has been transformed to make them more attractive or useful.

However, placing domesticated animals on the side of culture, rather than nature, is misleading. The natural world and the human environment do not stand separate and apart from each other. Domestication, even with human manipulation, is a product of evolution. Natural selection still operates on domestic animals.

The Human–Animal Relationship

While domestic animals constitute a crucial resource to human culture and have been given special human protection so that they now live almost exclusively within the bounds of human culture, regarding domestic animals as a product of human culture separate and apart from wild animals is an artificial distinction. Even those animals we think of as the wildest of wild animals—such as lions, tigers, elephants, rhinoceroses, and gorillas—live almost exclusively within culturally constructed environments. National parks and nature reserves set up to preserve endangered species and their natural habitats are just as much cultural artifacts as are zoos and wild animal parks.

Even when the environmental debate does consider domestic animals, the discussion is usually not about the animals themselves, but is about the pollution caused by animal waste, the plight of wild animals being threatened by human activity, or about the rights of animals involved in medical research. The discussion rarely considers human-animal relations.

The human-animal relationship has changed significantly since animals were first domesticated. Early pastoralists lived with their flocks, aiding in birth and protecting the flocks from predators. Modern human society has become increasingly more dependent on animal products while the separation between most humans and the agricultural animals we depend on has become more dramatic. We are more dependent, but less aware. The domestic animals that provide us with the wide variety of valuable products we depend on have become essentially invisible to most people.

As the divide between domestic animals and us grows ever wider, we have seemingly become more dependent on a special class of animals kept as pets. We keep pets to satisfy emotional needs rather than material needs. We enjoy stroking and cuddling our pets and seem to receive substantial emotional benefit from doing so. Thus the human-animal relation has pro-

> The relationships of animals to each other and to their environment give us something to compare ourselves to, and thus form a basis for describing our relations to each other. Many of the phrases we use to describe human characteristics are drawn from the animals we live with, such as "eats like a pig," "stubborn as a mule," or "fierce as a lion." These phrases anthropomorphize animal behavior and then use the imagined behavior as a description of human behavior.

foundly shifted from a relation with domestic animals to a very different sort of relation with our pets.

Humans and Their Pets

Humans keep a variety of animals as pets—snakes, lizards, roaches, spiders, fish, gerbils, rats, mice, birds—but the two most common are cats and dogs, with cat-owning households slightly outnumbering dog-owning households in the United States. Most pets serve no utilitarian purpose (although some dogs contribute to household security by barking at intruders). Pets are kept because they evoke affection or curiosity and often are given a special status as companions for members of the family. Cattle, horses, and other large domestic animals usually serve a more utilitarian purpose and are not ordinarily considered pets. However, elderly horses that can no longer serve a specific purpose are often kept as pets out of respect for the long years of service and companionship they provide.

> Cats have not always been honored. During the Middle Ages, cats were associated with witchcraft and were slaughtered in large numbers. This slaughter may have led to an explosion in the rodent population. As fleas carried by rodents can transmit bubonic plague, the destruction of cats may have contributed to the spread of the plague epidemic known as Black Death.

Cats. Modern domesticated cats (*Felis sylvestris catus*) are generally considered to be the descendants of the European wild cat, *Felis silvestris silvestris*, and the African wild cat, *Felis silvestris libyca*. Domestic cats probably evolved from African and European wild cats around 6,000 years ago.

The cat seems to have domesticated itself. In northern Africa, several cultures had developed well-established agricultural societies. Agriculture meant grain, and stored grain invited rodents. Out of the population of wild cats in the area, some had a higher tolerance for the presence of humans and a willingness to be near other cats (most cats are solitary creatures). Cats with these characteristics were able to move into the cities and onto the farms, where they found abundant prey. Keeping the rodents in check benefited the humans, so the cats were adopted and gradually increased in status. By 1600 B.C.E., cats were accepted as pets and by 1500 B.C.E. were regarded by the Egyptians as personal representatives of a deity, Bastet.

Dogs. The dog was probably the first animal to be domesticated by humans. This apparently occurred about 12,000 to 10,000 years ago. Domesticated dogs are classified as *Canis familiaris.* Some experts think that dogs are descendants of wolves (*Canis lupus*) and even go so far as to assign them to the subspecies *Canis lupus familiaris*. Dogs certainly freely interbreed with wolves and produce fertile off-spring. Others suggest they are descendants of a now extinct wild dog similar to the pariah dog of India.

How dogs were domesticated is still being debated. One suggestion is that dogs began to follow humans around, living off of discarded scraps of food. Through a gradual process of acclimation, both dogs and humans become more accepting of each other. Because dogs are natural **scavengers**, village trash heaps would be perfect places to find food. The wild dogs would scavenge through the scraps removing all the meat that would attract more dangerous scavengers. In this way, the dogs provided a substantial benefit to the humans.

Another suggestion is that humans deliberately domesticated dogs to aid in hunting. Dogs that had begun to hang around human settlements but were still interbreeding with wild dogs were first captured and kept in pens. Selective breeding gradually eliminated the wild characteristics. Subsequently, specialized dogs were bred by selective breeding. Also, to prevent cross-breeding, the remaining wild dog population was systematically exterminated.

Dogs often are put to work. This work includes sheep herding, rescue work, drug sniffing, pulling a sled, sentry duty, and serving as guide dogs for hearing- or vision-impaired persons. During World War I, the Red Cross used dogs to help search for wounded men on the battlefield. The U.S. Army started officially using dogs around the time of World War II.

Domesticated dogs have been trained to help humans with a variety of tasks. Here, a team of dogs pulls a sled in the Beargrease Sled Dog Marathon in Duluth, Minnesota.

scavengers animals that feed on the remains of animals that they did not kill

Problems in the Human–Pet Relationship. Abandoned pets are an enormous problem in most cities. In some cities, hundreds of cats and dogs are euthanized each day. Those euthanized may be the lucky ones, because house pets abandoned or released back to the wild almost always suffer a short, miserable existence, inevitably resulting in the animal's death.

The number of feral cats and dogs is a significant problem in most countries in the world. Feral animals are domestic animal breeds that live wild. One strategy that has been attempted to reduce the number of feral cats is to capture the cats, neuter them, and then return them to their original territory. The theory is that the cats will remain in the same approximate area, thus keeping new cats out in addition to their not being able to reproduce to replace the population. Results of this experiment are still being debated. This technique will not work for feral dogs because their behavior is different. They run in packs and defend a territory as a pack. Feral cats and dogs are a major concern in many countries because they can act as disease vectors (rabies) or carry the parasites (fleas and ticks) that act as disease vectors (plague and Lyme disease).

The relationship between humans and domesticated animals is loaded with contradictions. Dogs are often kept as cherished, pampered pets, but may also be severely maltreated and abandoned by their owners. An animal destined for the dinner plate may nevertheless receive a great deal of respect, care, and affection during its lifetime, demonstrating that the boundary between pets and livestock is blurred.

Both the manner in which we perceive animals and the way in which we treat them is evidence of the contradictory nature of the human-animal relationship imbedded within our cultures. For example, humans (who are not prohibited by religious belief) regularly consume the flesh of pigs. On the other hand, most Westerners are repelled by the idea of eating dog meat. Yet we keep both pigs and dogs as pets. In other parts of the world dog meat is regularly consumed, even by people who also keep dogs as pets. People from Western European culture are disgusted at the thought of eating insects, but readily consume many other arthropods with apparent gusto. In other parts of the world, insects form a significant portion of human diet. Although the relationship between humans and other animals has received increasingly more attention within the social sciences, only a few authors have explicitly drawn attention to the ambiguities that pervade everyday human-animal interactions.

Animals as Entertainment

Since 1958, the World's Largest Rattlesnake Round-Up, an event that benefits local charities, has been held in Sweetwater, Texas. It takes place annually around the first of March. The project was begun by local farmers and ranchers in an attempt to rid the area of an abundance of rattlesnakes that were endangering people and livestock. Over the years, more than 100,000 kilograms of rattlesnakes have been collected in the region.

The rattlesnakes are displayed for entertainment and most are "milked" to obtain venom to be used in the manufacture of antivenom vaccine. Events include a parade, the Miss Snake Charmer Pageant, snake-handling shows, brisket and chili cook-offs, and plenty of fried rattlesnake meat to snack on. Animal rights activists and environmentalists from all over the world have protested and criticized this event for many years. However, the event continues and the local rattlesnake population seems to be very little affected by this human tradition.

In the name of entertainment (sometimes thinly disguised as education), circuses, dog races, horse races, and marine parks often use animals. Unfortunately, some of these animals are not well treated. Orcas and dolphins in marine parks live only 25 percent as long as animals in the wild. These animals regularly swim long distances, up to 100 kilometers (62 miles) per day, in the wild. When kept in small pools the animals are not able to swim such long distances, hence, they suffer from stress and increased rates of disease. Circus elephants also experience stress when kept in captivity for entertainment purposes. Since 1990, circus elephants have killed 43 people. Elephants are not normally aggressive animals, but the stress of captivity can cause these highly intelligent animals to go insane.

Animals and World Religions

Religion, whether organized or not, is an intimate part of human culture. All of the world's major religions have explicit or implicit principles concerning the proper character of the human-animal relationship. Most of the world's religions recognize the importance of animals and the animal-human interaction. However, few major religions hold ceremonies to mark the birth or death of animals that are the equivalent of ceremonies marking the birth or death of humans. This seems to indicate that many world religions relegate animal life to a secondary status when compared to human life. Nonetheless, ethics and morality concerning the use of animals is an important issue that most world religions consider to be within their domain. Sometimes, the religion's standpoint on issues relating to animals is clearly stated in holy writings. In other instances, an interpretation of a written passage is made by a person or official body within the religion.

With few exceptions, the general attitude of most of the world's religions toward the relation of humans and animals can be characterized by five general principles. 1) Human life is more valuable than animal life because humans have a "soul" (or something equivalent to a soul). (2) Humans have a God-given authority over other animals. This is usually expressed as "dominion" or "stewardship." (3) The right of humans to consume animals for nutrition and to use the labor of animals is recognized by several, but not all world religions. (4) Cruelty to animals—pointless acts that will cause an animal to experience pain or suffering—is prohibited by most religions because it displays attributes that are undesirable in civilized societies. Even religions that previously or currently practice animal sacrifice often specify that the animal be killed in as painless a manner as possible. (5) Most religions urge kindness toward animals.

All of the world's major religions have explicit or implicit principles concerning the proper character of human–animal relationships. These Hindu women are petting a sacred cow during a religious festival in Nepal.

Christianity. For many Christians, an indicator of the desired relationship of humans to animals is found in Matthew 10:29–31 in the Christian New Testament. The verses suggest that, although the life of a sparrow is of much less value than a human life, "not a sparrow dies without God taking notice." For Christians, humans may have a soul but God still considers the life of a sparrow important enough to take notice of its passing.

Judaism. The God-given authority of humans over animals is recognized by Judaism, but not without restrictions. The prohibition of cruelty is so strong in Jewish law that the slaughter of animals for human consumption is carefully scrutinized by a specialist in the field. If there is any indication that the animal suffered unnecessarily, it is considered unclean (unfit for human consumption). There are exceptions to this rule for medical research. The Polish rabbi Moses ben Israel Isserles (1525–1572) taught that anything necessary for medical or other useful purposes is excluded from the prohibition of cruelty to animals.

Islam. The right of humans to consume animals for nutrition and to use their labor is recognized by most Muslims. The Qur'an is neutral on the subject of the consumption of meat. However, moderation in all things, including eating, is encouraged (Qur'an 7:31; 5:87). If animals are slaughtered for food, the slaughter must be done in strict accordance with Islamic law and in such a way as to cause as little pain as possible. Most Islamic scholars hold that the Qur'an prohibits animal cruelty, which is defined as causing unavoidable pain and suffering. This last prohibition is generally applied to sport hunting as well.

Hinduism. The Hindu religions also denounce cruelty to animals. The *Bhagavad Gita* (verse 5:18) proclaims that a self-realized soul is able to understand the equality of all beings. To a Hindu, animal souls are the same as human souls, progressing to higher means of conscious expression in each life. Hinduism teaches that every soul takes on a life for a specific purpose and that to kill an animal stops the progression of the soul and may cause great suffering. For this reason, most devout or orthodox Hindus do not consume meat or use meat products in any form.

Many Westerners have difficulty understanding why a country as poor as India allows cows to wander the streets, break into gardens, and pilfer food from market stalls. To a devout Hindu, the cow is sacred. The *Mahabharata*, an epic poem of ancient India, teaches that spiritual sacrifice must be accompanied by milk curds and ghee (clarified butter). Ghee and the cow that produces ghee becomes the very root of spiritual sacrifice. Hindus hold cows sacred because cows are the symbol of everything that is alive. In the same way that Roman Catholics and many other Christians revere Mary as the Mother of God, Hindus revere the cow as the mother of life. To a Hindu, there is no greater sacrilege than harming a cow. Even the taking of a human life lacks the symbolic defilement attached to cow slaughter.

Buddhism. Like Hinduism, Buddhism also teaches reincarnation, the belief that sentient beings are subject to rebirth as other sentient beings and that consciousness cannot be killed. The interconnectedness of all living organisms is an important precept of the faith. The first of the Five Precepts, the foundation of Buddhist ethical conduct, is not to harm sentient beings.

The relationship between humans and animals is evident in the literature, folklore, and practices of cultures around the world and through the centuries. Yet ambiguity and inconsistency often characterize this relationship. We love our pets and we depend on our domestic animals for food and valuable products, yet we sometimes mistreat our pets and we have almost completely separated ourselves from domestic animals.

Anthrozoology. There is a growing body of literature and an emerging scientific discipline concerning the human-animal relationship, sometimes called *anthrozoology*. The field includes social scientists, psychologists, zoologists, ethologists, historians, philosophers, veterinarians, and physicians. Several groups have been organized to study the human-animal relationship, such as CENSHARE at the University of Minnesota. However, these groups tend to focus on the relationship between humans and their pets. Issues concerning factory farming, vivisection, zoos, and pet-abandonment have generally been addressed by animal rights activists, ethicists and moral philosophers, such as Peter Singer and Thomas Regan. Singer writes about the ethical treatment of animals as a part of human ethics in general.

Humans are dependent on domestic animals for food and companionship. Perhaps the increasing study of human-animal relationships can help us better understand our relationship to the animal species on which we depend and that share our homes and our planet. SEE ALSO Animal Rights; Human–Animal Conflicts; Hunter-Gatherers; Hunting.

Elliot Richmond

Bibliography

Borowski, Oded. *Every Living Thing: Daily Use of Animals in Ancient Israel.* Walnut Creek, CA: Altamira Press, 1998.

Budiansky, Stephen. *The Covenant of the Wild: Why Animals Chose Domestication.* New York: Morrow, 1992.

Caras, Roger A. *A Celebration of Cats.* New York: Simon and Schuster, 1986.

Clutton-Brock, Juliet. *A Natural History of Domesticated Animals.* London: Cambridge University Press, 1987.

Ember, Carol R., and Melvin Ember. *Anthropology.* Upper Saddle River, NJ: Prentice Hall, 1999.

Harris, Marvin. *Cows, Pigs, Wars, and Witches: The Riddles of Culture.* New York: Random House, 1974.

Regan, Thomas. *The Case for Animal Rights.* London: Routledge and Kegan Paul, 1983.

Serpell, James, ed. *The Domestic Dog: Its Evolution, Behavior and Interaction with People.* New York: Cambridge University Press, 1995.

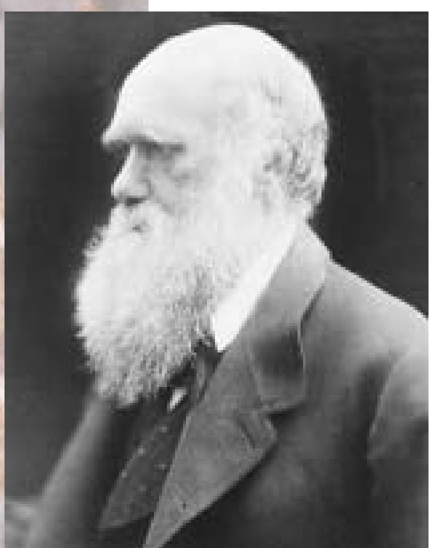
Singer, Peter. *Animal Liberation: A New Ethics for Our Treatment of Animals.* New York: New York Review, 1975. Rev. ed., 1990.

Tabor, Roger. *Cats: The Rise of the Cat.* London: BBC Books, 1991.

Understanding Cats: Their History, Nature, and Behavior. Pleasantville, NY: Reader's Digest Association, Inc., 1995.

Thurston, Mary E. *The Lost History of the Canine Race: Our 15,000-Year Love Affair with Dogs.* Kansas City, MO: Andrews and McMeel, 1996.

Zeuner, Frederick E. *A History of Domesticated Animals.* New York: Harper and Row, 1963.



Charles Darwin's theory of evolution, with its emphasis on natural selection, was the first to win wide approval from the scientific community.

Darwin, Charles

Naturalist
1809–1882

Charles Darwin was born on February 12, 1809 in Shrewsbury, England. He died at the age of seventy-three on April 19, 1882. Darwin revolutionized biology with his theory of evolution by **natural selection**. Although others contributed to the theory of evolution, Darwin was the first to win wide approval from the world's experts in biology.

Darwin was the son of a physician and the grandson of the physician and **naturalist** Erasmus Darwin. In the 1790s Erasmus Darwin proposed a theory of evolution. Darwin studied medicine at Edinburgh University and religion at Cambridge University. He received a Bachelor of Arts degree from Cambridge in 1831. There, his interest in biology was encouraged by his friendship with John Stevens Henslow, who studied plants. Henslow recommended Darwin as naturalist for a scientific expedition to South America. In 1831 Darwin began the five-year journey aboard the ship HMS *Beagle*. He gained valuable knowledge about the plants, animals, and natural features of the lands that he visited. In 1839 Darwin married his first cousin, Emma Wedgewood. They had ten children, seven surviving past childhood.

By 1846 Darwin had published several works on his discoveries about coral reefs and volcanic islands. For his writings and other scientific activities, he became greatly respected in the scientific community. Darwin spent years developing his theory on evolution. It is believed that he waited a long time to share it with the world because he feared the religious **controversy** that would result. He finally was moved to go public when he received a paper from Alfred Wallace in 1858. Wallace had the same ideas that Darwin had been pondering for 20 years. Darwin and Wallace presented their theories in a joint paper to the Linnean Society in 1858. In 1859 Darwin published his famous book *On the Origin of Species by Means of Natural Selection* *or The Preservation of Favoured Races in the Struggle for Life*. While the theory was accepted quickly in most scientific circles, religious leaders strongly opposed it. Many religious persons felt that the theory was inconsistent with the biblical book of Genesis. They feared that God had no place in Darwin's world. They claimed that in Darwin's theory, man was descended from apes and not placed in a superior position over other animals.

natural selection a process by which organisms best suited to their environment are most likely to survive and reproduce

naturalist a scientist who studies nature and relationships among organisms

controversy a discussion marked by the expression of opposing views

Darwin expanded his theory in other publications. His theories included the following: (1) most evolutionary changes were very gradual, requiring millions of years; (2) natural selection was the driving force behind evolutionary change; and (3) today's millions of species branched out from a single, original life form.

Darwin's theories spurred further research in biology. Charles Darwin is considered one of the greatest figures in the history of biology. SEE ALSO Adaptations; Biological Evolution; Natural Selection.

Denise Prendergast

Bibliography

Muir, Hazel, ed. *Larousse Dictionary of Scientists.* New York: Larousse Kingfisher Chambers Inc., 1994.

The Year 2000 Grolier Multimedia Encyclopedia. Danbury, CT: Grolier Interactive Inc., 1999.

Internet Resources

AboutDarwin.com. <http://www.aboutdarwin.com>.

Darwin. <www.public.coe.edu>.

DDT

DDT (dichloro-diphenyl-trichloro-ethane) is an insecticide that was first used worldwide in 1946 to increase agricultural production and to reduce disease vectors (carriers). Although formulated in 1874, DDT's insecticidal properties were not discovered until 1936. Paul Muller of Switzerland won the Nobel Prize for that discovery in 1948.

The neurotoxin DDT interferes with the **action potential** along **neurons**. It affects insects and vertebrates by means of this same primary mechanism. It has a greater effect on insects simply because they are smaller and absorb it more readily. At a high enough dosage, DDT can have as detrimental an effect on vertebrates, including humans. Symptoms of DDT toxicity include apprehension, headache, anorexia, nausea, hyper-excitability, muscle fibrillation, respiratory arrest, coma, and death.

action potential a rapid change in the electric charge of the cell membrane

neurons nerve cells

DDT is relatively inert and stable, and is nearly insoluble in water. This combination of attributes allows it to be stored easily in fat. As a result, fatty tissues act as biological magnifiers by slowing the excretion of DDT after it is absorbed. Like other fat-soluble compounds, DDT is transferred up the food chain more efficiently than are water-soluble compounds, thereby achieving higher concentrations among carnivores. Because DDT toxicity is a function of concentration, this **biomagnification** is most likely to cause problems for a predator species, such as eagles, ospreys, and falcons, at the end of a long food chain.

biomagnification increasing levels of toxic chemicals through each trophic level of a food chain

An airplane dusts DDT over sheep in Medford, Oregon, in 1948. First used worldwide as an insecticide in 1946, DDT came under fire in subsequent decades for its detrimental effect on vertebrates.

During the 1950s, United States efforts to control Dutch elm disease consisted primarily of killing its vector, elm bark beetles, with DDT. Soon after, communities in the Midwest and Northeast began to notice an accumulation of dead robins and other birds. Roy Barker discovered that earthworms were consuming DDT sprayed on the elm trees which was seeping into the soil. Robins in turn ate the earthworms, receiving a lethal dose of DDT from as few as eleven worms. Birds that did not die often suffered reduced fertility.

Other predatory bird species also appeared to decline during the 1940s and 1950s. Hawk Mountain, Pennsylvania, is a stopover for many migrating hawks and eagles. From 1935 to 1939, 40 percent of the eagles were yearlings. Between 1955 and 1959, only 20 percent were yearlings. The percentage of juveniles in eagle populations along the Mississippi, Illinois, and Susquehanna Rivers also declined after 1947. In 1950, there were two hundred mating pairs of ospreys at the mouth of the Connecticut River; by 1970 the number had dropped to six. One study suggested that DDT interfered with **calcium** deposition in eggshells, thereby potentially reducing the reproduction rate of susceptible bird species. However, subsequent studies found no correlation between DDT levels and eggshell thickness either in nature or in controlled experiments.

calcium a mineral form of calcium carbonate

DDT may adversely affect whole ecosystems. In the 1950s, the Canadian government instituted a policy of eradicating the spruce budworm. This native insect attacks several species of evergreens. Millions of acres of the Northwest Miramichi watershed were sprayed to save balsams, the pulp industry's most valuable cash crop. Soon trout and salmon began to turn up dead along the streams. Their prey, caddis fly larvae, stonefly nymphs, and blackfly larvae, were being killed along with the spruce budworm. In 1959, the watershed produced less than a third of the smolt (young salmon) it had produced before the most recent spraying.

Rachel Carson's book *Silent Spring*, was released in 1962 and documented the adverse effects of DDT on the environment. Her book catalyzed the modern American environmental movement. Over the years a variety of objections have been made to her characterization of DDT as an absolute detriment to human and ecological health. For example, studies on the role of DDT in breast cancer have yielded ambiguous results. It is also possible that the correlation between DDT use and the decline of fish and bird populations was caused by the simultaneous use of other pollutants such as PCBs.

The Environmental Protection Agency banned DDT in 1971 as a potential human carcinogen. Since then most countries have banned the chemical for agricultural purposes. However, DDT continues to be a cheap and effective way to kill mosquitoes that transmit malaria, requiring lower concentrations than those for agricultural use.

In 2000, more than 100 governmental and nongovernmental agencies gathered to formulate a treaty to completely phase out DDT and eleven other pollutants. The World Health Organization warned that a sudden worldwide ban on DDT could result in an epidemic of malaria in countries that cannot afford other effective insecticides. Until safe, affordable alternatives are developed, DDT will continue to be used in many countries where malaria is endemic, and its residues will be found in soils and human breast milk around the world. SEE ALSO CARSON, RACHEL; PESTICIDES; SILENT SPRING.

Brian R. West

Bibliography

Carson, Rachel. *Silent Spring.* Boston, MA: Houghton Mifflin, 1962.

DDT and Its Derivatives: Environmental Aspects. Geneva, Switzerland: World Health Organization, 1989.

Internet Resources

Note for the Press No. 15. *World Health Organization*. <http://www.who.org>.

Defense

Animal defense mechanisms include a stunning array of behaviors and adaptations. Defensive behavior of prey takes four forms: anti-detection, anti-attack, anti-capture, and anti-consumption. Every animal has perfected some form of anti-predator adaptation, whether they attempt to go undetected by camouflaging themselves against their surroundings, or keep themselves from being eaten because they are wildly colored and dangerous-looking.

Camouflage and Mimicry

Cryptic coloration and behavior, also known as camouflage and mimicry, are common methods of anti-detection in insects, birds, fish, amphibians, and mammals. Combining camouflage with hiding behavior is a phenomenon widely used among insects. Cryptic moths and butterflies have wing colors and patterns that mimic the plants found in their environments. The

Porcupines display sets of spiny quills as part of their unique defense system.

Catocala moth has whitish wings with dark linear patterns resembling birch bark so that when it rests upon a birch tree it is barely detectable.

Many animals mimic leaves. Again, most tend to be insects. Probably the most successful of all leaf-mimickers are the leaf insects of the genus *Phyllium*, the so-called walking leaf, from Malaysia and Indonesia. Its detailed body parts perfectly resemble a cluster of green leaves and leaf fragments. The disguise is enhanced by its behavior. By moving very slowly, advancing one leg at a time, it sways slightly like leaves being nudged by a gentle breeze.

Chemical defenses. Even cryptic prey can be detected by keen predators. Some animals have the ability to ward off enemies with noxious tissues, stinging hairs, sticky secretions, painful injections, and foul-smelling excretions. The creatures that rely on chemical defenses also tend to have warning coloration, meaning that their bodies are boldly hued in red, black, orange, or bright yellow. This helps to remind predators of past unpleasant experiences with these species. After having eaten a warning-colored toxic prey, many predators quickly learn to retreat whenever they see the same warning display. Some of the most poisonous species of all are the South American arrow-poison frogs, in the genus *Dendrobates*. These frogs are brilliantly colored with patterns of red, yellow, or white on backgrounds of black or electric blue. Their poisons, which affect the central nervous system, are so deadly that Colombian Indians use it to poison their arrowheads.

Batesian mimicry. Some edible prey have evolved to resemble bad-tasting species in an effort to take advantage of the visual response predators have to particular color patterns. These deceptive species are called Batesian mimics, named for the English **naturalist** Henry Bates, who discovered their ex-

naturalist a scientist who studies nature and relationships among organisms istence in Brazil during the 1800s. One Batesian mimic is the tephritid fly, which possesses a leglike pattern on its wings. It can wave these wings in ways that deceptively imitate the aggressive signals of predatory jumping spiders and ward off any possible fly-eating spiders lurking nearby.

Batesian mimicry can include acoustical, as well as visual, deception. For example, the ground-nesting burrowing owl makes the same sound as a rattlesnake. The owl and the rattlesnake share an underground habitat which makes the deception even more convincing.

Other Anti-Capture Methods

What if cryptic or warning behavior still doesn't keep the predator from closing in on its prey? Some animals use anti-capture methods. By startling the predator momentarily, the animal has a chance to escape. The catocala moth mentioned earlier shows only its white and dark-gray wings while resting. If attacked by a blue jay, the moth can display its hind wings, which are orange, yellow, or red bands on a dark background. The sudden flash of color will surprise the jay, who may inadvertently release the moth.

Another anti-capture weapon is sheer vigilance, or remaining alert so as to detect a rapidly approaching enemy in time to take effective action. Vertebrate prey are always scanning, sniffing, or listening for danger. The principle that many eyes, noses, or ears are better than a few could contribute to the tendency of animals to form flocks, herds, and other social groups. It also has been proven that the more animals scanning for danger, the faster the response to that danger.

Alarm calls. Most flock animals rely on alarm signals, or special calls that alert the others in the flock to a possible hazard. The risk of the signal-giver being singled out for predatory attention is lessened because the group flees together, which confuses the predator. In fact, non-calling animals attempting to escape are more than ten times as likely to be killed than alarm-givers. Ground squirrels that live in high densities in mountain meadows give a high-pitched whistle as they dash for cover when a hawk or falcon is spotted. The species has a separate alarm call for terrestrial predators such as coyotes.

Surviving Attack

What happens to the animals that wind up captured? If the prey can somehow convince its captor to let it go, being captured does not mean certain death. Sometimes, chemical deterrents are used to save the life of animal prey. Some salamanders excrete an adhesive that is used to ward off their enemies. If captured by a garter snake, for example, the salamander writhes and thrashes while releasing secretions from the tail and body. The snake can become so coated by the glue that its body becomes stuck to itself and it is rendered completely helpless.

Another way of surviving attack is to induce the predator to strike a body part other than the head. This is critical because brain damage quickly immobilizes prey and removes all chance of survival. This is why animals often hide their heads when under attack. Some animals have evolved false heads on body parts that can be sacrificed without causing death. Hairstreak butterflies have false heads on their hind wings so that when birds attack, the butterfly has a chance to fly away unharmed.

Expendable body parts are another lure used by animal prey. Some lizards, such as the young skins, have brightly colored tails. Skinks twitch their brightly colored tails when threatened to distract the predator's attention from their heads. When a snake attacks the tail, it breaks off and continues to wildly thrash on the ground. Distracted further, the predator generally attempts to subdue and eat the thrashing tail, giving the skink time to escape. SEE ALSO BEHAVIOR; CAMOUFLAGE; MIMICRY.

Ann Guidry

Bibliography

Alcock, John. *Animal Behavior*, 6th ed. Sunderland, MA: Sinauer Associates, 1998.

Macdonald, David. *Encyclopedia of Mammals*. New York: Facts on File, 1984.

McGrath, Kimberley A., ed. *World of Biology*. New York: McGrath Publishers, 1999.

Desert Adaptations

See Water Economy in Desert Organisms.

Devonian

The Devonian period, from 437 to 408 million years ago, was named for the English county where it was first identified. It has sometimes been called the Age of Fishes. Spectacular fish fossils abound in the massive Old Red Sandstone sediments that covered a large portion of Laurasia, the supercontinent that would later split apart to form Europe, Greenland, and North America. These fossils indicate that a vast radiation (or divergence) in size and function was taking place among Devonian vertebrates. The jawless Agnathans had multiplied into many groups distributed around the world by the late Silurian (438 mya). Then, in the Devonian, came the fish, which developed jaws and were such successful competitors that the Agnathans were reduced almost to extinction, with only the lampreys and hagfish as their descendants.

Vast schools of eight-to-ten-inch spined fishes, the Acanthodians, swam in the mid-deep waters (beyond the continental shelf). Some were toothless, but many had razor-sharp teeth and devoured huge quantities of the bony fish, which also swam in great numbers in the clear warm seas. The bony fish included the ray fin, the lungfish, and the fleshy, lobe-finned ancestors of amphibians. Enormous placoderms, up to thirty feet in length, dominated the oceans with their armored bodies and tooth-lined, hinged jaws. Early sharks arose, possibly from placoderms, whom they would replace as the

Devonain period and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

reigning predators of the deep by the end of the Devonian period. And vast coral reefs, some hundreds of miles long, transformed the shallow waters into virtual metropolises swarming with marine life at all levels.

Even more exciting than the proliferation of sea **fauna** was the evolutionary step toward dry land. Fish began exploring up the **brackish estuaries** into freshwater, followed by ravenous six-foot sea scorpions, the fearsome Eurypterids. The lobe-finned fish ventured into shallower and shallower water, eventually developing the rudimentary **lungs** that would allow them to breathe air. Next, their explorations on the muddy shores encouraged innovations in skeletons and fins that allowed them to support their weight in the stronger pull of gravity of the new environment. Gradually, the lower paired fins developed into the four limbs of amphibians. The most complete fossil of an early tetrapod (four-limbed) amphibian comes from the tropical swamps of Devonian Greenland. *Ichthyostega* was a lumbering, forty-inch carnivore, the ancestor of all existing land vertebrates.

fauna animals

brackish a mixture of salt water and fresh water

estuaries areas of brackish water where rivers meet the ocean

lungs sac-like, spongy organs where gas exchange takes place

Yet another major innovation occurred in the Devonian. As the earliest plants and invertebrates made their way onto land, they formed cooperative communities that make possible life as it exists today. Preserved in the Rhynie Cherts of Scotland are perfect slices of pondside life from the period. The minerals (silicon) in the water formed fossil images of the plants. These fossils show the first plants that grew and decomposed to form the first humus-rich soils on the Earth. Living amongst them were the earliest terrestrial **arthropods**: scorpions, mites, and spider-like arachnids. These tiny animals are responsible for breaking down organic material and releasing the nutrients back into the soil. Without this decomposition activity there could be no larger plants and therefore no land animals. This 400-million-year-old partnership between microscopic plants and animals is a fundamental feature of life as we know it. SEE ALSO Geologic Time Scale.

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

Nancy Weaver

Bibliography

Fortey, Richard. *Fossils: The Key to the Past.* Cambridge, MA: Harvard University Press, 1991.

Friday, Adrian, and David S. Ingram, eds. *The Cambridge Encyclopedia of Life Sciences.* London: Cambridge University Press, 1985.

Lambert, David. *The Field Guide to Prehistoric Life.* New York: Facts on File, 1985.

McLoughlan, John C. *Synapsida: A New Look Into the Origin of Mammals.* New York: Viking Press, 1980.

Steele, Rodney, and Anthony Harvey, eds. *The Encyclopedia of Prehistoric Life.* New York: McGraw Hill, 1979.

Diamond, Jared

American Physiologist and Biologist
1937–

In 1997, Jared Diamond won the Pulitzer Prize for Nonfiction with his book *Guns, Germs and Steel*, an analysis of the geographical and environmental origins of the long-term distribution of wealth and power in different regions of the world. Born in Boston, Massachusetts, on September 7, 1937,

Jared Diamond won a Pulitzer Prize for his analysis of the geographical and environmental origins of the long-term distribution of wealth and power.

Diamond was raised in an intellectually stimulating household by a physician father, interested in the **genetics** of childhood diseases, and a mother who was a linguist and teacher. Diamond became an avid bird watcher at the age of seven. All these influences led in 1958 to a biology degree from Harvard, where he studied biological research, language, history and writing. Diamond earned a Ph.D. in **physiology** from Cambridge, and then a professorship at UCLA in 1968 where he taught molecular physiology, evolutionary biology, and evolutionary **biogeography**.

Through years of fieldwork in South America, southern Africa, Indonesia, Australia, and New Guinea, he wrote more than 200 papers on physiology, **ecology**, and **ornithology**. Diamond also began writing science books for popular audiences. *The Third Chimpanzee: The Evolution and Future of the Human Animal*, 1992, discusses possible theories for the divergence between humans and chimps, who share 98.4 percent of the same genetic material. *Why Is Sex Fun? The Evolution of Human Sexuality*, 1997, examines aspects of human sexuality such as why only humans and pilot whales undergo menopause and why humans, dolphins, and chimpanzees are the only species to have sex for pleasure—that is, when the female is not fertile and there is no possibility of reproduction.

It was in the 1970s, while studying the ecological diversity of bird fauna in New Guinea, that Diamond was asked by his local guide why the white men had all the cargo, or technological goods. Thinking about it, Diamond couldn't come up with an answer. When he pursued the answer back in the United States with other scientists, the answers he received seemed to always come down to: We (being western Europe and the United States) are smarter than they are. Reflecting on his experiences in the jungle, Diamond knew that was untrue. The tribesmen were not only intelligent, but also far more observant and competent in their environment than Diamond thought he would ever be. *Guns, Germs and Steel*, he later said, was written to demolish the intellectual basis for racism. The book proposes that certain geographical regions of the globe lent themselves to the development of agriculture, which in turn encouraged technological growth. Diamond hoped that his work would show that historical studies of human beings can be pursued as scientifically as studies of dinosaurs—and can teach us what shaped the modern world, and what might shape our future.

Nancy Weaver

genetics the branch of biology that studies heredity

physiology the study of the normal function of living things or their parts

biogeography the study of the distribution of animals over an area

ecology the study of how organisms interact with their environment

orinthology the study of birds

Diffusion

See Transport.

Digestion

Digestion is the process of breaking down food into molecules that cells can absorb. Carbohydrates, proteins, nucleic acids, and fats are broken down into their smallest units (monomers) by digestive enzymes. These hydrolytic enzymes break chemical bonds through a reaction that requires water. Each hydrolytic enzyme is named after the substances it hydrolyzes. For example, carbohydrases break carbohydrates into single sugars (monosaccharides), proteases break proteins into amino acids, nucleases break nucleic acids into nucleotides, and lipases hydrolyze fats to fatty acids.

The Digestive System

The digestive system of humans consists of a one-way digestive tract with several specialized chambers along the way—mouth, stomach, small intestine, and large intestine. Each chamber has a specific function. In the human digestive system, digestion starts in the mouth. There food is physically digested by the action of our jaws and teeth, which break it down into smaller pieces, increasing the surface area for the digestive enzymes to work on. While being chewed, the food is mixed with saliva. Saliva makes the food slippery for swallowing, and also contains the enzyme amylase, a carbohydrase that breaks down starch into smaller polysaccharides. Once food is swallowed it passes along the digestive system through the activity of peristalsis (wavelike smooth muscle contractions). The passage of food from one chamber to the next is regulated by sphincters, or ringlike muscles.

Once the food arrives in the stomach, it is mixed with gastric juice, which contains hydrochloric acid (HCL) and pepsin. HCL kills most swallowed bacteria, and breaks down most food into individual cells, further increasing the surface area for enzyme attack. Pepsin (a protease) begins the hydrolysis of proteins into smaller polypeptides. The main site of human digestion and absorption of nutrients is the small intestine. There accessory glands of the digestive system, such as the pancreas and the liver, secrete their products into the digestive tract. The pancreas secretes bicarbonate ions that neutralize the acid from the stomach, protecting the digestive enzymes of the small intestine. The pancreas also releases a carbohydrase (pancreatic amylase), which continues the carbohydrate digestion started by salivary amylase in the mouth. The resulting disaccharides (e.g., maltose) are further hydrolyzed into monosaccharides (e.g., glucose) by enzymes (e.g., maltase), which are built into the membranes of cells lining the small intestine. This is also where sugar is absorbed from the lumen of the digestive tract into the cells lining the digestive tract.

Other enzymes that are produced and released by the pancreas are proteases (e.g., trypsin), nucleases, and lipases. Proteases attached to the membrane of cells lining the walls of the digestive tract are responsible for hydrolysis of small peptides to amino acids (which are then absorbed), and attached nucleases process nucleotides whose components are also taken up.

For the pancreatic lipases to be efficient, the lipid clumps that form in the watery environment of the digestive tract have to be broken into tiny droplets, which will increase the surface area for the lipases to work on. This is the function of bile salts, which are produced by the liver and stored in the gall bladder before being released into the small intestine. The fatty acids resulting from the action of the lipases are then absorbed.

While digestion and absorption of nutrients are taking place in the small intestine, peristalsis slowly pushes the content of the small intestine into the large intestine, where water and ion absorption are taking place. In the large intestine, populations of bacteria live on material that is not digestible by humans. As a byproduct of their metabolism, they produce gas as well as vitamins such as vitamin K that can be absorbed.

Control and Digestion

zymogens inactive building-blocks of an enzyme

How is it possible to digest food molecules and not the cells of the digestive system itself, which is made of the same molecules? Most enzymes are produced in an inactive form called **zymogens**, that do not affect the cells that produce them. These zymogens are then released into the digestive system where they are activated. The cells lining the digestive tract are protected from the active enzymes by a thick layer of mucus. However, the mucus lining is constantly eroded, and if the lining is eroded faster (e.g., by acid-resistant bacteria) than it is regenerated, stomach ulcers may occur.

To make efficient use of all the nutrients contained in food, control and coordination of the digestion process is crucial. This is accomplished by several negative feedback systems. For example, when we see, smell or taste food, our brain signals the stomach to secrete gastric juice. When food proteins are actually present in the stomach, they trigger the release of the hormone gastrin into the blood stream. This hormone causes the cells in the stomach wall to release even more gastric juice, ensuring that proteins in the stomach are properly predigested. If the stomach becomes too acidic, the release of gastrin—and thus the production of gastric juice—ceases. When the acidic content of the stomach enters the small intestine, another hormone, secretin, is released into the blood stream from the cells lining the small intestine. Secretin causes the pancreas to dump bicarbonate from the pancreas into the small intestine, buffering the acid. When amino acids or fatty acids are detected in the small intestine, another hormone, choleocystokinin (CCK), is released from the intestinal cells into the blood. CCK triggers the gall bladder to release bile and the pancreas to release its digestive enzymes. At the same time, CCK inhibits the peristalsis of the stomach thus slowing down food transport. This allows enough time for the digestion of the food already present in the small intestine before more food from the stomach arrives. SEE ALSO DIGESTIVE SYSTEM; HOMEOSTASIS.

Kathrin F. Stanger-Hall

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Eckert, Roger, David Randall, and George Augustine. *Animal Physiology*, 3rd ed. New York: W. H. Freeman and Company, 1988.

Kapit, Wynne, Robert I. Macey, and Esmail Meisami. *The Physiology Coloring Book*. Cambridge, MA: Harper Collins Publishers, 1987.

Purves, William K., Gordon Orian, and Craig H. Heller. *Life: The Science of Biology*, 4th ed. Sunderland, MA: Sinauer Associates, 1994.

Digestive System

The digestive systems of animals are quite diverse. Sponges, the simplest animals, do not have specialized digestive systems. Food particles filtered from the water are simply digested within individual cells (intracellular digestion). One of the first steps toward a complex digestive system in animals, and the processing of larger prey, is the evolution of a **gastrovascular cavity**, a digestive sac with a single opening to the external environment. The gastrovascular cavity serves as a protected space for extracellular di-

gastrovascular cavity a single cavity where digestions occurs gestion inside the animal, and at the same time allows distribution of the digested material to most cells of the body. Following extracellular digestion in the gastrovascular cavity, the digestion products from carbohydrates, proteins, and fats are taken up by cells lining the gastrovascular cavity, where digestion is completed intracellularly.

A One-Way Digestive Tract

Cnidarians and flatworms have a gastrovascular cavity. Cnidarians, such as the *hydra*, use their tentacles to move food through their mouth into their gastrovascular cavity. Then the cells lining this cavity excrete digestive **enzymes** that will start extracellular digestion and break the prey into smaller pieces. Any undigested remnants of the prey are expelled through the mouth opening. Like cnidarians, flatworms have a gastrovascular cavity with a single opening, but the cavity itself is highly folded. These folds greatly increase the surface area and extend throughout the body, bringing nutrients within the reach of all cells.

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

enzymes proteins that act as catalysts to start biochemical reactions

The gastrovascular cavity of cnidarians and flatworms allows them to digest larger prey than they could with intracellular digestion. However, the effectiveness of a gastrovascular cavity in supplying the animal with nutrients is limited. Because there is only one opening to the external environment through which prey is taken in and remnants are expelled, the animals have to complete digestion of the first prey and expel its remnants before taking in another prey. With the evolution of a second opening in the digestive system, the digestive system became a digestive tract, or alimentary canal, making it a one-way system between mouth and anus. Food could now be taken in and processed continuously, providing the animal with more nutrients. Most animals—including vertebrates, arthropods, **mollusks**, round worms and earthworms—have this form of digestive tract.

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

A one-way digestive tract is efficient because it allows the food to pass through a series of specialized regions. Such regions may be specialized for protein, fat, or carbohydrate digestion, making each step more efficient. Other regions may be used for food storage or for preparing the food for chemical digestion by physically grinding it into smaller pieces, which exposes more surface area to the action of digestive enzymes. These specialized regions eventually evolved into organs as parts of a complex digestive organ system. However, because nutrient dispersal, by the digestive system itself to all cells of the body, was no longer feasible with such a specialized digestive system (and animals became larger and bulkier) a separate cardiovascular system evolved to serve that function.

Simple animals such as earthworms suck soil into the mouth with the pharynx, pass it through the esophagus into the crop, where it is moistened and stored. From there it is moved into the **gizzard**, which contains small grains of sand that help grind down the food. The actual digestion and **absorption** of nutrients takes place in the intestine, and anything that remains is excreted through the anus. Insects also move food from the mouth through the esophagus into a crop (all parts of the foregut) for food storage and moistening. From there it is moved to a midgut where digestion and nutrient absorption through specialized extensions, or ceca, takes place. The hindgut functions mainly to reclaim water and ions from the gut content that would otherwise be lost in the feces.

gizzard a muscular part of the stomach of some animals where food is ground

absorption the movement of water and nutrients

This young South African spotted hyena licks its mother's mouth to stimulate regurgitation of partially chewed, digested food. The parental act of chewing and digesting food before it is eaten makes consumption easier for many juvenile animals.

Physical Digestion of Vertebrates

During the evolution of vertebrates, two trends can be recognized. First, animals became larger, requiring a more efficient digestive system to meet their nutritional needs. Second, some animals moved from living in water to living on land. This meant they required more energy for locomotion and a more efficient digestive system to provide that energy.

In vertebrates, the physical digestion of food begins in the mouth. Birds crunch seeds with their beaks, and mammals use their powerful jaws and specialized teeth to chew food into smaller pieces, increasing the surface area for digestive enzymes to work on. Salivary glands in the mouth coat the food with saliva to make it slippery for swallowing. After swallowing, the food is moved along the digestive tract with the help of involuntary **smooth muscle** contractions, called peristalsis. Sphincters regulate the passage of food from one chamber of the digestive tract into the next. First the food passes through the esophagus into the stomach. In the stomach, the food is stored and mixed with gastric juice. The gastric juice kills most swallowed bacteria, breaks down most food into individual cells (increasing the surface area for **enzyme** attack), and begins the digestion of proteins. Birds may store food in a crop without digesting it before passing it into the stomach. This allows parent birds to regurgitate food from their crops for their nestlings. Some birds move food from the stomach into a muscular gizzard containing swallowed stones that grind down seeds before digestion continues in the small intestine. The small intestine is the major site of digestion and absorption in vertebrates, and has three distinct regions—the duodenum, the jejunum, and the ileum. Accessory glands such as the pancreas and liver secrete digestive enzymes and other products into the duodenum. The jejunum also releases digestive enzymes. These enzymes digest carbohydrates, proteins, nucleic acids, and fat, and the products of the digestion are absorbed by cells lining the small intestine, especially the ileum. The large intestine is connected to the small intestine. The major function of the large intestine is to reabsorb water that was added to the gut content in the small intestine, and to absorb inorganic ions from the digested food. As a result the feces become more solid. The large intestine also contains many bacteria, which may produce gases as

smooth muscle the muscle of internal organs that are not under conscious control

enzyme a protein that acts as a catalyst to start a biochemical reaction byproduct of their metabolism, but also vitamins, such as vitamin K, that are absorbed into the blood. Feces are stored in the rectum until they can be eliminated through the anus.

Many grazing animals (e.g., deer, cattle, sheep, giraffes) who swallow grass hastily without chewing while watching out for predators, have a two-part stomach. In the first part of the stomach, the unchewed grass is fermented and predigested by bacteria before it is regurgitated back up into the mouth. There it can be chewed more thoroughly when the animal is in a safe place. After chewing, the food is swallowed again and passes into the second section where digestion takes place. **Herbivores** generally have a longer and more complex intestine than carnivores. This allows them to get as many nutrients as possible out of their more nutrient-poor food. SEE ALSO DIGESTION.

herbivores animals who eat plants only

Kathrin F. Stanger-Hall

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Eckert, Roger, David Randall, and George Augustine. *Animal Physiology*, 3rd ed. New York: W. H. Freeman and Company, 1988.

Kapit, Wynne, Robert I. Macey, and Esmail Meisami. *The Physiology Coloring Book.* Cambridge, MA: Harper Collins Publishers, 1987.

Purves, William K., Gordon Orian, Craig H. Heller. *Life: The Science of Biology*, 4th ed. Sunderland, MA: Sinauer Associates, and W. H. Freeman and Company, 1994.

Dinosaurs

The history of the Dinosauria begins with one of the dinosaur's small extinct ancestors called *Petrolacosaurus.* Around 270 million years ago, this animal was a member of the group of early land vertebrates called the diapsids that had skulls with two openings behind the eye socket (other evolutionary groups, like fish and amphibians, had one opening or none at all). The diapsids are believed to be the ancestors of the lepidosaurs (modern lizards and snakes) as well as of the archosaurs, the group that led to the dinosaurs.The lepidosaurs achieved great evolutionary success. The extra openings in their skulls led to the interesting structures found in modern snakes, including a light and flexible skull that allows them to catch and eat prey larger than their mouths.

Ancestry: Euparkeria

The first known archosaurs appeared in the Permian Period (319 to 286 million years ago) and they were well on their way to becoming large-sized animals by the early Triassic (about 245 million years ago). When discussing dinosaur ancestry, paleontologists prefer to examine an interesting little archosaur known as *Euparkeria. Euparkeria* had anatomical characteristics of most archosaurs (and eventually the dinosaurs), including deeply rooted, sharp, serrated teeth; two holes behind the eyes; and a broad space in front of the eye sockets. Their jaws had a distinctive opening that was different in shape and position from other tetrapods, and their spine had small bony plates suggestive of the beginning of armor plating. Perhaps the most important feature of *Euparkeria* is the arrangement of their hipbones.

As the archosaurs evolved, many species developed hipbones that allowed the angle of their hind limbs to change from a sprawling posture, such as a lizard or crocodile has, to an erect one, like a bird. The limbs came under the body instead of being spread out to the side. This leg position provided a firmer basis of support for a larger and heavier body. Dinosaurs became the largest land animals, and part of their ability to become so large was a direct result of this change in posture. When the legs are spread out to the side they can only support so much weight before the joints that attach them to the body give out. With the legs underneath the body, they form a kind of column that can support a great deal more weight. This means a larger animal can move around without being slow and sluggish or breaking its bones. This change in body posture is one of the main reasons dinosaurs were able to become so large.

One important group of archosaurs was the thecodonts, which included *Euparkeria*. During the Triassic period, thecodonts continued to evolve and undergo changes in body shape. By the end of the Triassic 213 million years ago), there were two groups of thecodonts, the saurischians and the ornithischians. The saurischians ate both plants and meat. Their pelvis was distinctive in that the three bones that made up the hip—the ilium, the ischium, and the pubis—were joined so that they angled away from each other in a triangular shape. There were two distinct groups of saurischians, the theropods ("beast feet") and the sauropods.

carnivorous describes animals that eat other animals

The theropods were **carnivorous** dinosaurs that walked upright on two feet. Some of the most famous dinosaurs we know today are theropods, including *Tyrannosaurus rex*, *Velociraptor*, and other swift and dangerous predators. The other group of saurischians, the sauropods, were herbivores and moved about on four legs. Some sauropods, including *Brachiosaurus*, *Camarasaurus*, and *Ultrasaurus*, were the largest animals that ever lived on Earth. The other evolutionary offshoot of the ancestral thecodonts was the ornithischians. The hip structure of the ornithischians differed from that of the saurischians in that their forward-extending pubis bone was turned toward the back. Because this bone structure also occurs in modern birds, the ornithischians are called bird-hipped dinosaurs. (The ornithischians are not ancestors of birds, they just have a similar hip structure.) The legs, feet, and anklebones of ornithischians were similar to those of the saurischians.

A peculiar adaptation of ornithischians was the beaklike covering of the front of the mouth, which is characteristic of the ceratopsians and duck-billed dinosaurs. Ornithischians also had a complex network of bony rods along their spine which supported the spine. All ornithischians were herbivores. The group contains some of the more distinctive-looking dinosaurs, including *Stegosaurus*, which had a series of large, triangular, horn-covered bony plates along its back and tail; the heavily armored *Ankylosaurus;* and the ceratopsians, including *Triceratops*, with its huge bony hood and horns.

The First True Dinosaurs

The first groups of true dinosaurs, the coelurosaurs, appeared about 210 million years ago in the late Triassic period. These dinosaurs were carnivorous theropods. They were agile and lightly built; most species were smaller than an adult human. Some of the best fossil specimens of the coelurosaur known as *Coelophysis* were discovered in the United States in New Mexico.

Other coelurosaurs were the smaller *Ornitholestes*, a heavily jawed predator with nostrils that faced upward on its skull, and *Coelosaurus* perhaps the best-known coelorosaur. All coelorosaur feet had three toes pointing forward and a fourth facing back. The fifth toe was greatly reduced. This pattern persisted throughout the history of all the dinosaurs and is one way to document change within the group.

From the remains of dinosaurs that appear in the fossil record, paleontologists can infer what those animals looked like, how they moved, and what and how they ate. But paleontologists today are also asking: What dinosaur behavior can we infer from fossils? The Maiasaura ("Good Mother" dinosaur) eggs and young found in Montana in 1978 are an excellent example of one way paleontologists can hypothesize dinosaur behavior. In this case, the young dinosaurs at the site were too big to fit in the fossil eggs in nests that were found nearby. Paleontologists think that the parent dinosaurs brought food to the baby dinosaurs and protected them from predators. Also, since many nests were discovered together in a small area, the scientists think that these dinosaurs many have lived together in some sort of herd.

This *Triceratops* skull is on display in the Graves Museum of Archaeology and Natural History in Dania, Florida. The *Triceratops* skull made up nearly one-third the length of its body. The skull featured a large "frill" (bony plate) at the dinosaur's neck, two large horns placed just above its eyes, and a nose that looked like a bird's beak.

The thinking is that if the baby dinosaurs were too big to fit in the eggs, but were still in the nest they probably remained in nest for some time after hatching. They would have to had food brought to them by the parents until they were large enough to forage for food on their own. Many birds care for their young this way by bringing them food until the fledglings are old enough to feed and fly on their own. This is another piece of evidence that links birds and dinosaurs.

At the end of the Cretaceous era (around 64 million years ago), something happened that caused the remaining dinosaurs to die out. No one knows for sure what the event was. Many scientists believe an asteroid hit Earth, causing harsh atmospheric conditions that led to the dinosaurs' extinction. However, very few species of dinosaurs remained by the end of the Cretaceous. Scientists will probably never know what actually happened to the dinosaurs. Most think they are still here as birds. This is not difficult to imagine when you look closely at the characteristics of birds. It is comforting to imagine that these fantastic and lively creatures are still among us, only much smaller.

Recent discoveries of many species of feathered dinosaurs in China have really supported this idea. Most scientists know agree that birds are very closely related to dinosaurs, if not actually dinosaurs themselves. The so-called "missing links" between dinosaurs and birds have been found.

Leslie Hutchinson

Bibliography

Carroll, R. *Vertebrate Paleontology and Evolution.* New York: W. H. Freeman and Company, 1988.

Czerkas, S., and E. Olsen. *Dinosaurs: Past and Present*, vols. I and II. Los Angeles: Natural History Museum of Los Angeles County, 1987.

Farlow, J. O., and M. K. Brett-Surman, eds. *The Complete Dinosaur.* Indiana University Press, 1997.

Horner, John R. *Digging Dinosaurs.* New York: Workman Publishing, 1988.

Norman, D. *Encyclopedia of Dinosaurs.* New York: Crescent Books, 1985.

Sloan, Christopher. *Feathered Dinosaurs.* Washington, D.C.: National Geographic, 2000.

Diurnal

Diurnal organisms are those that are active mainly during the day. When activity patterns of an organism occur in cycles of about twenty-four hours, the pattern is called a **circadian rhythm**. Diurnal animals, which sleep during the night and are active during the day, or, conversely, **nocturnal** animals, which sleep during the day and are active at night, follow a circadian rhythm. Scientists believe that circadian rhythms are controlled by an internal timing mechanism called a biological clock. The exact nature of this internal timing is not known, but varying levels of hormones are thought to play a role.

circadian rhythm a daily, 24-hour cycle of behavior in response to internal biological cues

nocturnal active at night

Scientists generally concur that the evolution of species on Earth has proceeded in the direction to take full advantage of all possible niches (the specialized role of an animal in its environment). Thus some organisms have evolved to be better suited for nighttime, which is relatively darker, cooler, and more humid. Other creatures have become more specialized for daytime, which is lighter, warmer, and drier. In a sense, then, organisms work in "shifts" so as to use the environment at all times. This allows a greater number of organisms to occupy the same area without excessive competition for space and food at any one time. The day shift includes animals such as humans, dogs, songbirds, elephants, squirrels, gorillas, deer, hawks, lizards, butterflies, honeybees, and chimpanzees. The night shift includes such animals as owls, bats, and mice.

Some animals have both nocturnal and diurnal species. In the tropics, mosquitoes transmit two serious human illnesses, malaria and dengue fever. The *Aedes aegypti* mosquito, which carries dengue fever, is diurnal. The *Anopheles* mosquito, which carries malaria, is nocturnal.

Adaptations of animals to diurnal activities are evidenced by the differing properties of some animals' eyes. For example, nocturnal birds like the owl generally have larger eyes than do diurnal birds like the hawk, for which more light is available. Larger eyeballs assist the nocturnal species in getting as much light as possible to the **retina**. SEE ALSO NOCTURNAL.

retina a layer of rods and cones that line the inner surface of the eye

Denise Prendergast

Bibliography

Towle, Albert. *Modern Biology.* New York: Holt, Rinehart, and Winston, 1993.

"Behaviour, Animal." *The New Encyclopedia Britannica*, Vol. 1. *Macropedia*, 15th ed. Chicago: Encyclopedia Britannica, 1998.

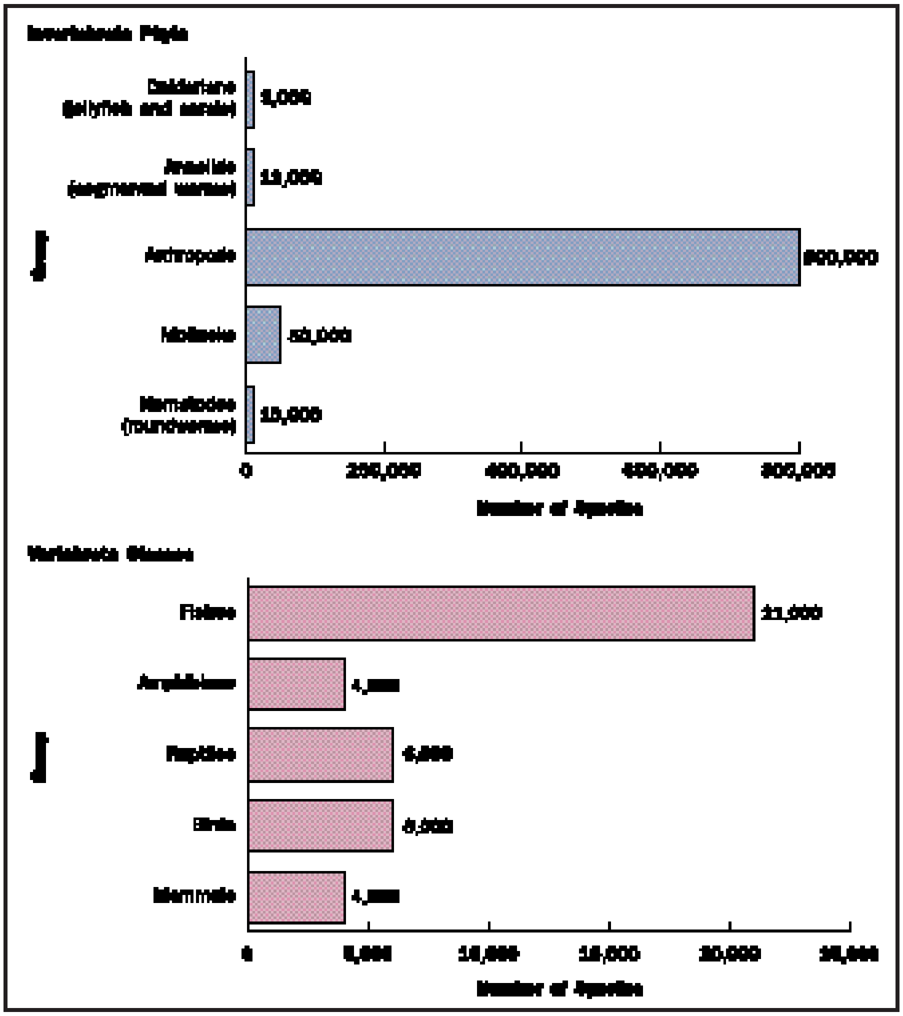
Diversity of Major Groups

archae an ancient lineage of prokaryotes that live in extreme environments

horseshoe crabs "living fossils" in the class of arthropods

crustaceans arthropods with hard shells, jointed bodies, and appendages that mainly live in the water

The diversity, or variety, of animal species in the major groups is staggering. Scientists currently recognize more than one million species of animals, and this number does not include all species of bacteria, **archae**, and protozoa. Invertebrates make up 95 percent of the more than one million known species. Arthropods—spiders, **horseshoe crabs**, **crustaceans**, insects, centipedes, millipedes, and scorpions—are the most successful phylum in the animal kingdom. Arthropods account for 80 percent of all



Graphic representation of the wide diversity of life forms on Earth.

known species of animals. Insects are the most successful arthropods. Scientists estimate that there are one billion insects for each human on Earth! SEE ALSO Biological Evolution; Phylogenetic Relationship of Major Groups.

Allan B. Cobb

Bibliography

Barnes-Svarney, Patricia. *The New York Public Library Science Desk Reference*. New York: Macmillan USA, 1995.

Ruppert, Edward R., and Robert D. Barnes. *Invertebrate Zoology*. Fort Worth, TX: Saunders College Pub., 1994.

Domestic Animals

The domestication of animals for agricultural purposes dates back to the beginning of the Neolithic period, 9,000 years ago. Early agriculturalists in the Fertile Crescent of the Near East began breeding goats first, then sheep, pigs, and cattle. The stimulus for this advance was probably **global warming** at the end of the Ice Age, which caused drought in the Near East and

global warming a slow and steady increase in the global temperature forced people to congregate around reliable sources of water. The subsequent increase in **population density** strained the ability of hunting and gathering to meet the demand for food. Herding animals provided a reliable source of protein-rich food during times of scarcity.

population density the number of individuals of one species that live in a given area

A domestic animal is characterized by several attributes. First, it is bred in captivity for economic profit. Second, humans control its breeding, territory organization, and food supply. Animals bred in captivity tend to have different anatomies and behavior from their wild ancestors. Stress and dependence on humans causes hormonal imbalances and disrupts growth in different parts of the organism. Captive breeding exaggerates these effects, leading to the retention of juvenile characteristics, such as submissive behavior, a smaller body, fat deposition under the skin, shortening of the jaws, and smaller teeth and brain. Domestic animals also tend to appear quite different from their wild ancestors, as animal breeders selected them for a variety of idiosyncratic traits in order to identify them easily as property.

Dogs

The first animal species to become domesticated was the dog (*Canis familiarus*), occurring more than 12,000 years ago in west Asia. Modern-day mastiffs and greyhounds have changed little from their ancestors 4,000 years ago in Egypt and Asia. Each of the more than 400 breeds of dog is the same species. Many experts think dogs descended from the wolf (*Canis lupus*). Other researchers suggest that the domestic dog may have descended from a now extinct wild dog. In either case, breeders selected dogs to look different from their ancestors by favoring those with black, white, or spotted coats, long ears, and curled tails. Dogs possess many juvenile characteristics of wolves, including submissive behavior, short jaws, and smaller brains.

Some believe that dogs descended from wolves and that dogs were easily domesticated because of the similarity between wolves' and humans' social behavior. Both species are acutely aware of social hierarchies, making group living more organized and complex than in any other species. When wolves began to scavenge around human settlements, people adopted pups to serve as guards and hunting companions. The human-raised wolves adapted well to human society and likely treated their human companions as if they were a wolf pack. Eventually, humans started to control the breeding of these proto-domestic wolves and the evolution of *Canis familiarus* began.

Livestock

Livestock were the next species to be domesticated. Archaeological evidence of domestic sheep and goats in the Jordan Valley dates back to 7,000 B.C.E. Sheep were domesticated from the Asiatic moufflon (*Ovis orientalis*), a grass grazer found in hills and foothills. Domestic goats were derived from the bezoar goat (*Capra aegagrus*), a hardy browser found in mountainous terrain. Both species were relatively easy to breed in captivity because they were social and adapted to harsh environmental conditions.

ruminant a plant-eating animal with a multicompartment stomach such as cows and sheep

Domestic humpless cattle. Domestic humpless cattle (*Bos taurus*) appear in the archaeological record 6,000 years ago in Egypt and Mesopotamia. Their ancestor was the wild ox (*Bos primigenius*), a browsing and grazing **ruminant** in forests and scrub, now extinct. They provided a multitude of uses,

Ranchers herding cattle in Utah's Salt Lake Valley. The domestication of animals—including sheep, pigs, goats, and cattle—for agricultural purposes dates back thousands of years.

including labor, milk, meat, bone, and tallow (for burning). Domestic humped cattle (*Bos indicus*) were domesticated independently in Southeast Asia. The domestic yak, water buffalo, and mithan were each domesticated independently from a different bovine species.

Pigs. Pigs were domesticated from the wild boar (*Sus scrofa*) around the same time as cattle. They resemble dogs and humans more than other livestock in several ways. Pigs enjoy body contact with other family members and build nests and beds. They are physically weak at birth, requiring significant parental investment. These similarities may underlie the variation in cultural attitudes toward pigs as agricultural products. Whereas Muslims, Hindus, and some Christians traditionally considered pigs taboo as a source of protein, the Chinese bred both pigs and dogs specifically for their meat.

Horses

Horses were domesticated in the third millennium B.C.E. in Russia and western Asia from the wild horse (*Equus ferus*). In early 2001, scientists from the University of California, Los Angeles, and three Swedish universities

mitochondrial DNA DNA found within the mitochondria that control protein development in the mitochondria

published research indicating that the domestic horse was so genetically diverse, it could not have originated at one place. **Mitochondrial DNA**, which is genetically transmitted from mother to children, indicated several different matrilineal (female-based) lines. Based on this finding, the researchers suggested that wild horses were tamed independently in several different parts of the world. The "idea" of domesticating horses may have originated in one place, probably central Asia, but various cultures captured and tamed their own horses.

Horses are grass grazers, making them especially well suited to dry plains. At first they were used for food, then as vehicles for travel. Their ability to carry people had an enormous impact on human economies by speeding travel and transport and was probably a necessary step in the development of civilization.

Cats

Domestic cats are an exception to the rule of domestication. Feral cats (*Felis silvestris*) helped rid rats and mice from stored grains once agriculture became widespread. Because cats are territorial, nocturnal carnivores, controlled breeding was exceptionally difficult. Consequently, there are relatively few cat breeds even after thousands of years of domestication, and those that exist are not much different from their wild ancestor or each other. The weakness of the effects of domestication on cats has made it difficult to determine when or where they were domesticated, but archaeological evidence indicates that ancient Egyptians kept cats as pets by 1000 B.C.E. SEE ALSO ANIMAL RIGHTS; BIOETHICS; FARMING; HUNTER-GATHERERS.

Brian R. West

Bibliography

Clutton-Brock, Juliet. *Domesticated Animals from Early Times.* Austin: University of Texas Press, 1981.

Darwin, Charles. *The Variation of Animals and Plants Under Domestication.* New York: New York University Press, 1988.

Dominance Hierarchy

Dominance hierarchies characterize many species in which individuals live in close proximity to one another. The dominance hierarchy is a social structure within a group of animals in which certain individuals are dominant over others, and are therefore able to claim access to better resources in the form of food, mates, shelter, and other desirable commodities.

The evolution of dominance hierarchies in a species is indicative that there is competition for resources. Members of a dominance hierarchy are aware of how they are positioned within that hierarchy and they behave appropriately. Of particular importance, the establishment of dominance hierarchies allows for the resolution of conflict between individuals without costly fighting that can result in serious injury or even death. In species where organized group living is essential to survival, it also serves to maintain order among pack members.

Establishment of Dominance Hierarchies

Dominance hierarchies are often established through ritualized displays or mild fighting, rather than all-out battle. The loser in a battle for dominance typically moves away from a choice habitat or a disputed mate. Among primates, dominance conflicts frequently involve no more than the display of enlarged canines, sometimes through yawning. Bears, also, will roar or wave their open mouths at social inferiors. Behaviors like these do not require fighting, but do result in the prominent exhibition of potentially formidable fighting weapons. In other cases, as in elephant seals, there actually can be prolonged, often bloody fighting. However, once the hierarchy is established, subsequent fighting is less frequent. In many cases, there is a strong correlation between dominance and large size.

Dominance hierarchies have to be reestablished when certain individuals feel prepared to move up within the hierarchy, or when new individuals are introduced into an area. During such time a series of challenges may occur. This can be a stressful period for all individuals involved.

Dominance and Mate Competition

Mate competition is extremely common in the animal kingdom, and many dominance hierarchies relate to competition either for mates, or for those resources such as admirable territories that will attract them. In most cases males compete for females, although there are also a few instances of females fighting for males.

There are clearly advantages to dominance. Dominant males have been shown in many species to copulate more frequently or to produce more offspring. In cowbirds, for example, only the dominant male is allowed to sing the songs that are most effective in attracting females. If subordinate males attempt to sing these highly charged songs, they are attacked, often brutally, by more dominant individuals.

Elephant seals are another group in which reproductive success is linked to dominance. Dominance battles in this species involve two males posturing chest to chest and attempting to bite each other, with the loser ultimately retreating. In a few species, such as wolves, the dominant members of a group are the only ones that reproduce.

One tell-tale sign of competition for mates is **sexual size dimorphism**, which describes a situation where one sex of a given species has much greater body size than the other. In the case of mate competition, it is the males that are larger than females. (There are other species where the females are larger, including, the large majority of frogs. However, in these species the large size of females appears to be associated with increased fertility rather than with the establishment of dominance.)

sexual size dimorphism a noticeable difference in size between the sexes

Sexual size dimorphism is often particularly pronounced in species where it is possible for a single male to monopolize many females, as in elephant seals. In fact, a study across various pinniped species (seals, sea lions, etc.) suggests that the degree of sexual size dimorphism is positively correlated with the size of the harem.

The spotted hyena. A particularly interesting example of the dominance hierarchy is that of the spotted hyena. It is the largest species of hyena and has also been called the laughing hyena because of the calls that individuals

Dominance hierarchies are often established through mild fighting. In this case, the dominant grey wolf establishes superiority by nosing a lower-ranking wolf into submission onto the ground.

make when they are in danger. Spotted hyenas live in social groups that vary greatly in size, with the largest having as many as eighty members. Each group defends a territory and hunting occurs in packs.

What is unusual about social organization in this species is that females are dominant within the group and at the same time possess reproductive organs that very much resemble those of males. In fact, female genitalia resemble the scrotum and testes of males so closely that it is almost impossible to determine the sex of individuals in the field.

One early hypothesis to explain this male-mimicking anatomy was that females evolved it in order to participate in the hyena greeting ritual, in which members of the same social group sniff each others' erect penises when they meet again after an absence. Because greeting behavior is important to group solidarity, it was argued that females evolved male-like anatomy so they could participate as well.

However, the greeting ritual theory has since been abandoned in favor of an argument based on fighting for dominance within the hierarchy. There are numerous benefits to being the dominant female within a spotted hyena clan. Females who are high in the hierarchy have priority at kills, and obtain more food than subordinate females or males. Dominant females tend to be the largest hyenas of a pack. They also tend to produce dominant offspring. The production of a dominant male is particularly advantageous because only the dominant male within a pack mates.

Many scientists believe that because aggressive behavior is advantageous in competitions for dominance, female hyenas have evolved high circulating levels of androgens (male sex hormones) such as testosterone, which promote aggression. The curious male-mimicking genitalia are now believed to be a mere side effect of the unusually high testosterone levels. The testosterone circulating in the female's bloodstream while she is pregnant results in the masculinization of the anatomy of both her male and female offspring. It was indeed confirmed that female spotted hyenas do in fact have unusually high testosterone concentrations in their blood. SEE ALSO Behavior; Social Animals.

Jennifer Yeh

Bibliography

Alcock, John. *Animal Behavior*, 4th ed. Sunderland, MA: Sinauer Associates, 1989.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Halliday, Time. *Animal Behavior.* Norman: University of Oklahoma Press, 1994.

Krebs, John R., and Nicholas B. Davies. *Behavioural Ecology: An Evolutionary Approach*, 4th ed. Cambridge, MA: Blackwell Science, 1997.

Drosophila

The common fruit fly *Drosophila melanogaster* is a human **commensal** typically seen hovering around garbage cans or the bananas in kitchen fruit bowls. These small flies have been model organisms for genetic studies since about 1910. The reason these flies have been so useful to biologists is because they are small and thus take up little lab space, they are easily cultured, they have a short generation time, and they are extremely fertile.

commensal a symbiotic relationship wherein one species benefits and the other is neither helped nor harmed

In 1910 Thomas Hunt Morgan of Columbia University in New York City discovered a white-eyed mutant in *Drosophila melanogaster* which differed from the standard red-eyed fruit fly. Mutations such as this allow geneticists to narrow down the chromosomal location of the gene or genes responsible for a particular phenotype, such as eye color. Since then thousands of other mutations in *Drosophila* have been identified and mapped, including mutations that alter behavior and learning. At the genetic level, more is known about *Drosophila* than any other multicellular organism. Furthermore, much of our knowledge of *Drosophila* is relevant to humans. For example, genetic mutations causing tumors in flies have homologues in other animals. With the sequencing of the entire genome of *Drosophila* in 2000, *Drosophila* will continue to be an important tool in understanding how the genotype controls the phenotype of complex organisms.

One aspect of biology in which *Drosophila* proved to be extremely useful was in the study of development. The life cycle of *Drosophila* is made up of four stages: egg, larva, pupa, and adult. Eggs are typically laid in a food source such as a rotting fruit and develop into larvae after about one day.

A fruit fly, also known as *Drosophila melanogaster.* Fruit flies are are a favorite subject of genetic studies, in part due to their compact size and short developmental cycle.

The larvae resemble small segmented worms, and rove about eating the food for several days until they pupate. At pupation the larvae encase themselves and remain stationary for four days as they **metamorphose** into adult flies. As are all arthropods, the adult flies are composed of three main sections—the head, thorax, and abdomen.

metamorphose a drastic change from a larva to an adult

In 1995, three developmental biologists—Americans Edward B. Lewis and Eric F. Wieschaus, and German Christiane Nüsslein-Volhard—won the Nobel Prize for Physiology or Medicine for determining the genes that control the developmental processes in *Drosophila.* They showed that once maternally transcribed genes determine the **anterior/posterior** polarity of the egg, the zygote's own genes control the rest of development. First the zygote's gap genes divide the embryo into broad bands. This activates the pair-rule genes which further divide the embryo into seven bands, each representing two of the larval segments. The pair-rule genes then activate the segment polarity genes, which establish the anterior/posterior polarity of each segment. Finally, the segment polarity genes activate the homeotic selector genes, which establish segment identity in both the larval and adult stages.

anterior referring to the head end of an organism

posterior behind or the back

Interestingly, complexes of the homeotic selector genes are arranged along the chromosome in the same general order that they are expressed along the length of the fly. For example, genes transcribed in the first segments of the fly are located in front of the genes transcribed in the last segments. Also, the first homeotic gene in the complex is active slightly earlier than the second gene and so on. The homeotic selector genes of *Drosophila* were later found to be arranged in the same order as the **homologous** homeotic selector genes in humans and other animals. This implies that the ordering of the homeotic selector gene complex has been conserved since the beginning of animal evolution.

homologous similar but not identical

Todd A. Schlenke

Bibliography

Ashburner, Michael. *Drosophila.* Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, 1989.

Greenspan, Ralph J. *Fly Pushing, the Theory and Practice of Drosophila Genetics.* Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, 1997.

Kohler, Robert E. *Lords of the Fly: Drosophila Genetics and the Experimental Life.* Chicago: University of Chicago Press, 1994.

Internet Resources

Aperia, Anita, Hugo Lagercrantz, Ralf Pettersson, Nils Ringertz, and Björn Vennström. *The Nobel Prize in Physiology or Medicine 1995.* Sweden: The Nobel Committee for Physiology or Medicine at the Karolinska Institute, 1995. <http://www.nobel.se/medicine/laureates/1995/illpres/index.html, Stockholm>.

The FlyBase Consortium. *The FlyBase Database of the Drosophila Genome Projects and Community Literature.* Nucleic Acid Research, 27:85–88, 1999. <http://flybase.bio.indiana.edu/>.

Echinodermata

The six thousand species of marine animals in the phylum Echinodermata ("spiny-skinned") are, like **annelids**, arthropods, chordates, and **mollusks**, characterized by a true **coelom**, or body cavity. However, echinoderms differ from all other coelomates (except for chordates) in their embryonic development. Very early in this development, a ball of cells called a blastula develops an infolding called a blastopore, which eventually reaches the other side of the embryo and forms the digestive tract. If the blastopore forms a mouth, the embryo is a called a **protostome**, meaning that the mouth (*stoma*) forms first (*proto*) after the anus. If the blastopore forms an anus, it is called a **deuterostome**, meaning that the mouth (*stoma*) forms second (*deutero*) after the anus. Echinoderm embryos are deuterostomes. This difference in development is so fundamental that protostomes and deuterostomes are thought to have diverged before any other branchings that led to the modern coelomate **phyla**. In other words, echinoderms and chordates are more closely related to each other than to any other organisms.

Although both are deuterostomes, echinoderms and chordates have significant differences. All echinoderms have a **calcium** carbonate skeleton just beneath the skin which typically bears projecting spines, hence the name of the phylum. Like **cnidarians** (jellyfish), echinoderms are **radially symmetrical** as adults, whereas chordates are **bilaterally symmetrical**. However, larval echinoderms are also bilaterally symmetrical. The late development of radial symmetry in echinoderms indicates that it is relatively recently evolved in the taxon. Modern echinoderms probably evolved from a mobile, bilaterally symmetrical ancestor by adding a sessile life stage, which then evolved radial symmetry. Many echinoderm species have since evolved mobility as radially symmetrical adults.

Echinoderms possess a unique water vascular system, which provides structural support for a set of tube feet used for locomotion. This system consists of internal canals lined with protruding tube feet and muscular sacs called ampullae. This system is also connected to the outside of the organism by an opening called a madreporite, through which water goes in and out of the system. When the ampullae contract, water is pushed into the tube feet, making them rigid. Most echinoderms have muscles in the ends of the tube feet that contract to create suction between the foot and a surface upon which locomotion occurs. The tube feet are also used for gas exchange.

annelids segmented worms

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

coelom a body cavity

protostome an animal in which the initial depression that starts during gastrulation becomes the mouth

deuterostome an animal in which the first opening does not form the mouth, but becomes the anus

phyla broad, principal divisions of a kingdom

calcium a soft, silvery white metal with a chemical symbol of Ca

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

radially symmetrical describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

bilaterally symmetrical describes an animal that can be separated into two identical mirror image halves

Echinoderms, such as this orange-footed sea cucumber, have a calcium carbonate skeleton just beneath the skin which typically bears projecting spines.

Phylum Echinodermata is made up of five classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies and feather stars), and Holothuroidea (sea cucumbers). Sea stars have the typical echinoderm **body plan**—a central disk from which five or more arms radiate. They have no head or brain, and their sensory perception consists of eyespots at the end of the arms and neurosensory cells scattered throughout the **epidermis**. A ring of nerves around the mouth connects to nerve cords extending down the arms and coordinates movement. Sea stars feed on **bivalve mollusks** by prying them open with their arms and tube feet, then turning their stomachs inside out into the opening to digest the prey while it is still in its shell.

body plan the overall organization of an animal's body

epidermis the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

bivalve mollusks mollusks with two shells such as clams

Brittle stars look like sea stars but have thinner arms. Like sea stars, they are mobile, but their tube feet lack suction and are not used for locomotion. Also like sea stars, brittle stars can regenerate limbs that have been lost. Incredibly, a leg can regenerate an entire body. Some species reproduce asexually by dividing and regenerating.

Sea urchins and sand dollars do not have arms, but retain radial symmetry in the rows of tube feet poking out of their hard skeleton. Whereas urchins are spherical, sand dollars are flattened along the axis of radial symmetry. They are armed with movable spines that can be poisonous. Many species have powerful jawlike structures called "Aristotle's lanterns," which they use for grazing on algae and other food attached to a surface, such as rock or coral. As with sea stars and brittle stars, the mouths of urchins and sand dollars are located on the bottom of the body.

Scientists believe that sea lilies and feather stars resemble the first echinoderms because they are sessile and their mouths and arms are oriented upward to gather food from the water. This was probably the intermediate evolutionary step through which the other echinoderms passed on their way to a more mobile adult stage. In fact, 500-million-year-old sea lily fossils are virtually indistinguishable from modern species.

Sea cucumbers are the most recently evolved echinoderms. They have lost most of the skeleton, which remains in the form of small bony particles in the skin. Although they retain five rows of tube feet, they are elongated from head to tail and display partial bilateral symmetry; some tropical species attain lengths of several meters. Sea cucumbers are the most mobile class of echinoderms, eating **plankton** from the water column or digging into the bottom sediments. They also have the ability to regenerate their guts after they expel them in response to predators, presumably as a deterrent.

plankton microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

Echinoderms play important roles in the ecological community of species. Ecologist Robert Payne conducted a famous experiment in Pacific-coast tide pools in which he removed *Pisaster*, a species of sea star. Because sea stars prey on mussels, removing them resulted in an explosion in the mussel population and disrupted the ecological balance of the entire community. Sea stars are so important to tide-pool communities that they are considered a "**keystone species**."

keystone species a species that controls the environment and thereby determines the other species that can survive in its presence

Echinoderms reproduce sexually, with male and female individuals releasing **gametes** into the water. The larvae that result are small and lightweight, like many other floating organisms. They transform into the relatively immobile adult form in order to grow and produce more gametes.

gametes reproductive cells that only have one set of chromosomes

Why did echinoderms evolve such a peculiar adult form of **sexual reproduction**? Why do the larvae not grow bigger and reproduce themselves? Like insects, echinoderms have evolved a strategy of specializing in different activities at different stages in the life cycle. The larval stage specializes in dispersal, which is important for finding new habitats and avoiding competitors. The adult stage specializes in growth and reproduction by moving only enough to capture prey or graze. The ability to **metamorphose** from a dispersal stage to a growth stage allowed echinoderms to perform each function more effectively than their ancestors did. But other primitive deuterostomes failed to evolve this sophisticated adaptation; one of them gave rise to the chordates, and eventually humans. SEE ALSO Keystone Species; Phylogenetic Relationships of Major Groups.

sexual reproduction a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

metamorphose changing drastically from a larva to an adult

Brian R. West

Bibliography

Campbell, Neil A. *Biology*, 2nd ed. Redwood City, CA: Benjamin/Cummings Publishing Company, Inc., 1990.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishers, 1989.

Ridley, Mark. *Evolution*, 2nd ed. Cambridge, MA: Blackwell Science, Inc., 1996.

Echolocation

Echolocation is the process of using sound waves to locate objects that may be invisible or at a distance. Some bats use sound to locate their insect prey. Bats have vocal chords modified to emit the high-frequency sounds needed for good resolution and specially adapted ears to receive the sound. Animals also use echolocation for orientation, avoiding obstacles, finding food, and for social interactions. The animal produces sounds and listens for the echoes reflected from surfaces and objects in its environment. By analyzing the information contained in these echoes, the animal can perceive the objects.

In all species that use echolocation, the sound pulses are short bursts at relatively high frequencies, ranging from about 1,000 Hz in birds to at least 200,000 Hz in whales. Bats use frequencies from about 30,000 Hz to about 120,000 Hz. The pulses are repeated at varying rates depending on what the animal is doing. A flying bat will emit about one pulse per second. In a hunting bat close to its target, the rate may increase to several hundred pulses per second.

microchiroptera small bats that use echolocation

megachiroptera fruit bats and flying foxes

baleen fringed filter plates that hang from the roof of a whale's mouth

krill an order of crustaceans that serves a food source for many fish, whales, and birds

insectivores animals who eats insects

Most bats, including all small bats (suborder ***Microchiroptera***) and one genus of large bats (***Megachiroptera***) use echolocation. Other animals thought to use echolocation are a few species of shrews and two kinds of birds. Echolocation is also used by most toothed whales and porpoises (*Odontoceti*). **Baleen** whales (those that exist primarily on **krill** and similar organisms) do not use echolocation.

Echolocation in Bats

There are two groups of bats, large bats and small bats. Large bats eat fruit and find their way around using their excellent eyesight. Small bats are mostly **insectivores** that find their flying prey at dusk using echolocation. Bats produce sounds with their larynx, or voice box, which has adapted to produce loud, high-frequency sounds. The quality, frequency, duration, and repetition rate of the sounds produced varies with the species of bat and with the situation. For example, as a bat closes in on its prey, it will repeat the pulses of sound more frequently.

sonar the bouncing of sound off distant objects as a method of navigation or finding food

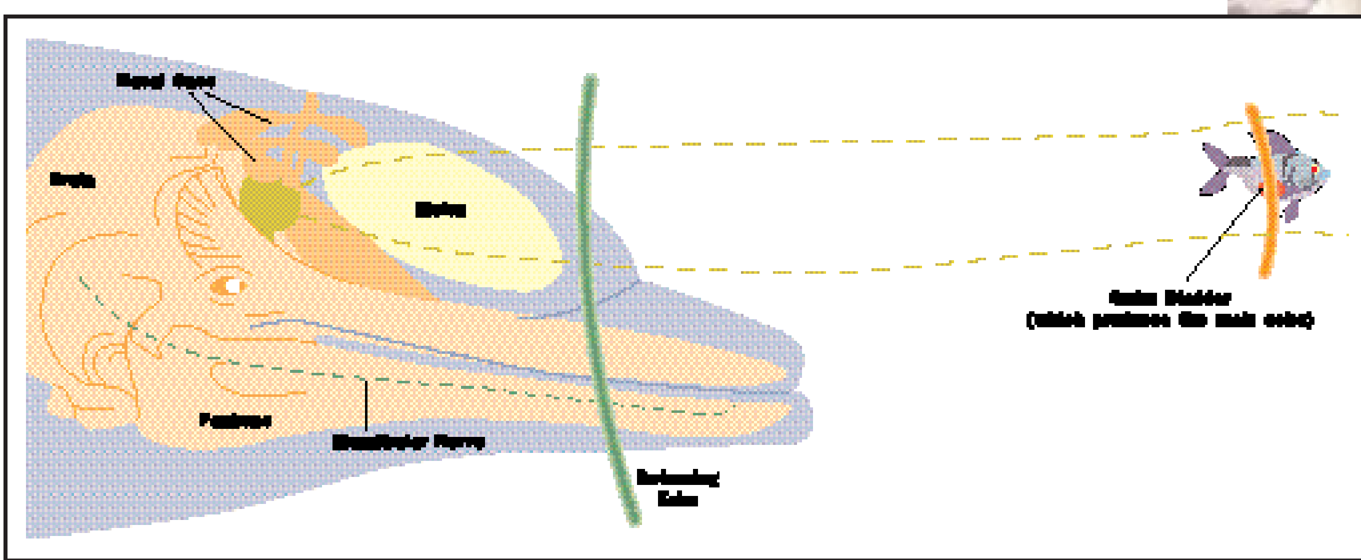
wavelength the distance between the peaks or crests of waves

Although the frequency of bat cries varies among species, the cries usually occur in a range between 30,000 and 80,000 Hz. The use of such high frequencies is an essential feature of the bat's **sonar** system. Because the target object (a moth or other small insect) is so small, a high-frequency, very short-**wavelength** sound must be used. A sound wave with a frequency of 80,000 Hz has a wavelength of around 4 millimeters (1/8 inch), which is suitable for locating a small moth.

Bat ears are well adapted to receive high-frequency sounds. In most bat species, the size of the outer ear is large relative to the size of the head. In some species that use relatively faint sounds, the outer ear is twice the size of the rest of the head. The large surface of the outer ear acts as an efficient collector of sounds. The outer ear is tuned to receive the frequencies emitted by the bat larynx, which helps the bat to hear the sounds it produces and tune out other sounds. The outer ear is also very mobile and can be rotated and tilted in various ways. The bat ear canal also contains a special organ that allows the canal to be closed to reduce the entrance of excessively loud sounds.

behavioral relating to actions or a series of actions as a response to stimuli

Neurophysiological and **behavioral** studies of bat hearing have revealed some curious features. One such feature is that bats do not respond behaviorally to frequencies below 10,000 Hz, although studies demonstrate that



Dolphins use echolocation to orient themselves in their surroundings. Redrawn from the *Greenpeace Book of Dolphins*, 1990.

they can hear these frequencies. This lack of a response is probably due to the bat's dependency on hearing for echolocation. Below 10,000 Hz, the wavelength is too long to be of any use in finding prey. It is also a frequency range where environmental noise is likely to occur, so bats have evolved the ability to selectively ignore sounds that are distracting and are not useful in finding prey. Researchers have also observed that bats are not easily disturbed by extraneous sounds of low frequencies, even very loud sounds. This peculiarity of hearing in bats may account for their resistance to distracting sounds.

Echolocation in Other Mammals

Dolphins and toothed whales use echolocation to orient themselves and locate objects in the water. These animals probably rely on sound production and reception to navigate, communicate, and hunt in dark or murky waters where sight is of little use. They produce sounds with their larynx and a complex system of cavities connected to their blowhole. The sounds used in echolocation are a rapid series of clicks. The clicks contain a wide range of frequencies, but most of the sound energy is in the 50,000 to 200,000 Hz range. These high frequencies are necessary for echolocation in water. Because the speed of sound in water is five times greater than in air, the wavelength of a sound of a given frequency is five times longer in water than in air. To achieve the same resolution, the frequency must be five times higher.

All toothed whales, including dolphins, have a fat-filled organ in the front part of the head called a melon. The melon acts like a lens for sound waves, focusing the sound waves into a narrow beam. Dolphins and other toothed whales generate a wide variety of clicks, whistles, and other noises used in communication and echolocation. The clicks they use for echolocation are of a higher frequency than those used for other forms of communication. This improves resolution and allows smaller prey to be located. The clicks are generated in a series of interconnected passages behind the melon. When the sound strikes an object such as a prey fish, some of the sound is reflected back toward the dolphin. Another fat-filled cavity in the dolphin's lower jaw acts as a receptor for this sound. The sound is carried from the fat-filled cavity to the middle ear and perceived by the animal's brain.

As soon as an echo from one click is received, the dolphin generates another click. The time lapse between click and echo enables the dolphin to determine the distance between it and the object. The difference in sound intensity received by each ear allows the animal to determine the direction. By emitting a series of clicks and listening to the echoes, the dolphin is able to locate and follow its prey. SEE ALSO Acoustic Signals.

Elliot Richmond

Bibliography

Allen, Glover M. *Bats.* Cambridge, MA: Harvard University Press, 1939. Reprint, New York: Dover Publications Inc., 1962.

Au, Whitlow W. L. *The Sonar of Dolphins.* New York: Springer-Verlag, 1993.

Bonner, Nigel. *Whales.* London: Butter and Tanner Ltd., 1980.

Fenton, M. Brock. *Bats.* New York: Facts on File Inc., 1992.

Gaskin, David Edward. *The Ecology of Whales and Dolphins.* London: Heinemann Educational Books Ltd., 1982.

Graham, Gary Lynn. *Bats of the World: A Golden Guide.* New York: Golden Press, 1994.

Harrison, Richard John, and Michael M. Bryden, eds. *Whales, Dolphins, and Porpoises.* New York: Facts on File, 1988.

Tuttle, Merlin D. *America's Neighborhood Bats*, rev. ed. Austin: University of Texas Press, 1997.

Wilson, Don E. *Bats in Question: The Smithsonian Answer Book.* Washington, D.C.: Smithsonian Institution Press, 1997.

Ecologist

If a butterfly flaps its wings in the Amazon, it causes a typhoon in Asia. This half-joke by ecologists illustrates their belief that all life on Earth is connected in a delicate and barely understood balance. Ecologists study the web of relationships between the plants, animals, microorganisms, climate, and geography of a given habitat.

The term "ecology" was devised by German zoologist Ernst Haeckel in the mid-1800s to mean the study of home. In his time, most scientists studied species in isolation. Haeckel realized the importance of looking at the links between animals and the places in which they live.

Biologist Rachel Carson enlarged on the ecological principle of the interconnectedness of life with her books in the 1950s about the sea. She described how living creatures interact to form communities of mutual dependency and how the vast currents of air and water connect the activities of one habitat with all others on Earth.

Once considered by science to be hostile and competitive with one another, species are now known to cooperate in elaborate ways, suggesting to some ecologists that the entire planet behaves as a single living organism, with the health of any one part mirrored in the whole.

The necessary coursework for a college degree in ecology includes chemistry, calculus, physics, genetics, biostatistics, and geology or biogeography. Ecologists also study neurobiology; cellular, developmental and molecular biology; physiology; and behavior. Their training consists of laboratory work and at least one semester of fieldwork.

Virtually any question concerning how life operates is open to an ecologist. Some of the fascinating puzzles investigated by ecologists include how **pesticides** cause bird species to decline, why pollution from fossil fuels could affect the atmosphere, and even how the flight of a butterfly might cause a typhoon.

pesticides substances that control the spread of harmful or destructive organisms

Nancy Weaver

Bibliography

Burnie, David. *Dictionary of Nature.* New York: Dorling Kindersley Inc., 1994.

Quinlan, Susan E. *The Case of the Mummified Pigs and Other Mysteries in Nature.* Honesdale, PA: Boyds Mill Press, 1995.

Ecology

Ecology is a branch of science that studies the ways in which plants and animals interact with one another and with their surroundings. Ernst Haeckel, a German zoologist, invented the word "ecology" in 1869. It comes from the Greek words *oikos*, which means "household," and *logos*, which means "discourse" or "study." In *The Riddle of the Universe*, Haeckel applied the term *oekologie* to the "relation of the animal both to its organic as well as its inorganic environment."

For many years, ecology was an obscure branch of biology. In the late twentieth century, however, as environmentalism became a popular movement, ecology moved to the forefront of public opinion and also rose to prominence as a discipline. Some of the late twentieth and early twenty-first centuries' thorniest problems—expanding populations, food scarcity, and environmental pollution—were and are essentially problems of ecology.

Ecologists study organisms in various kinds of environments by looking for patterns of interaction. An organism's environment includes both other organisms and physical surroundings. It involves relationships among individuals within a population and among individuals of different populations. These interactions among individuals, among populations, and between organisms and their environment form ecological systems, or **ecosystems**.

ecosystems self-sustaining collections of organisms and their environments

Background

The origins of ecology lie in the natural history studies of the Greeks, particularly the philosopher and scientist Theophrastus (c. 372–d. 287 B.C.E.), a contemporary and friend of the philosopher Aristotle. Theophrastus first described the interrelationships among organisms and between organisms and their nonliving environment.

In the early twentieth century, botanists in Europe and America began to study communities of plants that seemed to depend on each other. The Europeans looked at the composition, structure, and distribution of plant

Some of modern ecology's essential issues, such as environmental pollution and overpopulation, are cause for global concern.

communities. The American botanists studied how plant communities changed over time. Animal ecology developed along separate lines until American zoologists began to study the interrelation of plant and animal communities as a whole.

Around the same time, biologists began to study the interaction of predators and prey, competition among species, and territoriality (especially in nesting birds). Austrian zoologist Konrad Lorenz studied instinctive and **learned behavior** (such as imprinting in birds). In 1920 German biologist August Thienemann proposed the concept of **trophic levels** and energy flow in ecosystems. English biologist Charles Sutherland Elton developed the concept of ecological niches and trophic pyramids. Nutrient cycling was studied in the 1940s and 1950s.

learned behavior behavior that develops in reaction to the environment

trophic levels divisions of species in an ecosystem by their main source of nutrition

Modern ecology is now based on the idea of the ecosystem, a well-defined unit including the organisms and the nonliving environment in an identifiable region. Ecosystems have several structured interrelationships, and they function by maintaining a flow of energy and a cycling of materials through a series of processes such as the food chain. Ecosystems become more complex as they mature. Complex ecosystems are more stable. The organisms in an ecosystem occupy a niche, which includes their feeding and other behaviors as well as their physical position in the ecosystem.

Subdivisions of Ecology

Ecology is a multidisciplinary science. It draws from such disciplines as plant and animal biology, **taxonomy**, physiology, genetics, behavior, meteorology, pedology (the study of soils), geology, sociology, anthropology, physics, chemistry, and mathematics. Plant ecology centers on a descriptive study of

taxonomy the science of classifying living organisms the relationships of plants to other plants and their environment. Animal ecology studies population dynamics, distribution, behavior, and the interrelationships of animals and their environment. Plant ecology can often focus on just the plants. Because, however, animals depend on plants for food and shelter, animal ecology must include plant ecology. This is particularly true in areas of applied ecology, such as wildlife management.

Even within one of the subdivisions of ecology, ecologists usually concentrate on particular taxonomic groups, so that there are fields of insect ecology or the ecology of large mammals. Other ecologists may study particular ecosystems, such as marine environments or tropical rain forests. In applied ecology, basic ecological principles are applied to the management of plants and animals. Applied ecologists also study the effect of humans on their environment and on the survival of other species. Theoretical ecologists develop mathematical models and computer simulations of particular practical problems.

The study of an individual organism in relation to its environment is known as autecology. The study of groups of organisms in relation to each other and to their environment is called synecology. Autecology is closest to the original concept of ecology. When an individual organism is studied, it is possible to change variables in a controlled way. Thus, autecology is an inductive, empirical science. Synecology is more descriptive and deductive.

There are several other subdivisions of ecology. Ecological geography is the study of the geographic distribution of plants and animals. Population ecology is the study of population growth, mortality, **birthrates**, competition, and predator-prey relationships. Ecological genetics is the study of the genetics and ecology of local races and distinct species. Behavioral ecology is the study of the behavioral responses and social interactions of animals to their environment. Community ecology is the study of groups of organisms in a community. Systems ecology is the analysis and understanding of the structure and function of ecosystems by the use of applied mathematics, mathematical models, and computer programs. Finally, paleoecology is the study of the ecology of fossil organisms.

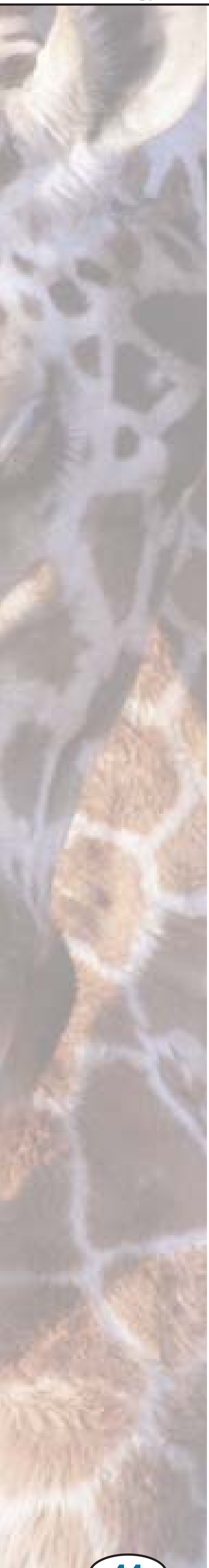
birthrates ratios of the number of births in an area in a year to the total population of the area

Methods

Ecologists work with living systems possessing numerous variables, so the techniques used by the other sciences are not directly applicable. It is obvious that an individual organism removed from its environment cannot be studied in the laboratory with any hope of **learning** about its relation to its environment. Ecologists must deal with many different variables, only a few of which can be controlled. Some of the variables are probably not known. Consequently, ecological measurements may never be as accurate or precise as measurements made in physics or chemistry.

learning modifications to behavior motivated by experience

In spite of these problems, statistical procedures and computer modeling are providing improved understanding of population interactions and ecosystem function. Computer modeling is becoming increasingly important in applied ecology, especially in the management of natural resources and of agricultural problems that have an ecological basis.



Several different modern techniques have improved the ecologist's ability to study animals in relation to their environment. Various techniques of telemetry can be used. For example, animals can be fitted with a radio transmitter and a global positioning system to provide a constant flow of information including body temperature, respiration, and position. Radioisotopes can be used to track nutrient cycling in an ecosystem. Laboratory microcosms can be constructed using living and nonliving material from natural ecosystems and can be held under conditions similar to those found in the field.

Interdependence in Nature

Ecology emphasizes the interaction between every organism with other organisms and with the natural resources in the environment, such as air, soil, and water. Nineteenth-century British naturalist Charles Darwin emphasized this interdependence in *On the Origin of Species*: "It is interesting to contemplate a tangled bank, clothed with plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp Earth, and to reflect that these elaborately constructed forms, so different from each other, and so dependent upon each other in so complex a manner, have all been produced by laws acting around us."

The well-established principles of ecology make it clear that humans cannot regard themselves as separate from and independent of the natural world. Nature is not just a place a person visits during a drive in the country. Changes made to the environment affect all the organisms in it. When vehicles and factories emit pollutants, plants and animals (including humans) are affected. Water contaminated by waste cannot support a mature, complex, stable ecosystem. Even the vast oceans cannot escape pollution.

Applications of Ecology

Early in the twentieth century, southern Ohio suffered massive flooding. To prevent a repeat of the disaster, residents in the area constructed large earthen dams across river valleys to contain floodwater. The dam slopes, however, were unstable and washed away easily. Ecologists were called on to devise a system for stabilizing the earthen dams. They recommended planting the fast-growing grasses alfalfa and clover. This was followed by planting bromegrass and Japanese honeysuckle. The combination of plants quickly produced a strong turf that was able to hold the soil and gravel in place.

Migratory waterfowl declined during the early part of the twentieth century. To reverse the trend, ecologists used banding and other techniques to study the migratory patterns and feeding habits. They discovered that springtime hunting was adversely affecting the population, but the major problem was the loss of breeding areas and resting areas. Wetlands were being drained across the northern prairies. Some of these wetlands were not well-suited for crops while others had stored water. Draining had reduced breeding and resting sites and contributed to downstream flooding.

keystone species a species that controls the environment and thereby determines the other species that can survive in its presence

Not all species in an ecosystem are of equal importance. Some, known as **keystone species**, are critical. For example, alligators in the Florida Everglades dig deep holes to collect mud and grass for nests. These holes become permanent ponds that survive periods of drought and provide a reliable source of water for many other species in the ecosystem.

Famous Ecological Mistakes

Well-meaning conservation efforts often turn out to be disasters when ecological relationships are not taken into consideration. To increase the number of deer in Grand Canyon National Park and the Kaibab National Forest, most American mountain lions or cougars (*Puma concolor*) were hunted out in the early part of the twentieth century. With no cougar to keep their numbers in check, the number of deer increased dramatically.

The deer stripped the forest of all undergrowth. They even ate the lower branches from the evergreen trees in the forest as high up as they could reach by standing on their hind legs. This gave the forest an unnatural appearance. With food supplies exhausted, the deer became feeble and many died of starvation. To reverse the damage, deer hunting was allowed and the remaining cougars were protected. The forest and the deer herd slowly recovered.

The Future

All over the world, human activity is dramatically altering natural environments. Natural communities are being replaced with human-made communities. These altered communities, however, still obey the same ecological principles. If these human-made communities are to thrive, people must recognize the ecological principles at work and strive for complex, diverse, and mature ecosystems. People must also recognize the interdependence of humans and the natural world and that human activities can adversely alter the natural balance. SEE ALSO ECOSYSTEM; HABITAT.

Elliot Richmond

Bibliography

Billington, Elizabeth T. *Understanding Ecology.* New York: F. Warne, 1971.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Darwin, Charles. *On the Origin of Species.* Danbury, CT: Grolier Enterprises, 1981.

Haeckel, Ernst. *The Riddle of the Universe*, trans. Joseph McCabe. New York: Buffalo Books, 1992.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth, 1990.

Pringle, Laurence. *Lives at Stake: The Science and Politics of Environmental Health*. New York: Macmillan Publishing Company, 1980.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer, 1987.

Sharpe, Grant William. *Interpreting the Environment*, 2nd ed. New York: Wiley, 1982.

Sharpe, Grant William, Clare W. Hendee, and Shirley W. Allen. *Introduction to Forestry*, 5th ed. New York: McGraw-Hill, 1986.

Ecosystem

An ecosystem consists of a biological community and the **abiotic factors** on which it relies. These factors include sunlight, water, elements, and minerals. Energy flows one way through an ecosystem, starting as sunlight absorbed by primary producers, passing through several levels of consumers,

abiotic factors pertaining to nonliving environmental factors such as temperature, water, and nutrients and eventually dissipating as heat. Materials cycle through an ecosystem by alternating between **biotic** and abiotic stages.

biotic pertaining to living organisms in an environment

The sun is the ultimate source of energy for most ecosystems. The distribution of solar energy around the world is dictated by the position of the sun and air and water movement. The variation in solar energy causes variation in temperature and rainfall in time and space, which in turn influences the type of ecosystem found in each place.

Ecosystems contain interconnected food chains known as food webs through which energy flows. Each food chain consists of a sequence of predator-prey relationships at different **trophic levels**. Each predator species can have more than one prey species and vice versa. Primary producers, which provide 99 percent of all organic material, are photosynthetic plants and algae. Primary consumers, or herbivores, eat primary producers; secondary consumers, or carnivores, eat herbivores. Tertiary consumers eat other carnivores. Most ecosystems contain no more than two carnivorous trophic levels, because only about 10 percent of the energy contained in the **biomass** at one level is passed on to the next.

trophic levels divisions of species in an ecosystem by their main source of nutrition

biomass the dry weight of organic matter comprising of organisms in a particular habitat

Detrivores, or decomposers, form yet another trophic level by scavenging or decomposing dead organic material. Decomposers are capable of gaining energy from materials that no other animals can, such as cellulose or nitrogenous waste, and may consume up to 90 percent of primary production (energy produced by plants) in forests.

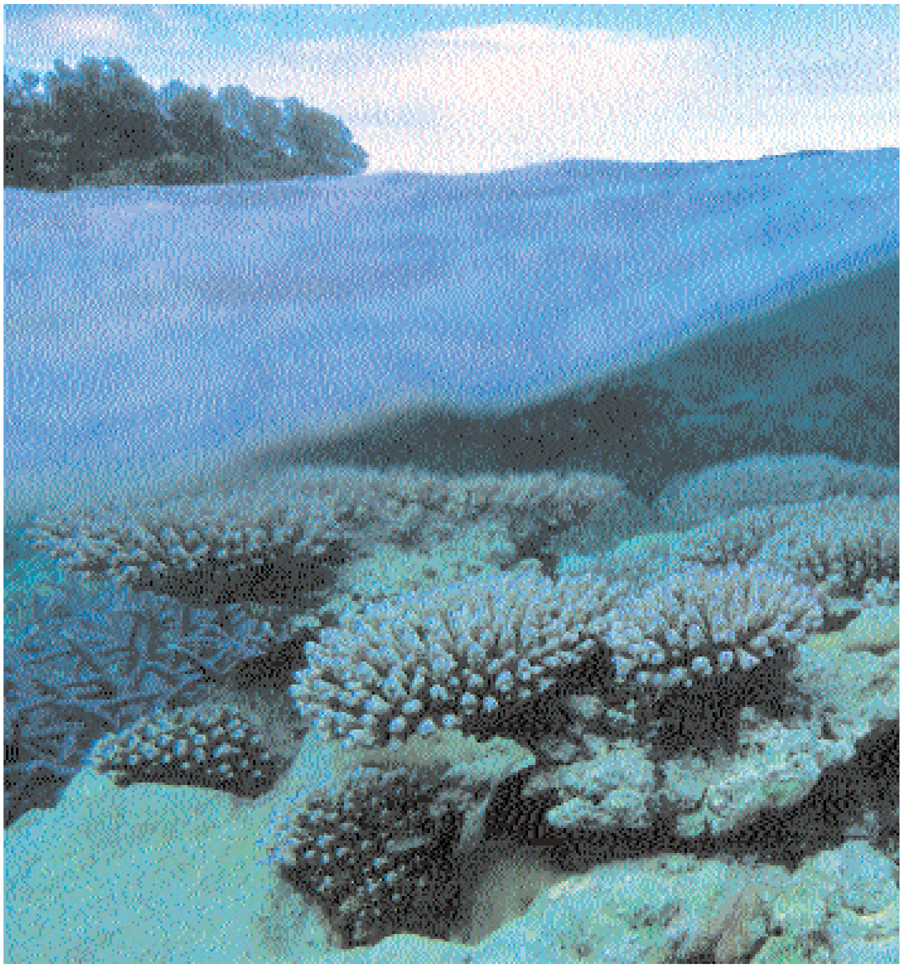
Trophic levels are characterized by their productivity. Gross productivity is the rate at which energy is assimilated by organisms. Gross productivity minus the amount of energy left over after the cost of metabolic activity is net productivity. Net productivity can be measured as accumulated biomass, which is the total dry weight of organic materials, and is the energy that is available to organisms at the next trophic level. The difference between gross and net productivity limits the number of trophic levels in an ecosystem. At some point, there is not enough residual energy to support a healthy population of predators.

The loss of energy at each trophic level would seem to dictate a pyramidal structure in which each trophic level contains less biomass than the one beneath it. However, productivity is a function of both biomass and reproduction rate. For example, a phytoplankton population often reproduces fast enough to support a larger population of **zooplankton**.

zooplankton small animals that float or weakly move through the water

Whole ecosystems can also be measured for their productivity. Algal beds and reefs, due to their rapid reproduction rates, are the most productive ecosystems on Earth. Temperate forests, however, contain the most biomass. Swamps and marshes rank as high as tropical rain forests in productivity, whereas the desert and the open ocean rank the lowest. Cultivated land has only average productivity.

Materials flow through ecosystems in biogeochemical cycles. These cycles include the atmosphere, the lithosphere (Earth's crust), and the hydrosphere (bodies of water). Decomposers play an important role in material cycling by separating inorganic materials, such as nitrogen, from organic compounds. A generalized biogeochemical cycle consists of available and



This coral reef in Palau offers a prime example of an ecosystem in delicate balance.

unavailable organic components and available and unavailable inorganic components.

Inorganic materials become organic through assimilation and **photosynthesis**. Organic materials become inorganic due to respiration, decomposition, and excretion. Sedimentation causes inorganic material to become unavailable, whereas erosion releases it. Fossilization stores organic material as fossil fuel, whereas erosion and combustion release fossil fuels as inorganic material.

photosynthesis the combination of chemical compounds in the presence of sunlight

The water cycle plays a significant role in terrestrial ecosystems because it is the major component, by weight, of all organisms. Water evaporates from oceans, rivers, and lakes and transpires from plants into the atmosphere. Precipitation occurs over land when the atmospheric water condenses, followed by runoff and percolation through the soil into ground water. Eventually, the water returns to the atmosphere by evaporation or transpiration, but in the meantime it can be assimilated by organisms.

Nitrogen also plays a vital role in ecosystems because it is necessary for the synthesis of both amino and nucleic acids, which makeup proteins and DNA. In order for plants to assimilate nitrogen, it must be in the inorganic form of nitrate (NO_3). Bacteria convert ammonia (NH_3) or ammonium (NH_4) into nitrate by nitrification, which requires the addition of oxygen.

A generalized biogeochemical cycle.

	Available	Unavailable
Organic	Organisms Detritus	Coal, petroleum oil, natural gas
Inorganic	Atmosphere Soil Water	Minerals in rocks

Plants convert nitrates into ammonium in order to synthesize organic compounds. Decomposers complete the cycle by ammonification, the separation of inorganic nitrogen from dead organic material. Nitrogen is lost from this cycle by denitrification, in which bacteria break down nitrates into oxygen and nitrogen in poorly aerated soils. Nitrogen is added to the cycle by nitrogen-fixing bacteria, which incorporate atmospheric nitrogen into organic compounds.

The fundamental element in organic molecules is carbon. Plants assimilate carbon from the atmosphere in the form of carbon dioxide, which is broken down during photosynthesis to produce oxygen and carbohydrate. Respiration in plants and animals reverses this process by using carbohydrate to fuel the conversion of oxygen into carbon dioxide. Thus, carbon may be thought of as cycling between gaseous and organic states.

nucleotides the building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

Phosphorus is necessary for the synthesis of ATP (adenosine triphosphate) and nitrogen-containing molecules called **nucleotides**. Phosphorus is separated from organic compounds by decomposers or excreted by animals as phosphates. Plants and algae then assimilate phosphates from the soil and water to produce organic compounds.

Humans affect the function of ecosystems in many ways. One effect is the increase in atmospheric carbon dioxide from the burning of fossil fuels, which was negligible until industrialization. Another is the diversion of water from rivers and ground water into reservoirs. Industrial fertilization has increased the level of phosphates in many waterways, causing blooms of phytoplankton that choke the oxygen out of the water. The long-term effects of human influence on ecosystems remain to be determined. SEE ALSO Biomes; Habitat.

Brian R. West

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Pianka, Eric R. *Evolutionary Ecology*. New York: Harper Collins Publishers, 1994.

Egg

The egg, or ovum, is the gamete (reproductive sex cell) produced by most female animals. It is fertilized by the sperm, which is the male gamete. The term "egg" is commonly used to include the acellular structures that surround the ovum.

In "higher" animals, including arthropods (such as crabs and insects), most fish, most amphibians, many reptiles (including birds), and some mammals (the echidna and the platypus), the egg is a relatively large structure in which the young matures outside the mother's body. This form of reproduction is called **oviparous**, or egg-laying. In the **viviparous**, or live-bearing, form of reproduction used by some fish, amphibians, and reptiles, as well as most mammals, the developing egg remains within the mother's body.

oviparous having offspring that hatch from eggs external to the body

viviparous having young born alive after being nourished by a placenta between the mother and offspring

The eggs of both amphibians and **amniotes** (reptiles and mammals) generally contain a protective covering and the cells from which the young develop. The protective covering may take on a number of different forms, depending on the animal. In amphibians the coating is gelatinous and clear. In amniotes, it may be leathery like the egg of a reptile, or hard like the egg of a bird. In live-bearing species of lizards and snakes, the shell is a thin membrane through which materials can easily pass.

amniotes vertebrates which have a fluid-filled sac that surrounds the embryo

In most amphibian and amniote eggs of both oviparous or viviparous species, a large yolk mass within the egg nourishes the developing embryo. In some viviparous reptiles and most mammals, nutrition comes directly from the mother through a specialized aggregation of blood vessels. In mammals, this structure is called a **placenta**.

placenta the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

The structure, size, and number of eggs produced depend on the lifestyle and environment of the animal that makes them, and there is a fair amount of variation. There are two general strategies involving the size and number of eggs: the mother's limited energy resources will either go toward making a smaller number of larger offspring or a larger number of smaller offspring.

Some species produce many offspring to increase the number that survive in a harsh environment. In this strategy, survival is largely dependent on chance, and many of the young die. Species that invest more energy into a smaller group of larger young increase the chance that each individual will survive, based on the assumption that larger young are stronger than smaller young.

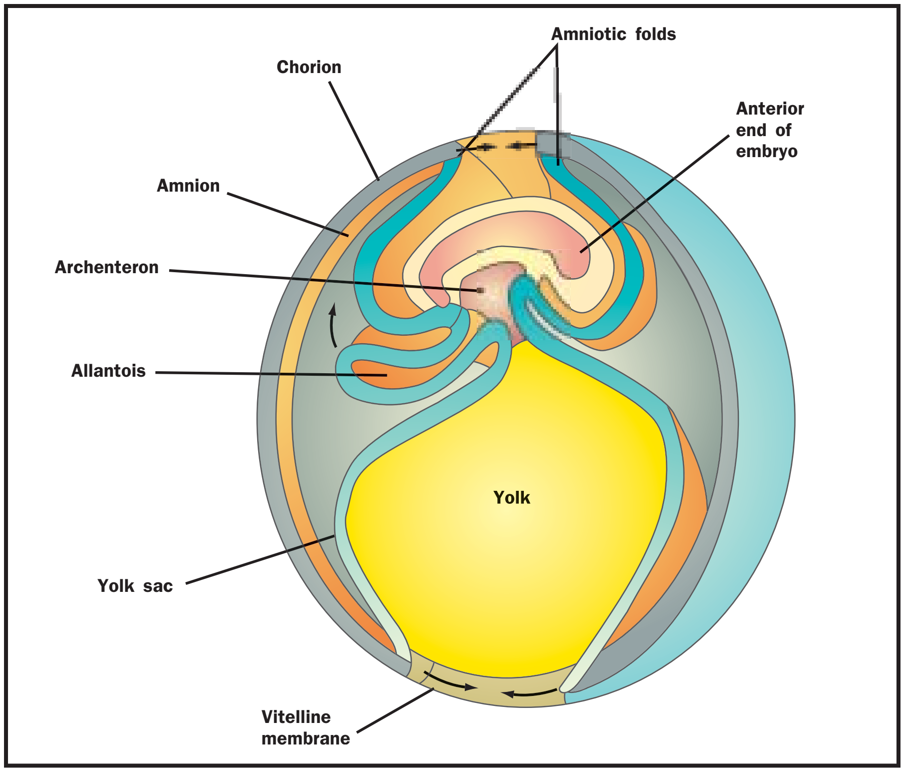
Both oviparous and viviparous strategies are represented among amphibians (frogs, **salamanders**, and the often-hiding, wormlike caecilians). The eggs of oviparous amphibians vary greatly in size. In addition, because the gelatinous membrane that surrounds an amphibian egg is not safe from losing internal fluids, desiccation (drying out) is a serious threat.

salamanders four-legged amphibians with elongated bodies

Most species lay their eggs in or near water, although some salamanders will bury their eggs to keep them moist and cool. Because an amphibian egg is not waterproof, it exchanges fluids and gases easily with the surrounding water. This is critical for supplying the egg with oxygen and for releasing harmful waste products from the confines of the egg.

The eggs of reptiles (including birds) and mammals have features that protect them from the challenges posed by a terrestrial (land) environment. In oviparous amniotes, the eggs are protected by a sturdy shell that safeguards the embryo against desiccation, although some air and moisture can pass through the shell.

The amniote egg has several specialized compartments. The yolk sac holds the yolk that feeds the embryo. The allantois, which is an extension



The development of embryonic membranes in a chicken egg. Redrawn from Campbell, *Biology*, 1993.

of the embryo's gut, stores solid waste products. Both the yolk sac and the allantois are connected to the developing embryo.

Various other egg layers and membranes form around the ovum as it passes from the ovary through a muscular tube called the oviduct to the cloaca. The materials that make up these layers and membranes are secreted by specialized glands that line the oviduct. A clear fluid layer called the albumen—the "egg white" of a chicken egg—supplies the embryo with water and inorganic nutrients and cushions the embryo from impact if the egg is jarred or dropped.

Albumen contains a protein (also called albumen), which binds to water and inorganic nutrients and aids in their transport. These nutrients diffuse through (pass through) the walls of the blood vessels that connect the embryo (through the umbilical cord) to the mother (at the placenta, or aggregation of vessels at the wall of the uterus/oviduct).

The albumen is enveloped within the chorion, a thin membrane which also surrounds the embryo, yolk sac, and allantois. The chorion regulates the passage of gas and moisture into and out of the egg. Finally, a shell surrounds and protects the entire egg. The shell allows moisture and gas to pass through it. The shells of most lizards and snakes have a leathery consistency, whereas birds have hard, **calcified** shells that resist denting. SEE ALSO EMBRYONIC DEVELOPMENT.

calcified made hard through the deposition of calcium salts

Judy P. Sheen

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman Inc., 1999.

Jameson, E. W. *Vertebrate Reproduction.* New York: John Wiley & Sons, 1988.

Elton, Charles Sutherland

British Biologist
1900–1991

Charles Sutherland Elton was born in Liverpool, England. Elton is considered the father of animal ecology. Ecology is the study of the relations between living creatures and their natural environment.

Elton was educated at Liverpool College and then at New College, Oxford. In 1922 he graduated from Oxford with a degree in zoology. At that time, most scientists studying animals emphasized their physical makeup and performed studies in laboratories. However, Elton was more interested in the scientific study of animals in their habitats. While still in college, Elton began this study, making numerous journeys to the Arctic.

In 1927 Elton published his first book, *Animal Ecology*. It was considered brilliant, and established many of the basic principles of modern animal ecology. He discussed food chains and the food cycle, niches, and the "pyramid of numbers." The pyramid of numbers is an observation about food relationships. A large number of plants feed a smaller number of animals, and these animals in turn provide food for an even smaller number of meat-eating animals. Elton addressed evolution in his 1930 book *Animal Ecology and Evolution*.

Elton concentrated his studies on how the number of animals in a population was affected by a changing environment. In 1932, he established the Bureau of Animal Population at Oxford, which for thirty-five years served as an important center for worldwide studies of ecology. In 1932 Elton became the editor for the newly established *Journal of Animal Ecology*.

In 1936 he was appointed to prestigious positions at Oxford and Corpus Christi College. Elton's research on mice populations enabled him to assist his country during World War II with the control of rodent pests. He published two books on rodents, *Voles, Mice and Lemmings* in 1942 and *The Control of Rats and Mice* in 1954. Other important books were *The Ecology of Invasions of Animals and Plants* (1958) and *The Pattern of Animal Communities* (1966).

In 1953 Elton was elected a member of the Royal Society of London and a foreign member of the American Academy of Arts and Sciences. He was awarded the Gold Medal of the Linnean Society in 1967 and the Royal Society's Darwin Medal in 1970. Elton retired from his studies in 1967.

Denise Prendergast

Bibliography

Elton, Charles S. *Animal Ecology.* London: Sidgwick & Jackson, Ltd., 1927. Reprint, London: Science Paperbacks and Methuen, 1966. Reprint: New York: October House, 1966. Reprint, Chicago: University of Chicago Press, 2001.

———. *Animal Ecology and Evolution.* Oxford: Clarendon Press, 1930.

———. *Ecology of Animals.* London: Methuen, 1933. Reprint, London: Methuen; New York: John Wiley, 1950. Reprint, London: Science Paperbacks and Methuen, 1966.

———. *Exploring the Animal World.* London: G. Allen & Unwin, 1933.

———. *Voles, Mice and Lemmings: Problems in Population Dynamics.* Oxford: Clarendon Press, 1942. Reprint, Codicote, Herts.: Wheldon & Wesley; New York: Stechert-Hafner, 1965.

———. *Ecology of Invasion by Animals and Plants.* London: Methuen, 1958. Reprint, London: Chapman & Hall, 1977. Reprint, Chicago: University of Chicago Press, 2000.

———. *Pattern of Animal Communities.* London: Methuen; New York; John Wiley, 1966.

McMurray, Emily J., ed. *Notable Twentieth-Century Scientists.* Detroit: Gale Research Inc., 1995.

Embryology

Embryology is the biological field of study that examines the early development of organisms. In general, a developing organism is considered an embryo until the point at which all the essential tissues and organ systems have developed. In humans, the embryonic stage covers approximately the first two months of pregnancy.

fertilization the fusion of male and female gametes

zygote a fertilized egg

cleavage the process of cytokinesis in animal cells; as cells multiply, the plasma membrane pinches off to make two cells from one

gastrulation the formation of a gastrula from a blastula

mesoderm the middle layer of cells in embryonic cells

Certain key events occur during the embryonic development of all multicellular animals. These include **fertilization**, the union of the sperm and egg to form the fertilized egg, or **zygote**; **cleavage**, when the fertilized egg divides in organized cycles to produce multicellularity; **gastrulation**, in which the three primary germ layers, the ectoderm, **mesoderm**, and endoderm, are differentiated; and finally organogenesis, during which the organs develop.

Two general approaches are often taken in the study of embryology: These are descriptive embryology and experimental embryology. Descriptive embryology dates from antiquity, and attempts to describe the normal sequence of developmental events that occur during embryonic development in a given organism. This information can be used to explain how adult anatomy is achieved. Understanding normal development also allows scientists to understand the origin of common birth defects.

Scientists interested in embryology study images such as this close-up of a 17.5 day old rat embryo without its yolk sac.

Experimental embryology attempts to shed light on the basic processes involved in development, particularly at the cellular level. Experimental embryologists want to discover how development is controlled and how ever more complex structures and organs are produced. They tend to focus on one of a few model organisms about which considerable developmental and genetic information is already known. These model organisms include the mouse, the chicken, the fruit fly *Drosophila melanogaster*, the African clawed frog *Xenopus laevis*, and the nematode *Caenorhabditis elegans.* One particularly effective approach in experimental embryology has been that of developmental genetics, which studies the effect of mutant genes on developmental processes. By comparing the developmental results of mutant versus normal genes, the role of individual genes in development can be assessed. This experimental strategy usually involves screening large numbers of animals for developmental abnormalities. SEE ALSO EMBRYONIC DEVELOPMENT.

Jennifer Yeh

Bibliography

Gilbert, Scott F. *Developmental Biology*, 5th ed. Sunderland, MA: Sinauer Associates, 1997.

Gould, James L., William T. Keeton, and Carol Grant Gould. *Biological Science*, 6th ed. New York: W. W. Norton & Co., 1996.

Embryonic Development

All embryonic structures are derived from a single cell formed by the union of two gametes. Every individual organism began as a single cell, which divided and differentiated into various types of cells that make up the diverse tissues and complex structures found in the adult. **Ontogeny**, or the development of an organism from fertilization to adult, begins with the **fusion** of two cells, the sperm and egg. The sperm and egg are **haploid cells** formed through the process of **meiosis**. The haploid cells have no function outside of their involvement in reproduction.

Many invertebrates have isolecithal eggs (yolk is evenly distributed throughout the egg). These eggs have relatively little yolk and various patterns of holoblastic cleavage (the cells divide completely and evenly). The **arthropod** egg has a moderate amount of yolk, concentrated in the egg's center. The eggs of amphibians and **cartilaginous** fishes have a moderate amount of yolk, mostly in the lower half of the egg (the vegetal hemisphere). Birds have extremely telolecithal eggs (yolk is concentrated in the vegetal pole, opposite the nucleus) that have a large amount of yolk.

A shell membrane surrounds the embryo, yolk, and albumin, or egg white. It offers mechanical protection and provides a surface for diffusion of oxygen and other gases. Within the egg the allantois acts as a compartment for the storage of nitrogenous excretory products such as **uric acid**, and may remain after birth or hatching as the urinary bladder. The **amnion** is filled with amniotic fluid to cushion the embryo that it surrounds. The chorion surrounds the amnion and yolk sac. Mammalian eggs contain some yolk but not nearly as much as found in bird eggs. The typical mammalian egg contains little yolk which is evenly distributed throughout the egg (it is microlecithal and isolecithal).

ontogeny the embryonic development of an organism

fusion coming together

haploid cells cells with only one set of chromosomes

meiosis a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

arthropod a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

cartilaginous made of cartilage

uric acid insoluble form of nitrogenous waste excreted by many different types of animals

amnion the membrane that forms a sac around an embryo

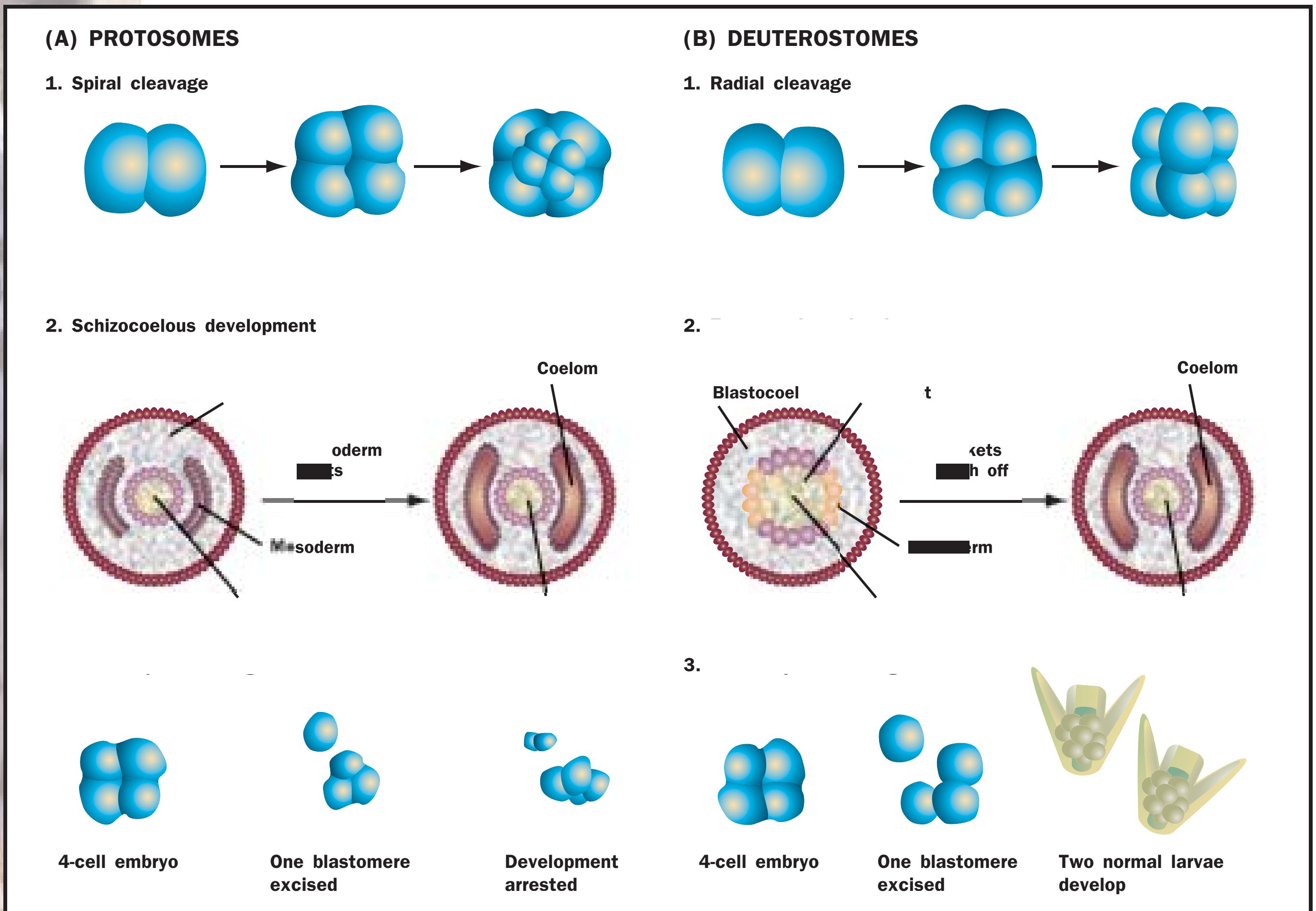
Stages of Development

In **deuterostomes** (one of two major groups of coelomate animals that includes echinoderms and chordates), early cleavage divisions are radial. In contrast, protostomes typically display spiral cleavage. Early cleavage divisions in most embryos are reductive, which means that they divide the original contents of the egg without an increase in the total cellular volume of the embryo. The average diameter of a cell decreases as cleavage continues so that the surface area increases relative to cellular volume.

deuterostomes animals in which the first opening does not form the mouth, but becomes the anus

Gastrulation occurs after several cycles of cleavage events. Several important events occur during gastrulation in multicellular animals:

- The three primary germ layers, ectoderm, mesoderm, and endoderm, are established.
- The basic body plan is established, including the physical construction of the primary body axes.
- Cells are brought into new positions, allowing them to interact with cells that were initially not near them. These cellular interactions alter the fate of individual cells, which begin to look and behave differently. This phenomenon is known as induction (cell–cell interactions which lead to cellular differentiation) and is a critical step in the formation of tissue layers.



A comparison of development cycles in protosomes and deuterostomes. Redrawn from Gilbert, 1994.

During **invagination**, a sheet of **epithelial cells** (cells that are in close contact with each other and adhere to a basement membrane) bends inward to form a "pocket." During ingression, cells leave an epithelial sheet by transforming into freely migrating mesenchyme cells. During involution, a sheet of tissue spreads inward from the lip of the newly formed cavity. As material moves in from the external portion of the sheet, material that was originally at the lip spreads further into the cavity, eventually forming a sheet of tissue that lines the invagination below the exterior tissue layers.

Intercalation is an expansion process during which cells from different layers lose contact with their neighbors and rearrange into a single layer, which increases in surface area and expands laterally. Intercalation is an important morphogenetic movement involved in the construction of the primary body axis in amphibians. A specialized form of intercalation is convergent extension. An epithelial sheet converges toward a central site, followed by its extension along a single axis through intercalation of the cells of the epithelium (picture a pile of poker chips arranging themselves into a stack). This rearrangement of epithelial cells is an important event during both **gastrulation** and subsequent neurulation. Convergent extension of the marginal zone (the region of intermediate pigmentation between the pigmented animal hemisphere and the unpigmented vegetal hemisphere) creates the **anterior-posterior**, or forward-backward axis. During neurulation,

invagination a stage in embryonic development where a cell layer buckles inward

epithelial cells cells that occur in tightly packed sheets that line organs and body cavities

intercalation placing or inserting between

gastrulation the formation of a gastrula from a blastula

anterior referring to the head end of an organism

posterior behind or the back

convergent extension of the central region of the neural plate (the region of embryonic **ectodermal** cells that lie directly above the **notochord**) occurs as the neural axis elongates and the neural tube closes. Also, during intercalation two or more rows of cells move between one another, creating an array of cells that is longer (in one or more dimensions) but thinner than the cell rows from which it formed. The overall change in shape of the tissue results from this cell rearrangement.

ectodermal relating to the outermost of the three germ layers in animal embryos

notochord a rod of cartilage that runs down the back of chordates

Intercalation can be a powerful means of expanding a tissue sheet. During convergent extension, two or more rows of cells intercalate. Cells converge by intercalating perpendicular to the axis of extension, resulting in the overall extension of the tissue in a preferred direction. Primary mesenchyme cells undergo ingression at the onset of gastrulation. During epiboly, a sheet of cells spreads by thinning which is accomplished by changes in the shape or position of cells.

In deuterostomes, the vegetal plate (a thin sheet of epithelial cells) undergoes invagination to produce the archenteron (the cavity formed by the endoderm during gastrulation). The blastopore (the external opening of the archenteron) forms the anus of the larva later in development. Secondary invagination involves the elongation of the archenteron across the blastocoel (the fluid-filled cavity of the blastula, as the embryo is known at this stage), where it attaches to the ectoderm near the animal pole (the pole nearest the nucleus) of the embryo. The onset of secondary invagination correlates with the appearance of long, thin filopodia extended by secondary mesenchyme cells at the tip of the archenteron.

One characteristic found in vertebrates is neural crest cells, derived from ectodermal cells. They develop along the top of the neural tube. As the neural folds close, most neural crest cells change into mesenchyme, an embryonic tissue that consists of star-shaped cells from all three germ layers. Mesechymal derivatives eventually give rise to the visceral skeleton (**gill arches**, some of which will develop into jaws), pigment cells, sensory and postganglionic **neurons** (the dentine-producing cells of teeth), Schwann cells that help protect neurons, and bony scales. **Differentiation** and derivation of tissues and organs during development is called organogenesis. After the production of the neural tube, differentiation of the germ layers occurs rapidly, and organogenesis begins, in which the primary tissues differentiate into specific organs and tissues.

gill arches arches of cartilage that support the gills of fishes and some amphibians

neurons nerve cells

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

Neurulation creates three important structures in the embryos of higher vertebrates:

- The neural tube, which gives rise the central nervous system;
- The neural crest, which gives rise to a diverse set of cell types; and
- A true epidermis, which covers over the neural tube.

Examples of Development

Four examples illustrate some aspects of embryonic development. All four are **metazoans**: Platyhelminthes (a nematode), Echinodermata (a sea urchin), and Chordata (represented by a frog, a bird, and a mammal).

metazoans a subphylum of animals that have many cells, some of which are organized into tissues

A worm. *Caenorhabditis elegans* (*C. elegans*) is a free-living nematode with two sexes: a self-fertilizing hermaphrodite and a male. The general body

concentric having the same center

pseudocoelom a body cavity that is not entirely surrounded by mesoderm

gonads the male and female sex organs that produce sex cells

osmoregulatory system a system that regulates the water balance between an organism and its environment

morphogenesis the development of body shape and organization during ontogeny

mitosis a type of cell division that results in two identical daughter cells from a single parent cell

plan of this worm is in the form of two **concentric** tubes separated by a space called the **pseudocoelom**. The intestine forms the inner tube and the outer tube consists of cuticle, hypodermis, musculature, and nerve cells. In the adult, the pseudocoelomic space also contains the tubular **gonad**. The shape of the worm is maintained by internal hydrostatic pressure, controlled by an **osmoregulatory system**.

C. elegans is a primitive organism yet it shares many embryological characteristics with members of higher phyla. The worm is conceived as a single cell that undergoes a complex process of development, starting with embryonic cleavage, proceeding through **morphogenesis** and growth to the adult worm-like animal.

Shortly after fertilization, the maternal pronucleus (the sperm nucleus and egg nucleus within the fertilized egg before their fusion to form the diploid zygote nucleus) migrates from the anterior to the posterior through the pseudocleavage furrow. It meets the paternal pronucleus in the rear, and they migrate forward before fusing and entering **mitosis**. Eggs are laid at about the time of gastrulation and hatch into first-stage juveniles. At hatching there are 558 cells in the hermaphrodite and 560 in the male. The animal matures through four larval stages, punctuated by molts and characterized by additional divisions of a few cells. These result primarily in elaboration of the nervous system and development of the secondary sexual characteristics.

Gonadogenesis, the formation of reproductive organs, begins in the first larval stage and ends in the fourth larval stage.

Sea urchins. Like all echinoderms, the purple sea urchin (*Strongylocentrotus purpuratus*) undergoes radial cleavage, as do typical deuterostomes, such as chordates, ascidians, and other echinoderms. As in embryonic cleavages in other metazoans, sea urchin cleavage divisions are reductive, that is, the cleavages result in more cells but without an increase in the total cellular volume of the embryo. The first two cleavages are meridional, meaning that the cleavage furrow passes through the animal and vegetal poles. The next cleavage is equatorial, that is, it passes through the embryo's midsection. The fourth cleavage is unequal. In deuterostome development, early cleavage divisions are radial. Protostomes typically display spiral cleavage. Early cleavage divisions in most embryos are reductive, dividing the original contents of the egg without increasing the total cellular volume of the embryo. The average diameter of a cell decreases as cleavage continues, and there is an increase in surface area relative to cellular volume. The embryo at this stage (known as the morula) is shaped like a blackberry made up of small, homogeneous cells. During the third cleavage, the surface area roughly doubles. The embryo then enters the blastula stage.

The blastula is a hollow ball of cells organized into an epithelial monolayer. The vegetal pole epithelium thickens to form the vegetal plate, which will give rise to primary mesenchyme cells and the archenteron during gastrulation. The epithelium is lined on its outer, or apical, surface by two extracellular matrice, an inner apical lamina and a hyaline layer outside it. Both are attached to the apices ("tips") of the cells in the wall of the blastula, which extend microvilli into these extracellular **matrix** layers.

matrix the nonliving component of connective tissue

Sea urchin gastrulae (as the embryo is called at this stage) elongate their archenterons via convergent extension during gastrulation. The epithelial cells of the archenteron rearrange as it elongates. Secondary invagination involves autonomous extension of the archenteron in the early phase of elongation, followed by mesenchyme-dependent pulling in the second phase. The sea urchin embryo possesses extracellular matrix layers lining the inside and outside of the embryo. The outer layer is divided into two layers, an apical lamina directly attached to the apical ends of the cells, and a hyaline layer on top of the first layer.

A frog. *Xenopus laevis* is a frog commonly used in embryological studies. The egg of this species is a huge cell, with a volume that is over one million times larger than a normal **somatic** frog cell. During embryonic development, the egg is converted into a tadpole containing millions of cells but with the same volume of material.

somatic having to do with the body

After fertilization, the cortical reaction (a wave of chemicals is released from the egg plasma membrane after fusion of the sperm and egg) results in loss of contact between the surface of the egg and the vitelline envelope (an extracellular membrane that encloses the embryo), permitting the reorientation of the egg via gravity. The varying densities of yolk in the egg result in a consistent orientation. The upper hemisphere of the egg, the animal pole, is dark. The lower hemisphere, the vegetal pole, is light. When it is deposited in the water and ready for fertilization, the haploid egg is at metaphase of meiosis II (the **chromosomes** are aligned at separate poles during second phase of reductive division).

chromosomes structures in the cell that carry genetic information

Entrance of the sperm initiates a sequence of fertilization events. After meiosis II is completed, the **cytoplasm** (the contents of the cell outside the nucleus and within the plasma membrane) of the egg rotates about 30 degrees relative to the poles, which is revealed by the appearance of a light-colored band, the gray crescent. This crescent forms opposite the point where the sperm entered. The crescent establishes the future pattern of the animal: its **dorsal** and **ventral** surfaces; its anterior and posterior; and its left and right sides.

cytoplasm fluid in eukaryotes surrounding the nucleus and organelles

dorsal the back surface of an animal with bilateral symmetry

ventral the belly surface of an animal with bilateral symmetry

The haploid sperm and egg nuclei fuse to form the diploid nucleus of the zygote. The zygote nucleus undergoes several cycles of mitosis (the nuclear division that follows duplication of the chromosomes, resulting in daughter nuclei with the same chromosome content as the parent nucleus). During cytokinesis, a belt of actin filaments forms around the perimeter of the cell, midway between the poles. As the belt tightens, the cell is pinched into two daughter cells. The first cleavage occurs shortly after the zygote nucleus forms and begins with the appearance of a furrow that runs longitudinally through the poles of the egg, passing through the point of sperm entry and bisecting the gray crescent. This divides the egg into two halves, forming the two-cell stage. During the second cleavage, the cleavage furrow again runs through the poles but at right angles to the first furrow, forming the four-cell stage. The third cleavage furrow runs horizontally but in a plane closer to the animal than to the vegetal pole. It produces the eight-cell stage.

The next few cleavages proceed in a similar fashion, producing a sixteen-cell and then a thirty-two-cell embryo. As cleavage continues, the cells in the animal pole begin dividing more rapidly than those in the vegetal pole and thus become smaller and more numerous. Subsequent cleavages produce a hollow ball comprised of thousands of cells called the blastula, which contains a fluid-filled cavity, the blastocoel.

Gastrulation begins with the invagination of cells in the region of the embryo once occupied by the middle of the gray crescent. This produces an opening, the blastopore, that will be the future anus and a cluster of cells that develops into the Spemann organizer (a cluster of cells which act as powerful inducer of surrounding cells). As gastrulation continues, three distinct germ layers are formed: ectoderm, mesoderm, and endoderm.

spinal cord thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

The ectoderm eventually forms the skin, brain, **spinal cord**, and other neurons. The mesoderm forms the notocord, muscles, blood, bone, and sex organs. The endoderm eventually forms the linings of the gut, lungs, and bladder, as well as of the liver and pancreas.

The Spemann organizer, which is mostly mesoderm, develops into the notochord, the precursor of the vertebral column, and induces the ectoderm lying above it to begin to form neural tissue instead of skin. This ectoderm will develop into two longitudinal folds, forming the neural folds stage. Eventually, the lips of the folds fuse to form the neural tube—which later develops into the brain and spinal cord—and the embryo elongates, forming an anterior-posterior, or front-rear, axis.

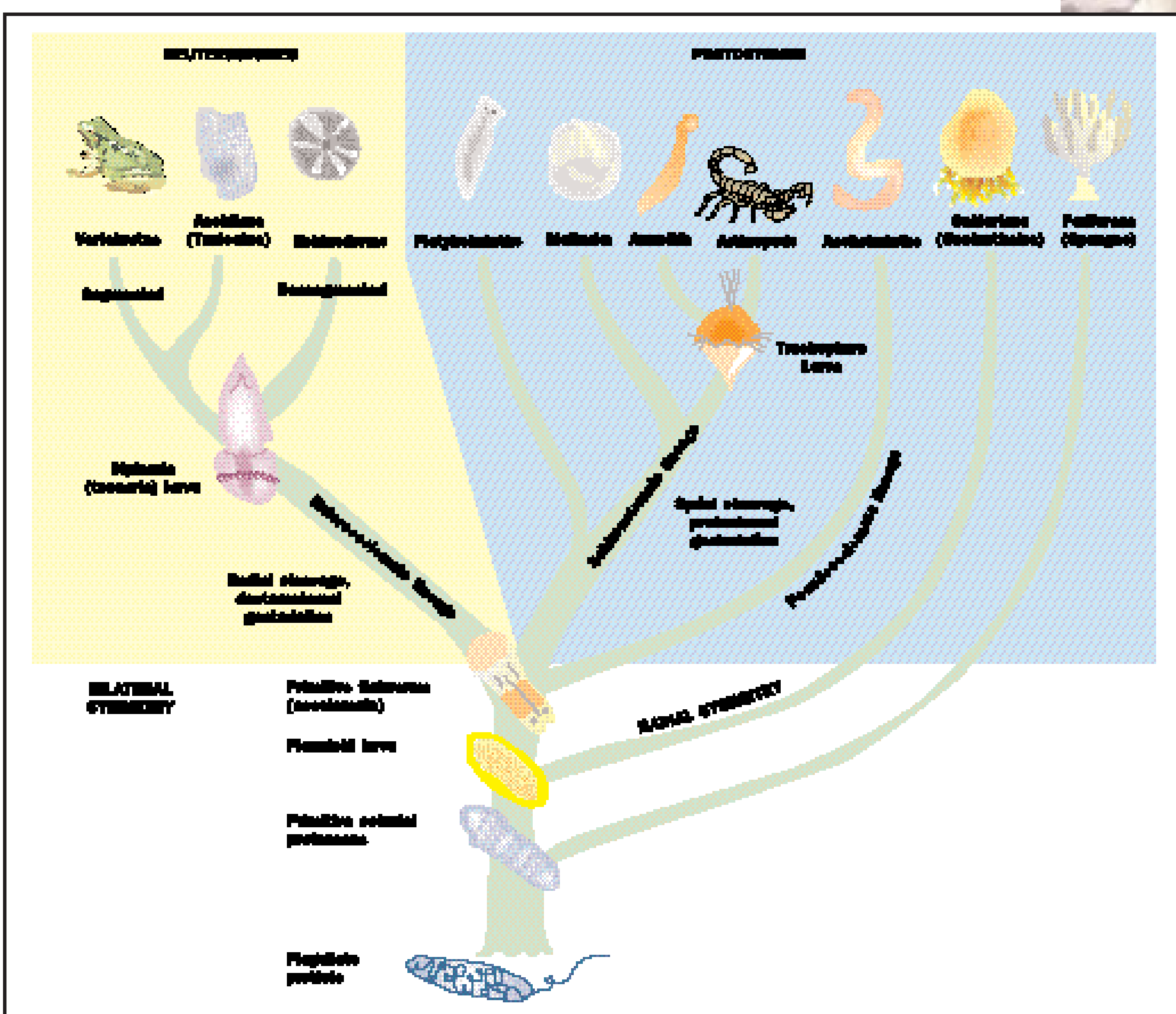
Each of the various layers of cells in the frog gastrula has a definite and different fate. Embryonic cells form many of the specialized structures in the tadpole, including neurons, blood cells, muscle cells, and epithelial cells.

Neurulation in *Xenopus* involves neural fold elevation and invagination of the neural plate to form the neural tube. The neural axis elongates as neurulation proceeds. The induction of convergence and extension behavior in cells of the neural tube is associated with neural induction, also known as primary embryonic induction.

The chicken (*Gallus gallus*). The chicken ovum consists of the yellow yolk and a small yolk-free area called the blastoderm (blastodisc or germinal disc). The nucleus of the ovum is in the blastodisc. The blastodisc appears as a small whitish area on the upper surface of the yolk. Albumin is added to the ovum as it moves down the hen's oviduct. Eventually, two shell membranes and a calcareous shell are added to form the complete egg.

Because of the large amount of yolk present in the chicken egg, cleavage, morphogenesis, and differentiation are confined to the blastoderm. Initially, the blastoderm becomes several cell layers thick and a cavity, called the subgerminal cavity, is formed under these layers. This stage of the embryo is comparable to the sea urchin morula. As cleavage continues and more cells are formed, the blastoderm splits to form two layers, a dorsal epiblast (ectoderm) and ventral hypoblast (endoderm). This embryonic stage corresponds to the sea urchin blastula and the cavity separating these two layers is called the blastocoel. Development to this stage takes place while the egg is still in the oviduct of the hen.

Gastrulation occurs by a process of involution. Involution is the curling inward and in-growth of a group of cells. Cells of the blastoderm surface migrate backward and medially (toward the middle of the embryo) and involute, or turn in, along a line called the primitive streak. These involuted



Comparison of development cycles in protosomes and deuterostomes. Redrawn from Gilbert, 1994.

cells will form the mesoderm germ layer. As gastrulation progresses, the anterior end of the streak moves backward so that the anterior region of the embryo is formed first. The primitive streak is functionally the same as the blastopore of the sea urchin gastrula.

The three germ layers, ectoderm, endoderm, and mesoderm, are created by involution following gastrulation. The coelom results from a separation of the lateral mesoderm. The involuted cells form the notochord anterior to the primitive streak and the lateral mesoderm (**somites**) laterally. After gastrulation, the process of neurulation, or formation of the neural tube and associated structures, takes place.

somites a block of mesoderm along each side of a chordate embryo

Neurulation occurs at or near the end of gastrulation and transforms the gastrula into a neurula by establishing the central nervous system. The ectoderm gives rise to neural folds flanking a neural groove along an axis from the blastopore toward the future head. These folds sink into the dorsum (back) of the embryo and meet mid-dorsally, forming a neural tube of which the anterior part becomes the brain and the rest the spinal cord. A population of mesodermal cells called the chordamesoderm aggregates, or gathers, to form the notochord. The chordamesoderm is required for the formation of the neural tube. During neurulation the portion of chordamesoderm that will form the notochord induces neural plate formation, which is the first stage in the formation of the neural tube. This process is characterized in most vertebrates by three stages. During the neural plate stage, the ectoderm on the dorsal side of the embryo overlying the notochord thickens to form the neural plate. During the neural fold stage, the thickened ectoderm curves inward, leaving an elevated area along the neural groove. The neural fold is wider in the anterior portion of the vertebrate embryo, which is the region where the brain will be formed. During the neural tube stage, the neural folds move closer together and fuse. The neural groove becomes the cavity within the neural tube, which will later contain cerebrospinal fluid that aids in the function of the central nervous system.

The mouse (*Mus musculus*). Embryos of the mouse develop in a very different environment than do those of the chicken. The relatively low yolk content in the typical, small mammalian egg requires that the embryo quickly implant, or adhere to the inner lining of the uterus, in order to obtain nutrients from the mother. Early cleavage in mammalian embryos is followed by the blastocyst stage. There are two groups of cells present at this stage. The outer layer of cells, called the trophoblast, and the inner mass of cells, called the blastocyst, will together go on to form the embryo.

During implantation of the fertilized ovum in the uterus the placenta is formed, which is a structure for physiological exchange between the fetus and the mother. The placenta consists of both a maternal contribution, the endometrium of the uterus, and a fetal contribution, the trophoblast. It is believed that the latter is used as an immunological barrier that prevents rejection of the fetus, and its paternal chromosomes, by the mother. The shape of the placenta varies, depending on the species. The inner cell mass of the blastocyst develops into the blastodisk, similar to that in chickens. Early stages of development of the mammalian embryo, such as the primitive streak stage, neurulation, and germ layer differentiation, are similar to those in birds and reptiles. The primary difference found in mammals is the development of the umbilical cord. The umbilical cord contains the allantois and yolk sac as well as circulatory system structures that connect the embryo to the placenta. SEE ALSO EMBRYOLOGY.

Andrew G. Gluesenkamp

Bibliography

Bruska, Richard G., and Gary J. Bruska. *Invertebrates*. Sunderland, MA: Sinauer Associates, 1990.

Butler, Harry, and B. H. Juurlink. *An Atlas for Staging Mammalian and Chick Embryos*. Boca Raton, FL: CRC Press Inc., 1987.

Gilbert, Scott F. *Developmental Biology*, 5th ed. Sunderland, MA: Sinauer Associates, Inc., 1997.

Gilbert, Scott F., and Anne M. Raunio, eds. *Embryology, Constructing the Organism*. Sunderland, MA: Sinauer Associates, Inc., 1997.

Johnson, Leland G. *Johnson & Volpe's Patterns & Experiments in Developmental Biology*, 2nd ed. New York: Wm. C. Brown Publishers, 1995.

Kalthoff, Klaus. *Analysis of Biological Development*, 2nd ed. New York: McGraw-Hill, Inc., 2001.

Mathews, Willis W., and Gary C. Schoenwolf. *Atlas of Descriptive Embryology*, 5th ed. Englewood, NJ: Prentice-Hall, Inc., 1998.

Raff, Rudolf A., and Thomas C. Kaufman. *Embryos, Genes, and Evolution: The Developmental-Genetic Basis of Evolutionary Change*. New York: Macmillan, 1983.

Schoenwolf, Gary C. *Laboratory Studies of Vertebrate and Invertebrate Embryos*, 8th ed. Englewood Cliffs, NJ: Prentice Hall, 2001.

Torrey, Theodore W., and Alan Feduccia. *Morphogenesis of the Vertebrates*. New York: John Wiley, 1991.

Wolpert, Lewis, R. Beddington, J. Brockes, T. Jessell, P. Lawrence, and E. Meyerowitz. *Principles of Development*. Oxford, U.K.: Current Biology Ltd., Oxford University Press, 1998.

Endangered Species

An endangered species is one that is likely to become extinct throughout all or part of its geographic range unless steps are taken to prevent its loss. Many of the species currently disappearing are tropical plants and insects that have not even been described by science but whose small ranges are being destroyed by deforestation. These species may contain valuable pharmaceuticals which could lead to cures for diseases, but they are also the irreplaceable products of millions of years of evolution.

The U.S. Endangered Species Act (ESA) protects any endangered species as well as the critical habitat on which it relies. Critical habitat does not necessarily include the entire ecosystem across the species' range. The ESA is the strongest ecological law in the world today because it has the power to restrict or eliminate human impact across an entire species range. Because the economic stakes can be high, officially designating a species as endangered can be a controversial process.

Given the costs of protecting endangered species, it is crucial to be certain that species are in fact endangered. The first step is to document a decline in population number. Doing so requires at least two population samples, using the same sampling methods, at different times. Even if a particular population shows no sign of decline, the species as a whole may decline as a result of range contraction and local population extinction; for example, deforestation eliminates whole populations while others remain intact.

Causes of Decline

Once a decline is established, the cause must be identified. First, natural history must be investigated in order to construct a list of possible agents. These may include prey extinction, pollutants, habitat change, habitat fragmentation, overharvesting, introduced species, disease, or **inbreeding depression**. Diagnosis requires the elimination of alternative hypotheses by observation and experiment.

inbreeding depression loss of fitness due to breeding with close relatives

A classic case of population decline was the decline and extinction of ten species of forest birds in Guam in the late 1960s. **Pesticide** use, hunting, competition from introduced bird species, habitat change, and disease were all measured and found to be uncorrelated with population densities of the forest birds. The only variable that was correlated with the decrease

pesticide any substance that controls the spread of harmful or destructive organisms

The bald eagle, an enduring symbol of the United States, remains an endangered species.

of the birds' range was the range of the brown tree snake, a species that was accidentally introduced to the island via an airplane wheel well in 1967. Subsequent live bait trapping indicated that brown tree snake predation on forest birds was higher where the birds were declining. An associated prediction that the snake would cause small mammal populations to decline was also supported.

Habitat change. Habitat change is any change in the suite of resources and environmental conditions on which a species depends. It is not enough to know that habitat change or loss is causing species decline; the particular factors relevant to the species must be discovered. For example, the northern spotted owl nests in the tops of dead firs. These "snags" are commonly found in old-growth forests. Young forests provide marginal habitat. Nevertheless, understanding the owl's behavior, hunting habits, nesting habits, and other factors may allow some human activity in owl habitat without endangering the owl.

Habitat fragmentation. This is a particularly harmful form of habitat change. Fragmentation is the loss of bits and pieces of habitat because of human activity, resulting in a patchwork habitat. Not only does this reduce the overall species range, it also changes the ratio of edge habitat to central habitat. For example, tropical forest fragmentation favors species that specialize in relatively open, sunny spaces such as treefalls, rather than the cooler, darker forest. This may cause forest specialists to decline as a result of competition as well as habitat loss. Demonstrating an effect of habitat fragmentation on population decline requires documenting fragment sizes and population densities.

Introduced species. Introduced species, such as the brown tree snake, have been responsible for 40 percent of all extinctions. The Nile perch, introduced into Lake Victoria (located in east Africa) in the nineteenth century,

caused the extinction of 200 species of cichlid by predation. To detect the impact of an introduced species, the timing of the introduction is compared to that of population decline. If there is a correlation, an experiment must demonstrate that the removal of the introduced species reverses the decline. Removal may involve surrounding the endangered species habitat with fencing or by poisoning the suspected introduced species. Unfortunately, it is difficult to remove a single species from a habitat without changing other variables. And introduced species, once established, are nearly impossible to eradicate.

Chains of extinction can make the diagnosis of species decline more complex. For example, Mauritanian kestrels declined because geckos, their food source, were eliminated by deforestation. Atlantic eelgrass limpets disappeared when a mold killed the eelgrass in which they lived. Black-footed ferrets declined along with their prey, the prairie dog. Saving one species may require saving several others as well.

Environmental contaminants. These may also play a role in species decline. The mechanism by which organochlorides, such as DDT, can cause eggshell thinning in raptors was discovered in the 1960s, and DDT was soon banned in the United States and other countries. Blaming a chemical for the decline of a species, however, can result in banning a harmless substance while ignoring the actual problem. For example, eggshell thinning due to insufficient calcium deposition occurred in the Netherlands in the 1980s, well after DDT had been banned. Further investigation concluded that **acid rain** had leached calcium from the soil, reducing the amount found in the calcium carbonate shells of snails; the birds were unable to obtain sufficient calcium from feeding on snails.

acid rain acidic precipitation in the form of rain

Disease. This factor is thought to have contributed to the decline of many species. Infections can cross from one species to another (called transspecies infections); for example, an introduced species can carry novel **pathogens** with it into a community that has evolved no resistance to it. Often, disease is the result of stress on the species' immune system from another source, such as pollution. Although the disappearance of amphibians around the world remains a mystery, it is likely exacerbated by the effect of acid rain on immune function in aquatic species. Establishing such a connection requires investigating beyond the appearance of disease into underlying causes.

pathogens disease-causing agents such as bacteria, fungi, and viruses

Hunting. Overharvesting occurs when the number of individuals lost to hunting consistently exceeds the number gained from intrinsic population growth in the absence of harvesting. Overharvesting is a particularly difficult factor to measure because both annual harvests and population sizes vary in time and space. Furthermore, hunting yields are often underreported, especially if they are illegal.

Inbreeding depression. This may be a factor in the decline of a population once the number of individuals is small. Inbreeding depression is the result of closely related individuals breeding, causing **recessive** harmful mutations to be passed on by both parents and therefore be expressed in subsequent generations. There is no evidence that inbreeding depression has ever caused extinction in the wild, though it can be a problem for captive-bred populations. It is likely that once a population is small enough for inbreeding depression to become relevant, extinction is inevitable for other reasons.

recessive hidden trait that is masked by a dominant trait

The Northern Spotted Owl

The case of the northern spotted owl in the Pacific Northwest region of the United States illustrates many of the issues surrounding the designation of an endangered species. The species is currently listed as threatened, meaning that it is at risk of becoming endangered in the foreseeable future. Its critical habitat is old-growth and late-successional forest with a dense canopy and open understory, which it requires for successful roosting. Such forests are extremely valuable to the timber industry. Since the spotted owl was listed as threatened in 1990, debate raged in the Pacific Northwest over the relative merits of a protection plan and the logging industry it would impact. At the beginning of the twenty-first century, there was no plan to protect the species, even though it was known that habitat destruction due to logging had caused the species' decline.

The current rate of extinction is greater than at any time in the last 65 million years. There have been only about five such mass extinctions in the history of the Earth, and they all occurred as a result of catastrophic changes in the environment. At no other time has the practices of a single species, humans, caused so many extinctions. SEE ALSO DDT; EXTINCTION; EXOTIC SPECIES; HABITAT LOSS; HABITAT RESTORATION; THREATENED SPECIES.

Brian R. West

Bibliography

Caughley, Graeme. *Conservation Biology in Theory and Practice.* Cambridge, MA: Blackwell Science, 1996.

Sutherland, William J., ed. *Conservation Science and Action.* Malden, MA: Blackwell Science, 1998.

Endocrine System

exoskeleton hard outer protective covering common in invertebrates such as insects

molting the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

metamorphosis a drastic change from a larva to an adult

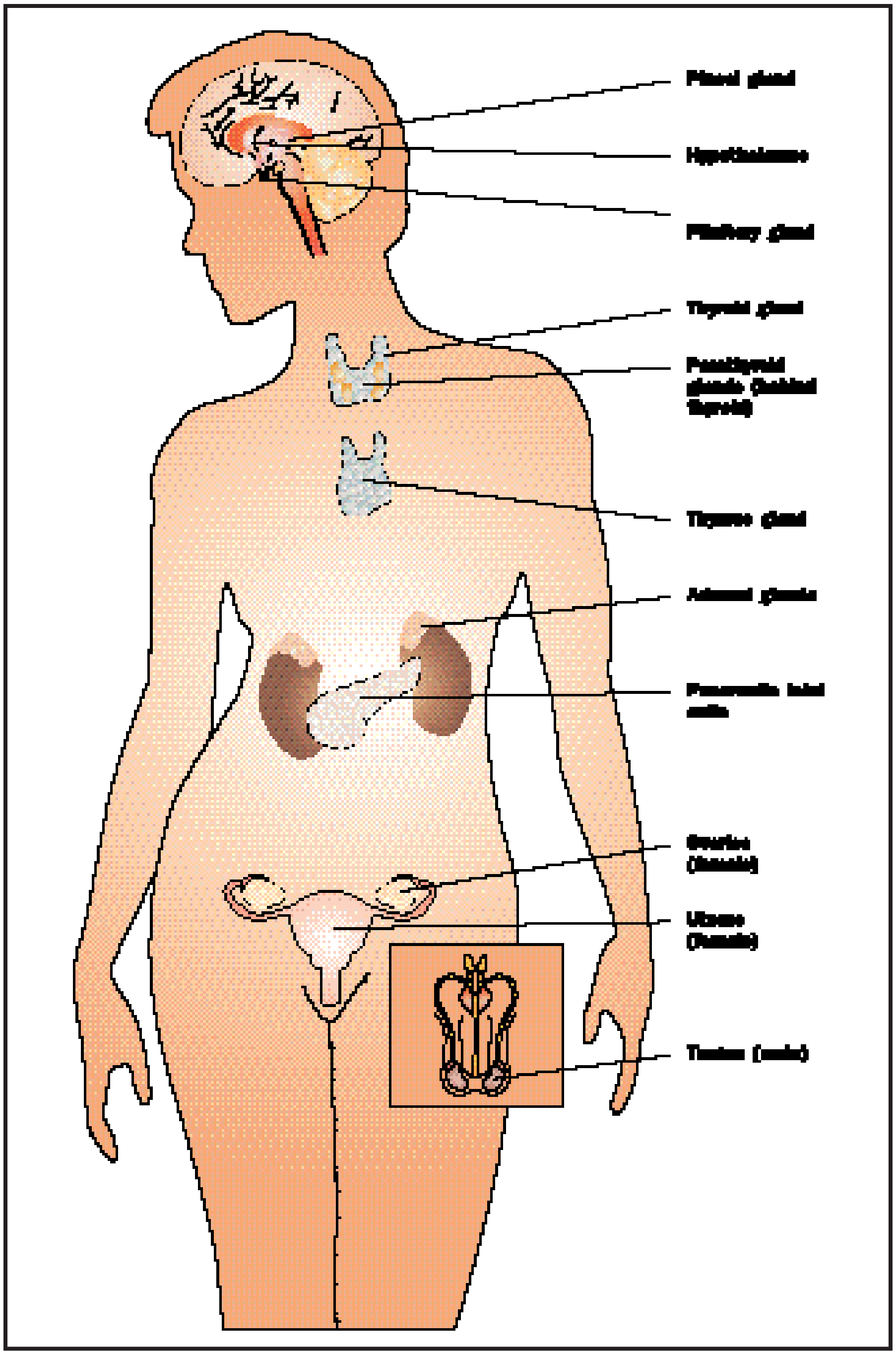
The endocrine system is part of the regulatory system in animals and helps maintain the internal balance of the body. Both vertebrates and invertebrates have endocrine systems. The endocrine system regulates many functions of the body, including growth and metabolism, water balance, sugar and calcium balance in the bloodstream, and several functions related to sexual maturity and reproduction. Two major functions under endocrine control in invertebrates are the shedding of the **exoskeleton** for growth, called **molting**, and **metamorphosis**, functions that do not occur in vertebrates.

The endocrine system is not as fast to respond to stimuli as is the nervous system (the other major regulatory system in animals), which can respond in less than a second. The endocrine system can respond within minutes, and the effects usually last longer than the effects of the nervous system.

The endocrine system is made up of organs that produce chemical messengers called hormones. Hormones are released directly into the bloodstream in vertebrates and the haemolymph in invertebrates. Hormones circulate with the blood, so they are everywhere in the body.

Only certain cells, however, are capable of responding to these chemical messengers. These are target cells, which have special receptors for different kinds of hormones. Every chemical messenger has a unique shape.

> Haemolymph is the "blood" of invertebrates. Similar to mammalian blood, it carries nutrients to cells and waste away from cells. Haemolymph does not carry oxygen to cells like mammalian blood.
>
> Hemolymph functions the same way as haemolymph, but works for insects instead of invertebrates.

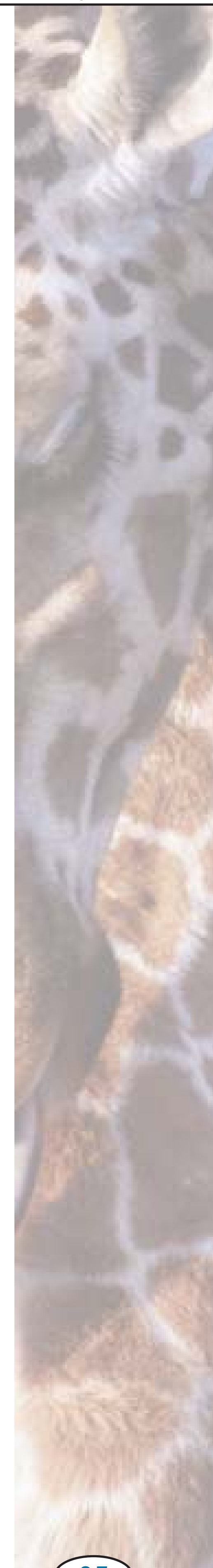


The endocrine organs and their locations in humans. Redrawn from Johnson, 1998.

The target cell has a receptor that corresponds to the shape of the messenger. Most receptors are outside of a cell, embedded in the cell membrane.

When a messenger binds to the target, a different messenger is released inside of the cell. This second signal inside the cell is called a secondary messenger. This secondary messenger then triggers other changes inside the cell, such as the release of a substance. Other target cells have receptors on the inside of the cells. Specifically, some hormones can go inside of the cell and bind to a receptor that turns on and off DNA **transcription** of specific genes.

transcription a process wherein enzymes are used to make an RNA copy of a strand of DNA



Endocrine Organs and Effects

The endocrine system works through the same process in vertebrates and invertebrates, although the organs and chemical messengers involved differ. In invertebrates, the nervous system has modified cells that secrete most types of hormones. The hormones released from within the nervous system regulate the other endocrine organs in invertebrates.

These other organs include the corpora cardiaca, the prothoracic glands, and the corpora allata. The corpora cardiaca are located next to the brain and secrete hormones that control the prothoracic glands. The prothoracic glands are located behind the brain and secrete **ecdysone**, which stimulates and controls molting, as well as other hormones involved in the molting process. The corpora allata is located near the digestive system and secretes juvenile **hormone**. Juvenile hormone is involved in growth, metamorphosis, and reproduction. The **gonads** (ovaries and testes) also secrete hormones in the invertebrates and are involved in reproduction.

ecdysone hormone that triggers molting in arthropods

hormone a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

gonads the male and female sex organs that produce sex cells

hypothalamus part of the upper end of the brain stem that regulates activities in the nervous and endrocrine systems

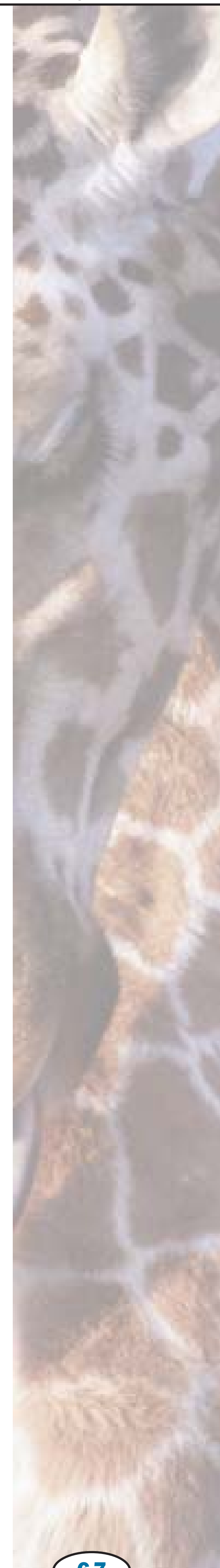
Vertebrates have more endocrine organs than invertebrates. The **hypothalamus**, pituitary gland, and pineal gland are located in the brain. The hypothalamus controls the pituitary gland. The pituitary gland controls water regulation and endocrine production of the gonads, and stimulates growth as well. The pineal gland controls biological rhythms such as sleep by producing melatonin.

All other endocrine organs are located in the body cavity. The pancreas controls blood sugar levels by secreting two hormones that have the opposing functions of raising and lowering blood sugar levels. The thyroid and parathyroid control calcium levels in a manner similar to the pancreas: one hormone raises calcium and another lowers calcium levels. The thyroid also controls metabolism. The adrenal glands are located above the kidney. They are involved in both long-term and short-term stress responses. The thymus is involved in immune responses. The gonads are involved in many functions.

The gonads consist of the ovaries and testes and in vertebrates control development and growth in addition to regulating reproduction. The gonads secrete steroid hormones. Steroids are one of the chemical messengers that have receptors inside of target cells and most cells have steroid receptors, so that steroids affect the entire body.

The gonads produce three classes of steroid hormones: androgens that include testosterone, estrogens, and progestins. Both testes and ovaries produce all three steroid types, but in different proportions. In humans, steroids determine the sex of a fetus during development. If androgens are present at high levels during fetal development, then the fetus develops as a male. If androgens are not present at high levels, then the fetus develops as a female.

Steroids are also responsible for sexual maturation and the development of secondary sex characteristics during puberty in humans. Secondary sex characteristics in males caused by high levels of androgens include changing patterns in hair growth such as baldness and facial hair growth and deepening of the voice. Estrogen in females cause secondary sex characteristics



such as the development of breasts. Progestins in females cause reproductive cycles and menstruation.

Supplemental Hormones for Humans

Humans sometimes take hormones by pills or injections to alter or supplement the body's own production of hormones. The best example of necessary hormone supplements is insulin replacement for diabetes mellitus. The pancreas secretes insulin, which lowers blood sugar levels, and glucagon, which raises blood sugar levels. When someone is diabetic, the body does not produce enough insulin and blood sugar remains at too high a level for normal water and metabolic functions.

Type I diabetes mellitus starts during childhood and is an autoimmune disease. Someone with Type I diabetes mellitus must take injections of insulin to control blood sugar levels. The insulin is either extracted from the organs of other animals or is produced by bioengineering bacteria to produce insulin. Those having Type II diabetes mellitus are often over forty years old and can control blood sugar levels with special diets and exercise.

Another common form of hormones taken by humans is steroids. A practice that is neither legal nor safe is that of individuals, usually males, taking steroids to increase muscle growth. Athletes of all types do this, not just bodybuilders. Androgens facilitate the acquisition of muscle mass, which is why men are more muscular than are women. However, taking supplemental androgens will cause the body to shut down its own production of androgens and interfere with the body's reproductive functions.

Common side effects of taking androgens include shrinking of the testes, impotence, the development of female secondary sex characters such as breasts, and a serious risk of heart attack. Additionally, sources for these androgens are usually other animals such as horses and illegal androgens are often impure, containing antibodies from the source animals. These antibodies can cause severe immune responses in humans and can even be fatal.

Birth control pills are another common form of steroids taken by humans. Birth control pills contain man-made estrogens and progestins. Birth control pills prevent ovulation, the development and release of an egg by the female, by disrupting the normal cycle of hormones that comprise the female menstrual cycle.

Environmental estrogens are chemicals that are thought to function as chemical messengers in animals. Examples of environmental estrogens include plastics and by-products of manufacturing. It is not completely understood at this point whether or not environmental estrogens can affect animals, and if so, to what degree.

Laura A. Higgins

Bibliography

Crews, David. "Animal Sexuality." *Scientific American* 270 (January 1994):108–115.

Johnson, George B. *Biology: Visualizing Life*. New York: Holt, Rinehart and Winston Inc., 1998.

McLachlan, John A., and Steven F. Arnold. "Environmental Estrogens." *American Scientist* 84 (September–October 1996):452–461.

Steinman, L. "Autoimmune Disease." *Scientific American* 269 (September 1993): 106–114.

Tjian, R. "Molecular Machines That Control Genes." *Scientific American* 272 (February 1995):54–61.

Endosymbiosis

Endosymbiosis is a mutually beneficial relationship between a host organism and an internal associate organism. The term is derived from the prefix "endo," meaning within, and the word symbiosis, which refers to a mutually beneficial relationship between two closely associated organisms. Another term for symbiosis is **mutualism**, which highlights the fact that both organisms are benefiting from the relationship.

mutualism ecological relationship beneficial to all involved organisms

Examples of Endosymbiosis

A well-known example of endosymbiosis is the relationship between a termite and the microorganisms in its gut. The termite consumes wood, but it cannot digest it without the help of protozoans in the termite's gut that break down the cellulose to a form that the termite can metabolize. Thus, the termite supplies food for the protozoan, and the protozoan provides food for the termite. In this example, the protozoan is the endosymbiont, or the internal organism in the endosymbiotic relationship.

There are a variety of levels of dependency between the two associates, including at one extreme an entirely voluntary relationship in which each partner can survive alone, and at the other extreme a situation where both are entirely dependent on the other. Also, the endosymbiont can be at different places within the host organism, from within a body cavity such as the gut to within individual cells. Endosymbiosis also plays a role in evolution, affecting the structure, behavior, and life history of the associated organisms.

Although there are various levels of dependency between the two organisms in an endosymbiotic relationship, it is nearly always advantageous for the two to stay together. An example that demonstrates this is the mutualism between corals and their endosymbiotic algae. The type of algae involved here are called dinoflagellates, and they are specialized to photosynthesize or use organic foods as their energy source. However, certain nutrients are not readily available in the ocean, so it is beneficial for the dinoflagelletes to live within the corals, where the nutrients are available. Similarly, corals can gather some dissolved organic carbon from the water or from prey items, but it is much easier and faster to gather them from the photosynthetic activity of dinoflagellate **endosymbionts**. A side effect of photosynthesis is that calcium carbonate is precipitated from the water that forms the coral structures of coral reefs.

endosymbionts the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

Both of these organisms have been cultured independently in the laboratory to show the extent of their interdependence. Under these circumstances, both have significantly reduced growth rates. Sometimes they even stop growing and rely on energy reserves. When they are allowed to circulate in the same water, but not make contact, their growth nearly doubles.

When put into contact, growth is even greater, indicating that actual contact can spur a higher than normal release and uptake of chemicals they exchange. Clearly, then, it is to the advantage of both to remain together.

Some sea anemones with these dinoflagellate endosymbionts have adapted their behavior to the needs of their algae. For example, free-swimming jellyfish will make vertical migrations to layers of water that are rich in ammonium for the dinoflagellates. During the day, **sessile** sea anemones expose those parts of their bodies where the dinoflagellates are located to allow for photosynthesis. At night they retract those parts and expose their stinging tentacles to catch prey in order to sequester food and provide nitrogen to their endosymbionts. These examples of behavior modifications by the host associate organism show how the two organisms have evolved to benefit one another, and, in turn, themselves.

sessile immobile, attached

Locations of Endosymbionts

Endosymbionts can live within their associate organism at a variety of places. They can be within a cavity of the organism, within cavities and within cells, or entirely within cells. Intracellularly, the location can be in cells that have special vacuoles for the isolation of the endosymbiont from the interior of the cell, or in cells that maintain the endosymbiont directly within the cell fluid.

Termites and their protozoan gut inhabitants are one example of the endosymbiont living within a cavity of the associate organism. Another common example is the **fauna** in the stomach of ruminating animals, or animals that regurgitate and rechew food particles, such as deer, cattle, and antelope. Stomachs of **ruminants** have chambers, the first of which is called the rumen and is specially designed to maintain populations of bacteria and protozoa that break down the food of their host using fermentation. The rumen is supplied with food and kept within a certain range of pH by specialized salivary glands. This affords the microbial community with a substrate to feed off of and a favorable environment to do so. There are a diverse number of microorganisms living there, including bacteria that digest cellulose, protozoa that digest cellulose with the help of their own endosymbionts, and others still that are predators on these protozoa. An entire community of different species with different lifestyles lives there.

fauna animals

ruminants plant-eating animals with a multi-compartment stomach such as cows and sheep

A common example of the endosymbiont living within the cells of the host is that of bacteria in the cells of insects. The cells of cockroaches contain bacteria, and cockroaches exhibit slowed development if the bacteria are killed with antibiotics. The growth of the cockroach can be restored, however, with certain additions to its diet that the bacteria presumably were providing.

The transmission of these bacteria from one cockroach to an offspring is hereditary, although not genetically based, because the bacteria invade the cytoplasm of the egg. Then, when the egg is fertilized and develops, it already has the endosymbiont that the mother had.

Another example of maternal transmission can be found in ruminating animals. In these animals, the mother passes the rumen microorganisms to her baby after it is born through her saliva and ruminated food, which contain all the microbial species the baby will need in life. If a baby ruminating animal is not allowed to be in contact with its mother, the baby may never get the microbes necessary for it to be able to digest plant material and will die.

Endosymbiotic Evolution

From behaviors such as the migration of jellyfish to different water layers, and special structures such as the rumen of the stomach, it is clear that endosymbiosis involves complex interactions and that these organisms have evolved together for many generations in order to develop such interactions.

eukaryotic cells cells that contain a membrane-bound nucleus and membrane-bound organelles

prokaryotes single-celled organisms that lack a true cell nucleus

Perhaps the oldest and most widespread example of this endosymbiotic co-evolution is in the origin of **eukaryotic cells**. They evolved from prokaryotic cells, with the primary differences being that eukaryotic cells are larger and more complex, containing a separate nucleus and numerous organelles (such as mitochondria), whereas prokaryotic cells are smaller with a few organelles floating freely in the cellular fluid. Examples of **prokaryotes** are simple unicellular organisms such as bacteria. Most multicellular complex organisms, however, from protozoans to fungus to animals, are eukaryotes.

How did eukaryotic cells arise? Athough there is no direct evidence, the most plausible theory is that an early prokaryotic cell, the ancestor to the mitochondrion, entered another prokaryotic cell, either as a food item or a parasite. Over time, the relationship between the two became endosymbiotic, with the mitochondrion supplying energy to the host associate and the host providing the proper environment and nutrients to the mitochondrion. Thus, a cell with a distinct organelle, or a eukaryotic cell, emerged. This means that every single cell in all prokaryotic organisms has endosymbiotic organelles.

Several characteristics of mitochondria support this widely accepted theory of an endosymbiotic evolution giving rise to eukaryotic cells:

- The mutually beneficial relationship between the cell, which provides nutrients and an environment for the organelle, and the mitochondrion, which provides energy for the cell, is seen in many other endosymbiotic systems, including those mentioned above.
- The modern role of the mitochondrion is to provide energy in a usable form for the cell.
- The mitochondrion has a genome within it that lets it reproduce itself and be largely independent from the cell and the cell's genome, which resides in the nucleus. Finally, the mitochondrion does not divide and reproduce in the same manner as the host cell. In sexually reproducing animals, for example, the mitochondria of the offspring are not a mix of both parents' mitochondria. Instead, they are all inherited from the mother. Thus, the mitochondria do not recombine as does the rest of the cell during sexual reproduction. Rather, they act more as independent organisms, maintaining their identity from host to host. SEE ALSO Interspecies Interactions.

Jean K. Krejca

Bibliography

Ahmadjian, Vernon, and Surindar Paracer. *Symbiosis: An Introduction to Biological Associations.* Hanover, NH: University Press of New England, 1986.

Begon, Michael, John L. Harper, and Colin R. Townsend. *Ecology*, 2nd ed. Cambridge, MA: Blackwell Scientific Publications, 1990.

Douglas, Angela E. *Symbiotic Interactions.* Oxford: Oxford University Press, 1994.

Marguilis, Lynn. *Symbiosis in Cell Evolution.* San Francisco, CA: W. H. Freeman, 1981.

Ridley, Mark. *Evolution*, 2nd ed. Cambridge, MA: Blackwell Scientific Publications, 1996.

Valiela, Ivan. *Marine Ecological Processes*, 2nd ed. New York: Springer-Verlag, 1995.

Entomology

Entomology is the study of insects. It is a major branch of animal zoology. Insects are one of the most successful and diverse groups of living organisms in the world today. Approximately 1.5 million species of insects have been identified by scientists as of the end of the twentieth century. However, it is estimated there may be as many as twice that number on Earth. The number of insect species is greater than the number of all other species of organisms combined. It is estimated that there are about 200 million insects for every living human. Insects are members of the kingdom Animalia, the phylum Arthropoda, and the class Insecta. Insects share the major group Arthropoda with creatures such as crabs, lobsters, shrimp, spiders, scorpions, ticks, mites, centipedes, and millipedes. Common insects include ants, butterflies, bees, cockroaches, beetles, flies, grasshoppers, mosquitoes, dragonflies, moths, wasps, and termites.

Insects have a tough **exoskeleton** (external skeleton) and three pairs of walking legs. The majority of insects have wings, and those with wings have two pairs, except flies, which have only one pair. Their bodies are divided into three regions: the head, thorax, and abdomen. All insects hatch from an egg in a form which is different from that of the adult insect. A well-known example of this is the caterpillar (the larval stage) and butterfly (the adult stage). Insects are characterized by their small sizes and short lifespans.

exoskeleton hard outer protective covering common in invertebrates such as insects

Scientists believe that insects have inhabited Earth for about 380 million years. They occupy nearly every type of environment except for salt water. They are most numerous in tropical climates and on land. Their enormous success is believed to be due to three main factors: their exoskeleton, size, and diet. Their tough exoskeleton protects them against physical damage and water loss. Their small size allows them to occupy many small areas unavailable to larger animals. Small size also allows for a faster reproductive rate. Finally, insects eat almost anything and everything.

Insects play many important roles in nature. Insects such as bees, butterflies, moths, and flies pollinate flowering plants. Many insects aid in the decomposition process and nutrient cycling, or exchange. Insects are important food sources for other animals, such as birds, and also eat other insects, thus keeping insect populations in control.

An entomologist looks through a microscope during a study of grasshoppers. Entomology is the study of insects and the further discovery of new kinds of insects on Earth.

Most entomologists work in the field of economic entomology, which is also called applied entomology. They study the small minority of insects that are harmful to humans. Harmful insects include those that destroy crops and buildings and those that transmit diseases to humans. Insects that feed on plants such as grasshoppers destroy plant crops and timber. Other insects transmit plant diseases. Insects such as termites destroy wood buildings. Bloodsucking insects such as mosquitoes, lice, and fleas transmit some of the most serious infectious diseases in the world. These include malaria, dengue fever, yellow fever, bubonic plague, and typhus.

Scientists attempt to reduce the number of insect pests through a variety of ways. Cultural controls include the draining of swamps where mosquitoes breed. Chemical controls include the use of pesticides and insect repellants. Biological controls include the use of animals that naturally prey on insect pests.

People are also inadvertently decreasing the number of insects by destroying their natural habitats. Destruction of natural areas by human activities is wiping out species of insects that we will never even know existed. What wondrous creatures are we missing?

Denise Prendergast

Bibliography

McGrath, Kimberley A. *World of Biology.* Farmington Hills, MI: The Gale Group, 1999.

Preston-Mafham, Rod and Ken Preston-Mafham. *The Natural History of Insects.* Ramsbury, Marlborough, Wiltshire, UK: The Crowood Press Ltd., 1996.

Environment

The term "environment" means the surroundings of a living creature. It can also refer to all the factors of the external world that affect biological and social activities. There are abiotic (nonliving) environmental factors such as sunlight, air, and water. There are also biotic (living or recently living) environmental factors such as plants, animal predators, and food. The total environment of an organism is the sum total of the biotic and abiotic environments. The study of the relationships between living creatures and their environments is called **ecology**.

ecology the study of how organisms interact with their environment

A human's abiotic environment includes things such as weather (sunlight, wind, air temperature) and items which give protection from the weather (clothes or houses). Other abiotic factors are the soil and water, and chemicals in the soil and water. A human's biotic environment includes things such as food (plants and animals), other humans, animals, trees, and grasses. The biotic environment also includes how living creatures interact with each other and their abiotic environments. Therefore, a human's biotic environment also consists of social or cultural surroundings. Humans learn from each other how to behave in socially acceptable ways. They also pass along knowledge about language, science, and art.

The major components of Earth's physical environment are the atmosphere, climate and weather, land, and bodies of water such as lakes, rivers, and oceans. The term "environment" is commonly associated with the impact that humans have made on the natural world. Increasing human population and industrial activities have led to problems associated with the pollution of air, water, and soil. Pollution has a negative impact on humans in terms of health and quality of life, as well as on other animals and plants.

Human activities such as the dumping of industrial wastewater and poorly treated sewage water have led to the pollution of fresh and salt water. Groundwater, water beneath the land surface that often serves as drinking water for humans, has also been negatively affected. Accidental oil spills from ships and untreated storm-water runoff from urban and agricultural areas also degrade bodies of water.

Air pollution results from human activities such as burning fossil fuels (oil, coal, and gasoline) to create electricity and power automobiles, and manufacturing industrial products such as chemicals and plastic. Burning fossil fuels releases carbon dioxide into the atmosphere, adding billions of extra tons of carbon to the natural carbon cycle. Deforestation and poor soil management also add carbon. Most scientists believe that the increased carbon dioxide in the atmosphere contributes to the potentially devastating warming of the global climate, the so-called "greenhouse effect." Another human impact on the atmosphere has been depletion of the ozone layer. The ozone layer helps filter ultraviolet light and protects Earth's surface from harmful doses of radiation. Many scientists believe that chlorofluorocarbons used as coolants in air conditioners and refrigeration units destroy ozone when released into the atmosphere.

Land pollution is caused by poor agricultural practices, mining for coal and minerals, and dumping industrial and urban wastes. The widespread usage of pesticides has led to pollution of both soils and bodies of water.

As more and more environmental problems become evident, humans will have to assess their activities and their impact on the natural world. SEE ALSO BIOME; ECOSYSTEM; HABITAT.

Denise Prendergast

Environmental Degradation

biotic pertaining to living organisms in an environment

abiotic nonliving parts of the environment

Humans, like all organisms on Earth, interact with both the **biotic** (living) and **abiotic** (nonliving) factors in their environment. Environmental degradation occurs when a potentially renewable resource—one of the biotic or abiotic factors humans need and use—such as soil, grassland, forest, or wildlife—is extracted at a rate faster than the resource can be replaced, and thus becomes depleted. If the rate of use of the resource remains high, the resource can become nonrenewable on a human time scale or even become nonexistent.

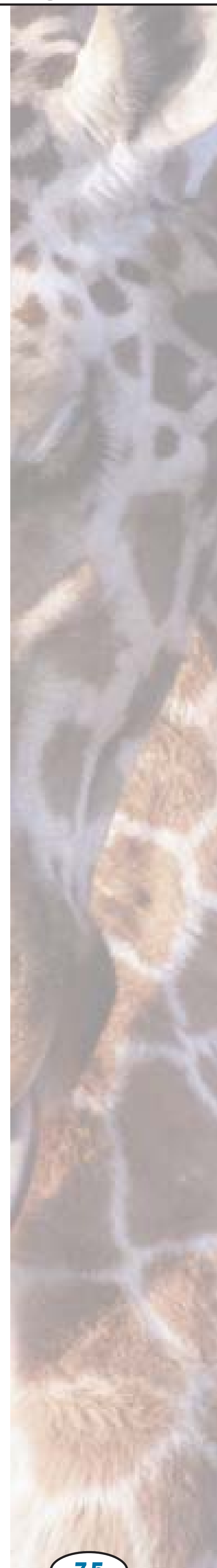
Toxic debris washed ashore at the Padre Island National Seashore in Texas.

For example, topsoil is important to farmers because crops are grown in topsoil. It can take as many as 200 years to form 1 centimeter (0.40 inches) of topsoil through natural processes. Topsoil can also be lost through various causes. One of the main causes of topsoil loss is erosion. Erosion can happen when water washes soil downhill or when wind blows unprotected soil away. Worldwide, topsoil is being lost to erosion much more quickly than it is being replaced.

If topsoil loss is allowed to continue unchecked, the land can be rendered permanently infertile through a process known as desertification. Many areas of the world suffer from desertification. Grasslands do not receive much rain. If the soil cover is removed by overgrazing or by poor farming practices, the topsoil can be rapidly removed by wind erosion. This happened in parts of Texas and Oklahoma during the 1930s, leading to dust-bowl conditions. Although drought contributed to dust-bowl formation, the main cause was overgrazing and poor farming practices.

biodiversity the variety of organisms found in an ecosystem

Loss of **biodiversity** is an important aspect of environmental degradation. Biologists agree that species are becoming extinct at an alarming rate. Biodiversity is also being lost at the ecosystem level due to environmental degradation. Tropical forests are recognized as the most diverse ecosystems on Earth and are experiencing the highest rate of ecosystem loss, but temperate habitats are also suffering degradation. Because the temperate parts of the world were settled first, the loss of biodiversity has been greatest there.



The quantitative loss of ecosystems is easy to measure. When a native prairie is converted to a cornfield or an open field is paved over to make a parking lot, the number of hectares can easily be calculated. Qualitative ecosystem degradation is harder to measure. The structure, function, or composition of an ecosystem can slowly change until the habitat is lost.

The Population Factor

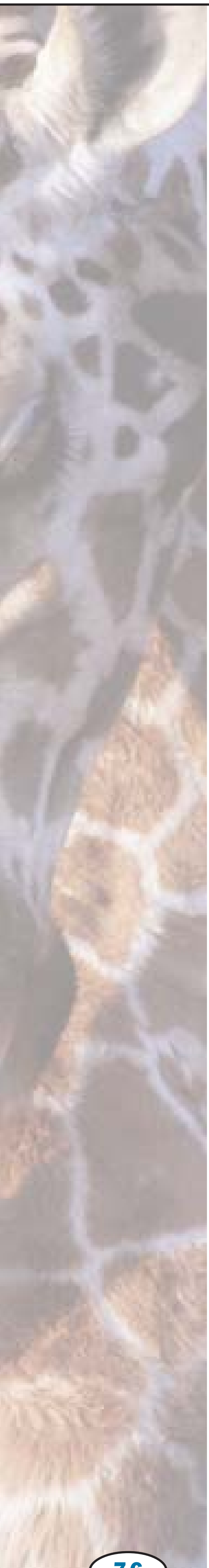
Who is responsible for degrading the environment? We all are. Ordinary human activity from even the most responsible individuals inevitably pollutes and degrades the environment to some extent. We degrade the environment directly when we consume resources (for example, burning wood in a fireplace), and indirectly when we extract resources and transform them into products we need or want.

In 1999, the number of people on Earth exceeded 6 billion. The population of the world increased fourfold in the twentieth century. This rapid increase in population was accompanied by an even more rapid increase in the use of resources to support the growing population and to raise living standards. During the twentieth century, global energy use increased by a factor of 20. Following World War II, the world became even more dependent on extractive industries, such as mining and oil exploration, to supply the various minerals and fossil fuels required to support a higher standard of living. Energy shortages have an even greater impact on developing nations that are heavily dependent on subsidized fuel supplies to maintain food production.

The role of agriculture. During the twentieth century, agriculturally productive land has been extensively modified to make it even more productive. This includes the widespread use during the twentieth century of chemical fertilizers (often produced from oil) pesticides, and extensive irrigation. To supply the needs of extensive irrigation, surface water has been diverted and many wells have been drilled seeking ever more subsurface water. At the same time that industrial agriculture was growing, agriculturally productive land was being lost to urban development and industry. In the twenty first century, competition for remaining land and water resources is expected to continue to increase.

Modern agriculture has been able to produce an enormous amount of food. Intensive agriculture is able to produce more food per hectare, but increases the need for fresh water and chemicals for pesticides and fertilizer. Much of the rise in the food supply since 1950 has been due to greatly expanded irrigation and the use of pesticides and fertilizers. However, reservoirs will eventually silt up and aquifers (subsurface water supplies) will be depleted. Irrigation with surface or subsurface water can also cause salt to accumulate in the soil. As the irrigation water soaks into the soil and evaporates, it leaves the minerals behind. Eventually, these minerals, including sodium chloride and other salts can build up to the point that the soil is rendered unsuitable for growing anything. This has already happened in much of the central valley of California. In addition, the simple ecosystems used by modern industrial agriculture are much less resilient than the complex ecosystems they replace. High-yield crops in **monocultures** are more susceptible to insect infestations and disease than traditionally farmed crops.

monocultures the cultivation of single crops over large areas



High-yield agricultural practices can also lead to soil erosion, and thus a further loss of topsoil.

Forests suffer similar pressures. Trees are harvested for timber and pulp. Land is cleared for agriculture. Mixed, old-growth forests are replaced with trees all of the same species planted at the same time. These forest monocultures suffer many of the same problems as food crop monocultures. They suffer from insect infestations and are much less stable than a diverse ecosystem. Grasslands have also been extensively modified and in many areas suffer desertification. As a consequence, there are significant losses of productivity in agricultural and forest lands from overcultivation, overgrazing, desertification, and deforestation around the world. The human population is expected to continue to grow rapidly during the twenty-first century. As it does, many of the environmental resources on which humans depend are being degraded.

Resource use. According to one simple model developed by G. Tyler Miller in *Living in the Environment*, the total environmental degradation, or total environmental impact, of a population depends on three factors: (1) the number of people, (2) the average number of units (kilograms, liters or pounds, gallons) of resources used by each person, and (3) how each person uses those resources. According to this model, there are different ways overpopulation can cause the environment to become unable to support the rate of resource consumption.

In some regions of the world, people use a relatively small number of units of any given resource, but there are so many people that the resource is still depleted. This is called people overpopulation and it is the principal cause of environmental degradation in the world's poorer developing nations. Because the population is already consuming the minimum amount of resources possible to sustain life, reducing consumption is not possible. In order to prevent or limit resource depletion, some countries have instituted family planning or have strictly limited the number of children allowed in each family.

In other regions there are relatively few people, but each person uses (on the average) so many units of a resource that the resource still becomes depleted. Miller calls this consumption overpopulation. The United States has the highest level of consumption of any nation, although the level of resource consumption in many other nations is rapidly increasing. Reducing resource consumption is certainly possible, but is politically unpopular. Many economists connect the high standard of living in the United States to a high level of resource consumption, and possible reductions in standards of living are never popular.

Population distribution. There are several other factors related to environmental degradation. The first is population distribution. When large numbers of people are concentrated in a small area together with industrial activity, air and water pollution can rise to unacceptable levels. Other factors are wasteful patterns of consumption and overconsumption. When people consume more than they need to maintain a high standard of living or fail to effectively control waste through recycling and conservation, then environmental degradation can occur.

Another factor related to environmental degradation is **carrying capacity**, the maximum population of a given species that an ecosystem can support for an extended period of time. Every habitat, ecosystem, or **biome** has a carrying capacity for the best population level of any particular species. This is the level that maintains ecosystem diversity (including genetic diversity) without depleting ecosystem resources. Humans now inhabit every portion of Earth and occupy a variety of different ecosystems. Discussions of carrying capacity for human population must include the whole Earth as an ecosystem. There is much debate and discussion of Earth's carrying capacity. Many scientists feel that Earth is already overpopulated and that drastic measures must be taken immediately to reduce population and resource consumption. Others feel, just as strongly, that Earth can support far more people than it does now at a high standard of living. New technology, including extractive technologies and genetic engineering of food crops, will continue to increase Earth's carrying capacity.

carrying capacity the maximum population that can be supported by the resources

biome major type of ecological community

global warming a slow and steady increase in the global temperature

A Global Issue

Environmental degradation affects everyone. International environmental concerns frequently focus on large-scale problems such as desertification or **global warming**. However, vulnerable groups, such as impoverished people living in marginal areas, are more concerned with local issues. They may worry about the loss of rangeland, soil erosion, or the need for more intensive farming. These and similar issues affect poor people because they are directly related to the household food supply and food security. Environmental degradation results in decreased production and lowered income. As the land is more intensively farmed, soil fertility decreases and crop yields are reduced. Unfortunately, rural poor people have few choices other than to overusing the limited resources available. The resulting environmental degradation can trigger a downward spiral in which the intensive use of resources results in more environmental degradation, which requires even more intensive use of resources. SEE ALSO Habitat Loss.

Elliot Richmond

Many of the resources to which humans have free access such as clean air, open oceans and the fishes in these oceans, wildlife, migratory birds, atmospheric gases, and stratospheric ozone are held in common. Everyone has the opportunity to use or even abuse these resources. Because it is each individual's self-interest to extract as much of a resource as possible, resources can easily be overharvested or converted to nonrenewable resources. This is often called the "tragedy of the commons," after the practice of grazing sheep or other animals on property held in common by the whole community. When there are relatively few users, the use of resources held in common has little effect. When there are many users, the cumulative effect of many people trying to maximize their use of the same resource can lead to degradation or destruction of the resource. Humans may be able to avoid the tragedy of the commons if they can convert their thinking from a self-centered viewpoint to a broader perspective.

Bibliography

Curtis, Helena, and N. Sue Barnes *Biology*, 5th ed. New York: Worth Publishing, 1989.

Dregne, Howard E., and Adli Bishay. *Desertification of Arid Land.* Newark, NJ: Gordon & Breach Publishing Group, 1983.

Ehrlich, Paul R. *The Population Bomb.* New York: Ballantine Books, 1971.

Findley, Rowe. "Will We Save Our Own?" *National Geographic* 178, no. 3 (1990): 106–136.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth Publishing Company, 1990.

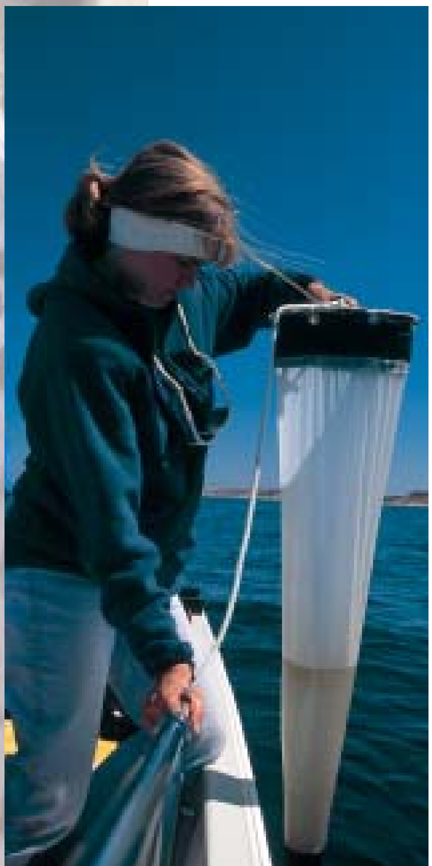
Noss, Reed F., Edward T. LaRoe III, and J. Michael Scott (1993). Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. United States Geological Survey.

Odum, Eugene Pleasants. *Fundamentals of Ecology*, 3rd ed. Philadelphia: W. B. Saunders Company, 1971.

Purves, William K. and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates Inc., 1987.

Terborgh, John. *Where Have All the Birds Gone?* Princeton, NJ: Princeton University Press, 1989.

Environmental Impact



A scientist takes a water sample from Monterey Bay in California to determine the environmental impact of pollution in the area's water.

The term environmental impact is a legal term introduced by the National Environmental Policy Act of 1969. This act requires federal agencies to conduct studies to determine the possible consequences for the environment of planned activity. Many states have enacted similar legislation. The results of the study are published as an environmental impact statement. These legal documents are often the basis on which an agency decides whether or not to proceed with a project.

All animals interact with their environment, so all animal activity, including human activity, has some environmental impact. However, human impact on Earth's environment far exceeds that of other species. Humans have altered the environment and landscape on a global scale.

Most species inhabit fairly limited regions within Earth's biosphere, but humans occupy every biome. Humans have the advantage of a high level of technology. Technology has enabled humans to create artificial environments that allow survival even in the harshest environments. Technology allows humans to move food and other materials thousands of kilometers from areas where the resources are plentiful to areas where resources are scarce.

Our ability to live just about anywhere in the world comes at a cost to the environment. Most animals require only a few resources to survive, such as air, food, water, and nesting material. These resources are obtained from a relatively small area. In contrast, humans living in highly industrialized nations rely on thousands of products that come from all parts of the world.

The worldwide extent of human activity, the shift to intensive agriculture, the demand for mineral and other resources, and rising standards of living have all created numerous global environmental problems as well as many regional and local environmental problems. These problems are our environmental impact.

There are several significant environmental issues, including the acquisition and use of natural resources, rapid population growth, soil erosion, desertification, diminishing water supplies, deforestation, loss of biodiversity, global warming, and **acid rain**.

acid rain acidic precipitation in the form of rain

Resource Acquisition

All organisms interact with their environment to acquire and use resources and thus have an impact on their environment. Most of the time, this is a sustainable impact in that resources are replaced at about the same rate as they are removed and waste is produced in amounts that can be easily absorbed by the ecosystem. Consequently, most animals living in a natural environment have no significant long-term environmental impact.

The maximum viable population of a particular species that an environment can support indefinitely is referred to as the carrying capacity. For most organisms, carrying capacity is determined by the ability of an ecosystem to provide resources, such as food, water, and shelter, and its ability to assimilate, dilute, or detoxify wastes.

Early humans interacted with their environment in a sustainable manner, and their environmental impact was localized and short term. However, the development of intensive agriculture (following the invention of the metal plow) beginning about 5,000 B.C.E. allowed humans to increase the carrying capacity of their environment. During this agricultural revolution, humans came to see the environment as something to be tamed and exploited. Farmers were able to produce a surplus of food that could be traded for other goods and services. This trade led to increased urbanization with the development of trade centers.

During the first half of the nineteenth century, the Industrial Revolution made manufactured goods cheap and readily available to everyone. The mechanization of agriculture allowed an even greater rise in food production and increased urbanization. The Industrial Revolution, therefore, expanded the carrying capacity of the environment even more. As methods of resource acquisition developed, including methods of mining, fishing, farming, and logging, humans have had an increasingly significant, and often harmful, impact on the environment.

Population Growth

Many environmentalists consider population growth to be the principal environmental problem facing the world today. Sometime during 1999, world population exceeded 6 billion. If the current rate of population growth continues, the world's population will exceed 10 billion by 2030, and will continue to double about every twenty-five years. A larger population creates a greater demand on energy and other resources to maintain current living standards.

Desertification

When topsoil is removed, forests are cut down, or grasses are overgrazed, the land can be permanently changed. The process of degrading grassland to infertile conditions is known as desertification. Many grasslands grow in semi-arid regions of the world. These areas average between 25 and 75 centimeters (10 and 30 inches) of precipitation per year. This rain or snow is trapped by a thick layer of humus-rich topsoil. Overgrazing can remove the grass cover, exposing the topsoil to wind and water erosion. Poor farming practices can also expose topsoil. In the 1930s in portions of Texas, Oklahoma, Kansas, and Colorado, overgrazing and poor farming practices combined with extended drought to create dust-bowl conditions. Once the topsoil is lost, it can take hundreds of years to replace.

Diminishing Water Supplies

Water comes from two sources, surface water and ground water. In many parts of the world, there is insufficient surface water to supply the needs of agriculture, so water is pumped from deep wells. Often, the aquifers supplying these wells are recharged only very slowly, if at all. Some of these deep wells pump water that was deposited in the aquifer during the Pleistocene, over 18,000 years ago. Since the climate has now changed, the water cannot be replaced.

Intensive agriculture requires lots of water. Industry, agriculture, and human populations also have a need for abundant supplies of water. Many experts believe the unavailability of sufficient supplies of fresh water will be

the most serious long-range problem confronting the United States and many other parts of the world in the years to come.

Deforestation

Deforestation occurs when trees are removed from a forest faster than they can be replaced by natural growth or replanting. Sometimes deforestation is deliberate. When Europeans first arrived, a dense hardwood forest covered much of the eastern United States. Settlers cut down the trees for fuel and building materials and cleared the land for farming.

In tropical regions of the world, the same thing happens today. Trees are removed to open up land for farming. Unfortunately, the soil under tropical forests is poor and lacks essential nutrients due to the heavy rainfall, so the land cannot support agriculture in the long term. After two or three years, the cleared land no longer supports crops and more trees are cut down. Harvesting tropical hardwoods for building materials also contributes to deforestation. The result of clearing land and cutting down hardwoods is an alarming loss of tropical and other forests worldwide.

Biodiversity

Worldwide, species are being lost at a rate equal to or greater than at any other time in the history of life on Earth. Entire ecosystems are lost through environmental degradation. The world's tropical forests contain the greatest variety of organisms on Earth. As these forests are cut down for timber or converted to rangeland, there is a great loss of species and diminished biodiversity. Temperate forests and other temperate habitats are also suffering degradation. While it is easy to measure the number of hectares of forest or grassland converted to cornfields or to parking lots, it is much harder to characterize the slow degradation in an ecosystem's structure, function, or composition.

Global Warming

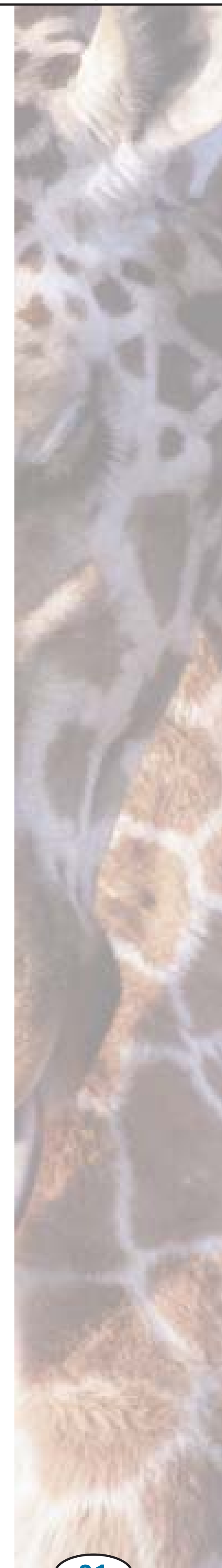
Research strongly indicates that the atmosphere of Earth is gradually warming. The best estimates are that the temperature has increased by 0.5°C (1.0°F) in the last century. This is a small but significant increase. What scientists cannot agree on is what causes global warming. Many researchers are convinced the data show unequivocally that global warming is directly related to the increase in greenhouse gases, such as carbon dioxide. Others feel it may simply be a short-term climactic phenomenon.

Acid Rain

acidic having the properties of an acid

Because acid "rain" may come in the form of rain, snow, fog, or dew, the best term is acid deposition. All rain is slightly **acidic**. As water falls through the atmosphere, it absorbs carbon dioxide. The carbon dioxide reacts with the water to form carbonic acid. This is normal and healthy. Plants and animals easily tolerate this natural acid rain.

The problem arises when other compounds dissolve in rainwater and make the rain even more acidic. Sulfur dioxide is emitted from power plants that burn high-sulfur coal, and from other sources that burn fuel with a high sulfur content. Sulfur dioxide particles can be carried over long distances by



winds and fall to the ground far from where they originated. If the sulfur dioxide dissolves in water in clouds, it forms sulfuric acid. Power plants and automobiles also emit oxides of nitrogen, which can dissolve in water to form nitric and other acids.

Natural precipitation has a pH of about 5.6. The pH of pure water is 7.0. A pH of 5.5 will reduce the ability of trout and salmon to reproduce. If the pH falls below 5.1, several serious effects can occur. Acid rain with a pH below 5.1 can damage buildings and statues, kill fish and aquatic plants, weaken trees, disrupt the nitrogen cycle, and stunt the growth of crops.

There is no escaping the conclusion that human activity has dramatically changed our planet, mostly for the worse. Many of these changes, such as open pit copper mines, are simply unsightly. Other changes, such as air and water pollution, have great potential to do harm to humans and other life. As we struggle with raising the standard of living of people all over the world, it is important to look for techniques of resource extraction and utilization that can minimize the adverse impact human activity has on the environment. All human and animal activity affects the environment in some way, but human activity need not harm our environment. SEE ALSO Global Warming.

Elliot Richmond

Bibliography

Art, Henry W., ed. *The Dictionary of Ecology and Environmental Science.* New York: Henry Holt, 1993.

Bowler, Peter J. *Norton History of Environmental Sciences.* New York: W. W. Norton & Company, Inc. 1993.

Caplan, Ruth. *Our Earth, Ourselves: The Action-Oriented Guide to Help You Protect and Preserve Our Planet.* Toronto, Canada: Bantam Books, 1990.

Carson, Rachel. *Silent Spring.* Boston: Houghton Mifflin, 1994.

Chiras, Daniel D. *Environmental Science: Action for a Sustainable Future*, 4th ed. Menlo Park, CA: Benjamin-Cummings Publishing Company, 1993.

Franck, Irene M., and David Brownstone. *The Green Encyclopedia.* New York: Prentice Hall General Reference, 1992.

Harms, Valerie. *The National Audubon Society Almanac of the Environment.* New York: Putnam Publishing, 1994.

Luoma, Jon R. *The Air Around Us: An Air Pollution Primer.* Raleigh, NC: Acid Rain Foundation, 1989.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth Publishing Company, 1990.

Mott, Lawrie, and Karen Snyder. *Pesticide Alert: A Guide to Pesticides in Fruits and Vegetables.* San Francisco: Sierra Club Books, 1997.

Newton, David. *Taking a Stand Against Environmental Pollution.* Danbury, CA: Franklin Watts Incorporated, 1990.

Parker, Sybil P., and Robert A. Corbitt, eds. *McGraw-Hill Encyclopedia of Environmental Science and Engineering*, 3d ed. New York: McGraw-Hill, 1993.

Rubin, Charles T. *The Green Crusade: Rethinking the Roots of Environmentalism.* New York: Free Press, 1994.

Thackray, Sue. *Looking at Pollution.* North Pomfret, VT: Trafalgar Square, 1987.

Trager, Oliver, ed. *Our Poisoned Planet: Can We Save It?* New York: Facts on File, 1989.

Environmental Lawyer

The field of environmental law began after World War II (1939–1945) as a response to growing public concern about the impact of the massive amounts of toxic chemicals used in the fields of agriculture and public health. American biologist Rachel Carson's 1962 book *Silent Spring*, which served as both a warning about the dangers of unregulated **pesticide** use and a reminder that human health is inextricably linked to the health of the planet, mobilized people around the world. The first lawyers to work with this growing "environmental" movement helped grassroots organizations investigate chemical claims and lobby for laws to regulate the proliferation of poisons flushed into the water and air and dumped by the planeload over farmland. Thanks to public pressure, the U.S. government in 1970 created the Environmental Protection Agency, charging it with enforcing environmental protection of land, air, water, and other species.

pesticide any substance that controls the spread of harmful or destructive organisms

Environmental lawyers choose from three broad areas in which to work. Many enter government agencies, writing laws and enforcing them, investigating violations, and prosecuting the violators. Many other lawyers choose to work for industry helping companies to understand and comply with the changing laws, permits, and regulations. These lawyers also defend their clients in violation lawsuits and help them to lobby for decreased regulations. The smallest group of environmental lawyers is composed of those who work as public advocates for citizen's groups, from the local to the international level. These lawyers describe their work as the least well paid yet the most rewarding in allowing them to use their career to pursue their ideals, whether they are protecting neighborhoods, clean air and water, wilderness, or other species.

The requirements for becoming an environmental lawyer are the same as for any law degree. A candidate with a bachelor's or master's degree applies to a three-year law program with a set curriculum. Elective courses could include studying the Clean Air Act, Superfund cleanup laws, or the laws governing mineral resources. Although not a requirement, a background in ecology, biology, chemistry, or engineering helps lawyers understand complicated pollution questions. The most important quality to bring to environmental law is a reverence for life and an understanding of the interconnectedness of all beings.

Nancy Weaver

Bibliography

Concise Dictionary of Scientific Biography. New York: Scribners, 2000.

Ethology

The study of behavior is divided into two sub-categories: learned behavior and **innate behavior**. Ethology is the study of innate, or instinctive, behavior. Scientists in this field study the mechanisms underlying specific behavior, as well as their evolution. Ethologists were the first to systematically and scientifically measure the natural activities of animals.

innate behavior behavior that develops without influence from the environment

Ethology had its origins in a middle ground between the behaviorists, who believed that all behavior must be learned, and the classicists, who held that all behavior was inborn. According to ethologists, animals are genetically predisposed to learn behaviors that benefit their species, but this natural behavior can be modified, within limits.

The field of ethology was pioneered by three prominent European scientists during the first half of the twentieth century: Konrad Lorenz, Nikolaas Tinbergen, and Karl von Frisch. Lorenz, an Austrian scientist and physician, is referred to as the founder of modern ethology. He discovered the process of imprinting, by which newly hatched ducklings and goslings follow the first animal they see and hear as if it was their mother. Lorenz also conceived of the **fight or flight response**, a theory that attributes an animal's reaction to conflict as a compromise between two inner drives: to attack or to flee. Nikolaas Tinbergen began by studying the homing behavior of wasps and later worked with Lorenz. Tinbergen applied ethological concepts to anthropology, the study of human interactions, by linking human instinct to rituals. Karl von Frisch studied the sensory systems of fish, discovering that fish are able to see many colors and have relatively sensitive hearing. Von Frisch also demonstrated that honeybees have a sophisticated ability to use the sun's position for orientation and to utilize different dances to indicate a target's direction and distance from the honeycomb. These three researchers won the Nobel Prize in Physiology or Medicine in 1973 for their combined contributions to the field of ethology.

fight or flight response an automatic, chemically controlled response to a stimulus that causes increased heart and breathing rates for increased activity

Neuroethology, a discipline that originated in the 1960s, combines ethology with neurobiology. It draws connections between outwardly observable, innate behaviors and the activity of particular regions of the brain.

Rebecca M. Steinberg

Bibliography

Bateson, Paul Patrick Gordon, Peter H. Klopfer, and Nicholas S. Thompson, eds. *Perspectives in Ethology*. New York: Plenum Press, 1993.

Krebs, John R., and Nicholas B. Davies. *An Introduction to Behavioural Ecology*, 3rd ed. Oxford, U.K. and Cambridge, MA: Blackwell Scientific Publications, 1993.

Tinbergen, Nikolaas. *Social Behaviour in Animals: With Special Reference to Vertebrates*. London: Chapman and Hall, 1990.

Eukaryota

The Eukaryota are one of the two major groups of biological organisms. The other is the **Prokaryota**, which contains the eubacteria and archaebacteria.

prokaryota a group of organisms that lack a membrane-bound nucleus and membrane-bound organelles

Differences Between Eukaryotic and Prokaryotic Cells

The key feature of all eukaryotes is that they possess eukaryotic cells. These differ from prokaryotic cells in several important respects. Eukaryotic cells are more complex and highly organized than prokaryotic cells. They are also, on average, ten times larger. Only eukaryotic cells have membrane-bound **organelles**. The organelles are separated from the cytoplasm by plasma membranes.

organelles membrane-bound structures found within a cell

In eukaryotic cells, the DNA is contained within a nucleus, an organelle bound by a double membrane. Eukaryotic DNA is linear, with a beginning and an end, and is divided into a number of separate chromosomes. Prokaryotic cells, on the other hand, have only a single circular-shaped chromosome of DNA that is not contained in a nucleus. One consequence of this difference is that eukaryotes can have much larger amounts of DNA than prokaryotes, which is necessary for the evolution of complex organisms.

ATP

ATP, or adenosine-triphosphate, is the organic molecule that forms the basis of energy in all living organisms. ATP is used in all cellular processes that require energy.

Other important eukaryotic organelles include the mitochondria, which are responsible for the cell's metabolism (the conversion of food into usable energy resources in the form of ATP), and the chloroplasts, which allow those species engaging in photosynthesis to use light energy to fix carbon, that is, to take in atmospheric carbon in the form of carbon dioxide and incorporate it into organic molecules for use by the organism. While both of these functions are also performed by prokaryotes, the machinery for these processes is not organized into organelles.

Eukaryotic cells also have an extensive system of internal membranes, including the endoplasmic reticulum (responsible for the synthesis of proteins) and the Golgi apparatus (responsible for processing and packaging proteins from the endoplasmic reticulum), which are not found in prokaryotic cells. Finally, unlike prokaryotes, not all eukaryotes have cell walls, and the cell walls of eukaryote species are composed of different materials from prokaryotic cell walls.

The Endosymbiotic Theory of the Origin of Eukaryotic Cells

Because of the relative simplicity of prokaryotic cells, it has long been supposed that they preceded eukaryotic cells in time. The endosymbiotic hypothesis for the origin of eukaryotic cells was first proposed by Lynn Margulis in her 1981 book, *Symbiosis in Cell Evolution.* The endosymbiotic hypothesis ("endo" means "within," "symbiosis" is a situation in which organisms live together in close association) suggests that eukaryotic cells arose when certain prokaryotic cells acquired **endosymbionts**, in this case other prokaryotic cells that lived within them. It is believed that the endosymbionts derived benefits from the host such as protection and organic nutrients, while the host obtained ATP (from the prokaryotes which evolved into mitochondria) or access to the products of photosynthesis (from the prokaryotes which evolved into chloroplasts).

endosymbionts the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

What were these prokaryotic symbionts? Likely candidates have been identified: mitochondria may have originated from endosymbiotic aerobic bacteria, while chloroplasts probably arose from endosymbiotic cyanobacteria, a prokaryotic group that had already evolved photosynthesis. There is considerable evidence supporting this hypothesis. Within eukaryotic cells, mitochondria and chloroplasts both have their own genetic material, separate from that of the nuclear DNA. It is in the form of a single circular chromosome, much like that seen in prokaryotes. Also, mitochondria and chloroplasts possess their own protein-synthesizing machinery, which again resembles that found in prokaryotes.

The evolution of the eukaryotic cell represented an advance in the degree of complexity present in cells. It allowed for the evolution of further

complexity of organization, including multicellular organisms. SEE ALSO Prokaryota.

Jennifer Yeh

Bibliography

Curtis, Helena. *Biology*. New York: Worth Publishers, 1989.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton and Co., 1996.

Margulis, Lynn. *Symbiosis in Cell Evolution: Life and Its Environment on the Early Earth*. San Francisco: W. H. Freeman, 1981.

Evolution *See Biological Evolution.*

Evolutionary Stable Strategy

An evolutionary stable strategy describes tactics employed by individual organisms when competing with one another for a given resource. These tactics can be behavioral or structural, and the organism does not consciously choose them, but adopts them as a natural consequence of evolution. Both structures and behaviors are heritable (capable of being inherited), and as some are successful and some fail, only the better ones are passed on. It is important to differentiate between a strategy employed by an individual, such as displaying brighter-colored feathers, and a strategic decision an individual might consciously make, such as going to medical school, because only heritable strategies get passed on to offspring. Decisions such as going to medical school, however strong in a family, are not heritable.

The idea of evolutionary stable strategy (ESS) was first conceived by the British biologist John Maynard Smith in 1974. The idea is that one strategy in a given contest, on average, will win over any other strategy. The strategy should also have the benefit of doing well when pitted against opponents employing the same strategy. This is important, because a successful strategy is likely to be common and an organism will probably have to compete with others who are employing it. There does not necessarily have to be a single evolutionary strategy. It can be a combination of strategies, or a combination of individuals who each employ only one strategy.

The workings of an evolutionary stable strategy can be illustrated by looking at a simple system of two strategies. Suppose a given population of organisms has to compete for food. In this particular population, there only two possible strategies. Individuals can act like "hawks," which will fight over a piece of food viciously and retreat only when seriously injured, or they can act like "doves," which will try to puff their chests out and pretend to be tough, but run away at the threat of any serious challenge. Hawks will always beat doves. When hawks fight hawks, there will be a winner and a loser, but the loser will be seriously injured. Doves fighting doves will display at one another for a period of time before giving up. Neither will be injured, but they will have wasted some of the time they could have spent looking for food.

Illustration of the Dawkins system.

		Opponent	
		Hawk	Dove
Player	Hawk	50 or –100, average –25	Always 50
	Dove	Always 0	40 or –10, average 15

Which is the better strategy? That is, is it better to be a hawk and win against all doves, but at the risk of serious injury, or is it better to be a dove and risk being trounced by hawks? To answer this question, the British evolutionary biologist Richard Dawkins assigned arbitrary scores to wins and losses. He awarded 50 points for a win, zero points for losing, minus 100 points for serious injury, and minus 10 points for wasting time with excessive displays. Under Dawkins's system, assuming a record of equal wins and losses for evenly matched competitors, a bird population consisting exclusively of doves would reward individuals with an average of 15 points per contest. If a dove wins a contest against a dove, he gets 50 points less 10 points for wasting time, for a total of 40 points. The loser gets minus 10. If an individual wins half his contests, his score averages to 15 points (40 points minus 10 points divided by 2).

However, we cannot assume that a population of only doves would be evolutionarily stable. Although such a population seems beneficial for all the individuals involved, what happens if a mutation takes place, or a sudden immagrant flies in, and a hawk appears in the population? The hawk will win all his contests, and reproduce quickly and often. Before long, the successful hawks could possibly drive the doves into extinction. However, at a price of minus 100 points per loss, a hawk surrounded exclusively by hawks will average minus 25 points, whereas a dove surrounded by hawks will score zero. So in a population of only hawks, doves will tend to do better. A population of only hawks would not be evolutionarily stable, either. Over time, a single strategy cannot sustain itself.

So what strategy is evolutionarily stable? In this particular population, the stable strategy is a mixture of doves and hawks. This could mean that individuals never change their strategies and that a combination of both strategies is stable, or that individuals may employ either strategy and switch strategies as often as they please. In this case, the average individual will employ the most advantageous proportions of either strategy. In a system with 12 individuals—5 doves and 7 hawks—the average payoff for any individual is 6.25. Thus, we could have 5 individuals that were always doves and 7 that were always hawks, or 12 individuals that were doves 5/12 of the time and hawks the rest.

Of course, this is a very simple system. If individuals switch strategies, it is assumed that the organism's opponents are unable to guess its intentions. If the organism could not disguise its intentions, enemies could quickly learn to detect outward signs of strategy choice and adjust their tactics accordingly. For example, if an individual scratched at the sand every time before deciding to be a dove, its opponents could learn to be a hawk every time sand was scratched, and they would always win.

In nature, of course, different strategies are tried all the time. Instead of just two, there is a nearly infinite number of potential tactics, and it is reasonable to imagine that mutations are happening at a constant rate that introduces new tactics, or reintroduces old ones, into the system. These new strategies may topple the old ESS, or they may not. A preexisting ESS has probably been challenged by any number of alternate strategies and has survived, but it might be expected that only a completely new and innovative strategy would have a fighting chance at defeating it.

In 1980, the American political scientist Robert Axelrod created a contest related to the hawks-vs.-doves scenario, but allowed fifteen different strategies to compete in a computer simulation. After hundreds of rounds, a consistent winner cropped up, which may be safely called the evolutionary stable strategy. Fifteen opponents with a variety of tactics could not defeat it. Axelrod held another contest, this one with sixty-three entrants, and came up with the same winning strategy.

Such contests happen constantly in nature. New strategies evolve and pit themselves against the present evolutionary stable strategy. Given the diversity of the opponents that show up, the strategy is tested in a variety of directions. A true ESS will be unshakeable regardless of the opponents. Of course, in nature, changes in an organism's physical environment or species invasion can change all the rules of the game, and strategies may topple and be replaced by others better suited to the new environment.

Ian Quigley

Bibliography

Dawkins, Richard. *The Selfish Gene.* New York: Oxford University Press, 1989.

Excretory and Reproductive Systems

Excretory and reproductive systems each have important but different functions in animals. The excretory system maintains water, ion, and nitrogen balance within the body and eliminates wastes. The reproductive system creates new individuals of a species. Both the excretory and reproductive systems are under endocrine control but are also influenced by the external environment.

The Reproductive System

The reproductive system functions to produce more individuals of a species. The reproductive system is regulated by the endocrine system and is affected by environmental conditions outside of the animal and internal conditions inside the animal. Reproductive cycles are influenced by the time of year, amount of daylight and rainfall, and temperature, in addition to nutrition and general health of the animal.

The main organs in the reproductive system are the **gonads**, which include the ovary and testis. The ovaries produce eggs and the testes produce sperm. The egg and the sperm are **gametes** that combine to form a **zygote** in a process called fertilization. The zygote will grow and develop into a new individual of the species.

gonads the male and female sex organs that produce sex cells

gametes reproductive cells that only have one set of chromosomes

zygote a fertilized egg

Timber rattlesnakes during mating.

The egg and sperm both carry DNA, the material that contains the genetic instructions for the growth and development of a new individual. Gametes are produced through **meiosis** and contain only one-half of the genetic information of the parent. When the gametes come together and form a zygote, the zygote will have half of its genetic information from the egg and half from the sperm.

meiosis a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

In vertebrates such as humans, egg and sperm come separately from different individuals. Humans and most other animals (both vertebrates and invertebrates) have different sexes commonly called males and females. In the case of animals without separate sexes, one individual produces both eggs and sperm and is called a **hermaphrodite**. Most hermaphrodites, including many **annelids**, pair with another individual and exchange eggs and sperm rather than fertilizing themselves. Some platyhelminthes self fertilize. Other animals switch between being male and female, a condition called sequential hermaphroditism.

hermaphrodite an animal with both male and female sex organs

annelids segmented worms

In addition to sexual reproduction, the fusion of the egg and sperm, some animals can reproduce asexually. In asexual reproduction, genetic material is not combined. Therefore, it produces an offspring that is genetically identical to the parent. Types of asexual reproduction include budding, fission, and parthenogenesis. Parthenogenesis occurs in rotifers, some bees, wasps, ants, and several species of fish, lizards, and amphibians. Some animals switch between sexual and asexual reproduction, and some reproduce only asexually.

Fertilization can happen internally or externally. External fertilization occurs in most sea-living creatures as well as freshwater fish and amphibians. In external fertilization both eggs and sperm are shed into water and fertilization, development, and growth of the zygote all take place outside the body. Internal fertilization occurs when egg and sperm are joined inside of the body. The zygote can develop inside of the reproductive tract, as in mammals. Birds and reptiles have internal fertilization but lay eggs. The zygote develops inside the egg but outside of the body. Invertebrates that have internal fertilization also lay eggs.

The Excretory System

Vertebrates have a closed circulatory system, which means that they have arteries and veins that transport blood. Cellular metabolism produces waste and uses nutrients and water. The circulatory system carries water and nutrients to cells and carries waste products away from cells. Water and nutrients come from ingestion and digestion. Waste removal is critical to maintaining internal **homeostasis**.

Nitrogen is the most toxic byproduct of cellular metabolism. The body must excrete nitrogen. Nitrogen is commonly produced as ammonia from cells. Many animals will convert ammonia, which is extremely toxic, into a less toxic form of nitrogenous waste. These include **urea** and **uric acid**.

The habitat of an animal determines which kind of nitrogenous waste it produces. Most aquatic animals, both invertebrates and freshwater fish, excrete ammonia. Ammonia dissolves in water and is easy to transport outside of the body by **diffusion** when an animal is surrounded by water. This happens primarily through the skin in invertebrates and through the **gills** of fishes. Ammonia must be diluted by a great deal of water to be nontoxic. There is not enough water in land animals to dilute ammonia enough, so ammonia is turned into either urea or uric acid.

homeostasis a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

urea a soluble form of nitrogenous waste excreted by many different types of animals

uric acid an insoluble form of nitrogenous waste excreted by many different types of animals

diffusion the movement of molecules from a region of higher concentration to a region of lower concentrations

gills the site of gas exchange between the blood of aquatic animals such as fish and the surrounding water

Which of these an animal produces is linked to where the offspring develop. Animals characterized by internal development of offspring such as mammals make urea. So do animals that have eggs which develop in water, such as amphibians, sharks, and some fish that live in saltwater.

Urea is not very toxic and can be concentrated by the kidney to conserve water. Urea is dissolved in water, so transport of waste out of a developing egg that is sitting in freshwater is done by diffusion. Uric acid is not water soluble and is excreted in a paste. Birds, reptiles, and insects all produce uric acid. These animals develop in an egg on land, and waste must accumulate in the egg as the individual grows and develops. Because uric acid is not water soluble, it can sit in the egg and not be reabsorbed by the developing zygote.

Water balance in the body is maintained through a process called osmoregulation. The vertebrate kidney is a specialized organ that both concentrates urea or uric acid and maintains water balance, mostly by filtering the blood. When blood passes through the kidney, water is reabsorbed and reused by the body. Additionally, almost all sugar, salts, and other nutrients are reabsorbed by the body from the kidney. Waste products are taken out and eliminated, the main waste product being nitrogenous waste. The kidney contains about 20 percent of the blood volume at any one time.

In invertebrates, a variety of specialized structures exist for waste removal. Flame bulb protonephridia in planaria are the most primitive specialized osmoregulation structure in invertebrates. Annelids have an excretory system called the metanephridium, and it functions for both osmoregulation and nitrogenous waste removal. Insects use Malpighian tubules for both osmoregulation and filtering the hemolymph. SEE ALSO Catadromous—Diadromous and Anadromous Fishes; Fertilization; Ontogeny.

Laura A. Higgins

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, 1999.

Crews, David. "Animal Sexuality." *Scientific American* (January), 1994.

Marieb, E. N. *Human Anatomy and Physiology*, 4th ed. Menlo Park, CA: Benjamin/Cummings, 1998.

Schmidt-Nielsen, K. *Animal Physiology*. Cambridge, U.K.: Cambridge University Press, 1997.

Exotic Species

Exotic species, which are also known as alien species, invasive species, nonindigenous species, and bioinvaders, are species of plants or animals that are growing in a nonnative environment. Alien species have been moved by humans to areas outside of their native ranges. Once transported, they become removed from the predators, parasites, and diseases that kept them in balance in their native environments. As a result of the loss of these controls, they often become pests in the areas into which they are introduced.

Many plants and animals can disperse naturally into new habitats. The colonization of North America by cattle egrets from Africa, and the slow spread of the nine-banded armadillo into Texas and Louisiana occurred without human intervention. But the most destructive invasions are invariably those caused by human activity, whether deliberate or inadvertent.

The introduction of exotic species into the United States probably began with the first colonists that came ashore. When the Pilgrims landed at Plymouth in 1620, various non-native rodents, such as *Rattus*, and the house mouse, *Mus musculus*, almost certainly disembarked right along with them. The problem of exotic species became even more acute in the eighteenth and nineteenth centuries, as the United States entered world trade.

Environmental Impact

Nonnative species are not always harmful. Ninety-eight percent of the food grown in the United States come from nonnative species of wheat, barley, rice, cattle, and poultry. The nonnative honeybee is essential in growing plant crops, as well as generally benefiting flower pollination. Non-native species add $500 billion a year to the United States economy.

However, many nonnative species do enormous environmental damage. Research has shown that more than 40 percent of species on the U.S. Department of the Interior's lists of endangered or threatened species are at risk primarily because of nonindigenous species.

The economic damage caused by rats is huge. Rats alone do more than $19 billion of damage per year. Damage caused by alien insects cost $20 billion. Altogether, the more than 30,000 nonnative species in the United States cost the country $123 billion a year in economic losses, according to a June 12, 1999 report by Cornell University ecologists. In that report, David Pimentel of Cornell said that the United States has become the land of a billion rats.

Constant motion allows these fire ants to breathe in the water.

Invading species can cause complex changes within the structure and function of their new ecosystem. Their presence can lead to the restructuring of established food webs, the importation of new diseases to the new surroundings, and competition with indigenous organisms for space and food. Other ecological changes may occur when the invading organisms reproduce with native species, possibly altering the gene pool. This may lead to hybridization and homogeneity, which reduces biodiversity, the primary element associated with an ecosystem's ability to adapt to natural or human-induced changes.

How Do They Get Here?

Introductions of nonnative species can be planned, incidental, accidental, or unintentional. They can also be caused by a natural disaster. Scientists have made several attempts to identify the possible pathways of introduction, with varied success.

The most common method of introduction into marine environments is through the ballast water of shipping vessels. A cargo ship floats high in the water and is very unstable when it is empty. To stabilize the ship, the crew fills the ballast tanks with water. When the tanks are filled, marine organisms are pumped in along with the water. Then, when the ballast water is discharged at the next port of call, exotic species can be introduced. Scientists estimate that as many as 3,000 alien species per day are transported around the world in the ballast water of ships.

Aquaculture, the cultivation of natural products of water such as fish, also introduces invading organisms. Although nonnative species can provide inexpensive food and sources of recreation for human communities, these same species can cause environmental damage if they are released or escape.

Extent of the Problem

Every state in the United States and nearly all communities have been affected by bioinvaders. However, two states have been especially hard hit—Hawaii and Florida—and for similar reasons. Both states are geographically isolated and both have a semitropical-to-tropical climate.

Hawaii. Hawaii has been geographically isolated from the rest of the world for millions of years. Because of this isolation, Hawaii originally had thousands of species that existed nowhere else on Earth. But it has suffered the highest rate of extinctions of any area of the United States and one of the highest rates anywhere in the world, with hundreds and possibly thousands of unique species already extinct. The tropical climate of Hawaii allows invasive plants and animals to thrive. Nonnative plants and animals frequently displace native species. Predation by nonnative rats, feral cats, dogs, and mongooses has led to the extinction of many species of birds. Habitat destruction by feral pigs has altered landscapes. To compound the problem, nonnative species are usually more aggressive at colonizing disturbed ground left behind by the feral pigs.

Florida. Like Hawaii, Florida has a subtropical-to-tropical climate that allows many plants and animals to thrive. The state is protected by ocean on three sides. On the fourth side, it is geographically isolated from the states further north by differences in climate. Because of this isolation, Florida is considered to have been somewhat species-poor, with many niches available for invasive species to colonize.

Florida now lays claim to 63 percent of the nonindigenous bird species, 25 percent of nonindigenous plants, 25 percent of land mammal species, and the largest number of established nonindigenous amphibian and reptilian species in the United States. Overall, approximately 42 percent of Florida's reptiles, 23 percent of its mammals, 22 percent of its amphibians, 16 percent of its fishes, 15 percent of its **flora**, and 5 percent of its birds are naturalized nonindigenous species.

flora plants

Florida's nonindigenous species cause severe problems for the state's ecology, economy, and resource management. This is largely because of their impact on fishing and water sports, the degradation of wildlife habitat, the reduction of biological diversity, and the alteration of natural ecosystems.

Well Known Invaders

Thousands of invasive species worldwide are notorious for their distinctive habits, destructive potential, or ecological damage. Other invaders seem to be having little environmental impact. A few of the more well-known exotic species in the United States are discussed here.

African Clawed Frog. The African Clawed frog, *Xenopus laevis*, was widely used in human pregnancy testing in the 1940s and 1950s, and as a result was shipped all over the world. The frog is native to southern Africa, but is now found around the world in suitable habitats, probably due to accidental or deliberate releases. It is voracious and prolific, preying on insect larvae, small fish, and tadpoles. It is a completely aquatic frog. The state of Washington prohibits importation of *Xenopus*, and other states require a permit for possessing it. *Xenopus* remains a popular laboratory animal and is still available as a pet in some areas. The environmental damage caused by *Xenopus* is due to its voracious appetite and fecundity. The frog competes with native species for small fish, insect larvae, amphibians, and other prey. However, researchers disagree as to the extent of environmental damage it causes.

Mediterranean Gecko. This small gecko (*Hemidactylus turcicus*) is a native of the Mediterranean, and apparently first arrived in the United States on cargo ships unloading in New Orleans. Some areas may also have been colonized by escaped pets. The lizard is primarily nocturnal, preferring rocky walls near bright lights. It is found all along the Gulf Coast of the United States and as far west as Arizona. Because there are no other nocturnal, insectivorous lizards in areas the gecko have colonized, it does not appear to be causing any environmental damage.

Zebra Mussel. Zebra Mussels (*Dreissena polymorpha*) originated in the Balkans, Poland, and areas within the former Soviet Union. The species was introduced into the Great Lakes in the ballast water of ships in 1988. It has been spread by barge traffic into all the major East Coast rivers of the United States that are connected through canals to the Great Lakes. At first, the zebra mussel was believed to be intolerant of the warm water in the southern parts of the United States, but it is now established in the lower Mississippi River. Many of the small lakes near the Great Lakes are not connected to the Great Lakes by waterways, but they still have zebra mussels. In these cases, the mussels were probably transported on boats moved from lake to lake on trailers. They would not necessarily have to be moved from lake to lake on the same day, because in cool, humid conditions, zebra mussels can stay alive out of water for several days.

The economic impact of zebra mussels is due to their habit of colonizing the pipes that supply water to electric power plants and public water supplies. The colonies can become so dense that flow through the pipes is restricted. At one power plant in Michigan, zebra mussel densities were as high as 700,000 individuals per square meter (80,000 per square foot), and the diameters of pipes had been reduced by two-thirds at some Michigan water-treatment facilities.

Imported Fire Ants. There are two species of imported fire ants, *Solenopsis invicta*, the red fire ant, and *Solenopsis richteri*, the black fire ant. *S richteri* was introduced first, but the much more aggressive red fire ant has displaced it and the native fire ant species across most of the south. Currently, *S richteri* is found only in a few areas of northeast Mississippi, northwest Alabama and southern Tennessee. The attempts to control these invaders have been controversial. Early efforts to eradicate the ants with the widespread application of pesticides severely damaged the environment and may have contributed to the spread of the insect. Recently, a small parasitic fly (*Psuedacteon*) which offers promise as a fire ant control has been successfully bred, and test releases are underway. Techniques are now being developed to breed large numbers of the tiny flies for more widespread release.

The red fire ant is well established from North Carolina to eastern Texas, although the further extension of its range may be limited by geographical factors such as dry summers or cold winters. The two fire ant species inhabit approximately 93,120,000 hectares (23,010,4531 acres) in nine southern states, making them a familiar feature of life in these areas. There are probably about 10 billion colonies. The ants are feared because, when a nest is disturbed, the ants swarm over any nearby object, delivering multiple, painful stings to the intruder. However, the greatest economic impact of the imported fire ant comes from their attraction to electrical equipment. Short circuits, fires, and other damage can occur after ants colonize the equipment.

Reptiles and amphibians. The native range of the giant toad (*Bufo marinus*) extends from southern Texas, through Mexico and Central America, to Brazil in South America. This marine toad is widespread, occurring outside its natural range in places such as Australia, Fiji, Guam, Hawaii, Japan, New Guinea, the Philippines, the Solomon Islands, Tonga, several islands in the West Indies, and southern Florida. In 1955 an accidental release of 100 frogs led to an established population around Miami International Airport. This population has now spread throughout southern Florida and into the fringes of Everglades National Park through an extensive system of canals and drainage ditches.

Giant toads have replaced the native toad *Bufo terrestris* in much of its range. Marine toads have voracious appetites and eat small, moving or nonmoving objects such as other toads, insects, snails, snakes, garbage, and dog food. If bitten by a pet, the toads release a milky bufotoxin from their parotid glands. Bufotoxin causes profuse salvation, twitching; vomiting; shallow breathing and collapse of the hind limbs. The toxin has been known to cause death in small mammals. The long-term environmental impact of this animal is unknown.

Birds. The parakeet or budgerigar (*Melopsittacus undulatus*), commonly known as the budgie, is indigenous to interior Australia. Budgerigars are popular as caged birds throughout the world, but escaped or released birds have become established as wildlife in Florida. Another small parrot, the Monk parakeet (*Myopsitta monachus*), is native to South America. It has established colonies in several cities around the United States, including one in Austin, Texas. This parrot is considered a pest in its native territory, causing substantial damage to grains and fruit crops. It is also a very aggressive bird, competing with other species for food sources. There are several reports of Monk parakeets attacking and killing other birds. The overall environmental impact of these birds is unknown at this time.

In the 1850s and 1860s, the weaver finch, *Passer domesticus* (also called the house sparrow) was deliberately introduced into North America at several different times and places. In 1853, a group of 100 birds from England were released in Brooklyn, New York, in a misguided attempt to control canker worms. Since its introduction, it has rapidly and aggressively colonized almost all of North America, displacing native birds by competing for nest sites and food. It is also hardy and fecund.

Where do we go from here? Many scientists think that the spread of exotic species is one of the most serious, yet largely unrecognized, threats to our environment. Nonnative animal species cause enormous economic each year to crops, waterways, and natural environments in the United States. Safeguarding our natural heritage from alien and exotic species involves stopping additional introductions, the early detection and quick eradication of pests, integrated systems for the control and management of existing pests, and the restoration of native species and ecosystems.

Elliot Richmond

Bibliography

Allen, Craig R., R. Scott Lutz, and Stephen Demarais. "Red Imported Fire Ant Impacts on Northern Bobwhite Populations." *Ecological Applications* 5, no. 3 (1995): 632–638.

Billington, Elizabeth T. *Understanding Ecology.* New York: Penguin Putnam Books for Young Readers, 1971.

Holt, Alan. "Hawaii's Reptilian Nightmare." *World Conservation* 28, no. 4 (1997): 31–32.

Kurdila, Julianne. "The Introduction of Exotic Species Into the United States: There Goes the Neighborhood." *Boston College Environmental Affairs Law Review* 16 (1995):95–118.

Lafferty, Kevin D., and Armand M. Kuris. "Biological Control of Marine Pests." *Ecology* 77, no. 7 (1996):1989–2000.

Laycock, George. *The Alien Animals.* New York: Natural History Press, 1966.

Long, John L. *Introduced Birds of the World: The Worldwide History, Distribution, and Influence of Birds Introduced to New Environments.* New York: Universe Books, 1981.

Nature Conservancy. *America's Least Wanted: Alien Species Invasions of U. S. Ecosystems.* Arlington, VA: The Nature Conservancy, 1996.

Roots, Clive. *Animal Invaders.* New York: Universe Books, 1976.

Silverstein, Alvin, and Virginia Silverstein. *Animal Invaders.* New York: Atheneum, 1974.

Simberlof, Daniel, Don C. Schmitz, and Tom C. Brown. *Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida.* Washington, D.C.: Island Press, 1997.

Wachtel, S. P, and J. A. McNeely. "Oh Rats." *International Wildlife* 15, no. 1 (1985): 20–24.

Wilcove, David S., and M. J. Bean. *The Big Kill: Declining Biodiversity in America's Lakes and Rivers.* Washington, D.C.: Environmental Defense Fund, 1994.

Williamson, Mark H., and Bryan Griffiths. *Biological Invasions.* Norwell, MA: Kluwer Academic Publishers, 1997.

Internet Resources

Pimentel, David, Lori Lach, Rodolfo Zuniga, and Doug Morrison. *Environmental and Economic Costs Associated with Non-Indigenous Species in the United States.* Cornell University. <http://www.news.cornell.edu/releases/Jan99/species_costs.html>.

Expenditure Per Progeny

The goal of each living thing is to pass on its own genetic information. The limited resources of the world have created a complex, biological community under intense selective pressure. In order to ensure survival of oneself and one's genes, an individual must utilize a competitive reproduction strategy. Genetic adaptations occur over time to make organisms run faster, grow more efficiently, or better detect their food. These evolutionary "decisions" are fairly easy to make: the tradeoff of spending energy on stronger muscles is easily worth it if stronger muscles keep their owner alive.

Numerous reproduction strategies and compromises are evident in nature, and certain constraints favor one or another. If you were given power to design a completely new organism, you would be forced to make a number of decisions regarding its production. Eggs or live young? How many eggs? How much time invested in raising them? Do the males care for the young? The females? Both? Neither? Organisms evolve to take the best strategy under the given circumstances, and one "choice" they have to make is how to allocate energy towards reproduction.

One variable is how many offspring to have. For example, long-term studies of the great tit, a bird in Britain, show that the optimal number of eggs for a great tit is about eight. If a pair of birds raises a larger brood, chicks in that brood get fed less often. They eat fewer caterpillars and weigh less when leaving the nest. However, heavier chicks tend to live longer and healthier lives.

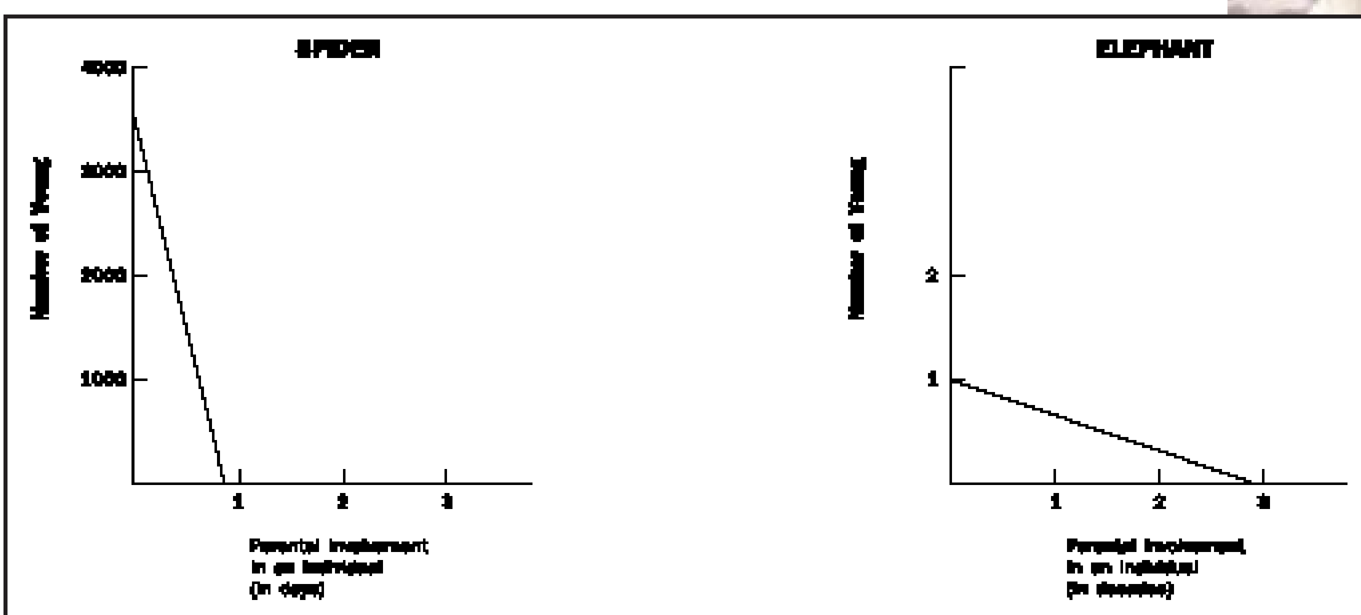
So if a parent wants to maximize the number of healthy young it can have, and maximize the chance that all of those young will live to be old enough to reproduce and generate healthy offspring of their own, it cannot raise too many. If it raises fewer than the optimal number, its chicks might well turn out healthy, but there will be less of them to pass on the family genes.

Christopher M. Perrins showed in 1979 that if the size of broods are artificially manipulated by sneaking into nests and adding or removing eggs, the optimum number is between eight and twelve eggs. We know this because Perrins tried to recapture chicks from the nests later on; he had the best luck recapturing chicks from the nests with eight to twelve eggs. More eggs meant the chicks were less healthy overall; fewer eggs simply meant there were fewer chicks to start with.

This assumes that parents will expend about the same amount of energy on a brood of chicks regardless of brood size. Raising chicks is an enormously expensive endeavor: parents must expend energy in making the eggs, making the nest, sitting on the nest and protecting it, and getting food for the brood once it hatches. Great tits bring back an item of food every thirty seconds as long as there is daylight. Plus there is the matter of multiple breeding seasons. Is it better to work like a horse for one season on one brood and be tired and inefficient for subsequent seasons, or more slowly expend oneself? In the end, each chick receives a certain amount of energy in metabolic production, feeding, and raising. This amount is known as the expenditure per progeny.

Predictably, differing species exhibit a wide range of "decisions" regarding expenditure per progeny. An organism as physiologically and socially complex as a human being requires a lot of energy to develop inside and outside of the womb, so any one individual offspring represents an enormous investment. The evolutionary "hope" is that an incredibly complex, adaptable individual will be able to reproduce, and thus only a few are made. This is a good thing, because human beings are so energetically expensive!

Contrast this reproductive strategy with that of a spider. Spiders have no social development and require little to no care after birth. They are also small and comparatively easy to make. Thus, a reproducing spider will invest all of her energy into making thousands and thousands of eggs. While



A comparison of the energy expended per progeny between a spider and an elephant.

baby spiders possess negligible learning capacity and are not as equipped as human beings to deal with complex, new situations, it is reasonable to assume that if a parent generates thousands of them, at least a few of them will make it to reproductive age.

Making energetic decisions like these, or tradeoffs, is part of the process of evolutionary development. As changing environmental circumstances dictate what might be the most effective reproductive strategy, parents must allocate their energies accordingly. SEE ALSO Reproduction, Asexual and Sexual.

Ian Quigley

Bibliography

Davies, Nicholas B., and John R. Krebs, eds. *An Introduction to Behavioural Ecology.* Cambridge, MA: Blackwell Science, 1993.

Dawkins, Richard. *The Selfish Gene.* Oxford, U.K.: Oxford University Press, 1989.

Extinction

Extinction is the irreversible disappearance of all signs of life pertaining to a particular group of organisms. This group can be any of the accepted categories of taxonomic nomenclature, including kingdom, phylum, class, order, family, genus, species, and even subspecies. Most often, extinction is used in reference to the species level organism. The organism may have gone extinct at any time within the past 600 million years of the **fossil record** or may be in the process of going extinct today. Furthermore, this phenomenon does not pertain only to animals but is also applicable to plants, fungi, protists, bacteria, and archaebacteria.

fossil record a collection of all known fossils

Many situations can theoretically lead to the extinction of an organism. Determining the cause of extinction is very difficult, especially when information from the fossil record must be used to reconstruct a sequence of events. In many cases, a direct explanation is not forthcoming, and many hypotheses must be examined. Unfortunately, present-day cases of extinction are becoming increasingly common, leading to the need to predict and counteract the disappearance of currently living organisms. Extinction is a natural occurrence well documented in prehuman fossil deposits, and there is evidence that it may allow opportunistic evolution of species that had previously been overshadowed. Human domination of the biosphere, however, is accelerating the extinction rate. For many reasons, human lives are negatively affected by mass extinctions, and humans are struggling to oppose further loss.

Causes of Extinction

niche how an organism uses the biotic and abiotic resources of its environment

Many mechanisms account for extinction. Although organisms depend on other species in their ecosystem for food and population control, this delicate balance may be upset through the pressure of interspecies interactions. If an organism serves as the food source for another, it may be overpredated or overharvested, leading to the death of all members of the taxonomic group. This can occur if the predator/herbivore evolves keener sensory or cognitive capabilities, making it a more efficient consumer. It can also be the result of a food web disruption, such as when an environmental change suddenly favors the propagation of the predator/herbivore without offering such a benefit to the prey. Similarly, when two species occupy the same environmental **niche**, meaning that they prefer similar habitats and food types, they can be in direct competition for limited resources. If the competing species is better able to inhabit that niche, by gaining more territory and consuming more food, it can drive its competitors to extinction. Humans sometimes hunt animals for sport. This is not exactly predation or competition, but it can also result in the death of an entire species, for example, the dodo bird.

habitat loss the destruction of habitats through natural or artificial means

Environmental alteration can also lead to extinction. This may be part of a global climate change, one of Earth's natural climate fluctuations. In this case, one might expect to find a high number of global extinctions, especially among animals in regions greatly affected by the temperature and weather pattern differences. The microenvironment also undergoes change over time. For example, a new mountain range may form along a plain, an island may sink into the ocean, and a river may divert its course. Each of these examples would strongly affect the organisms that depend on those particular microenvironments for sustenance. In some cases, this local regional change can be called **habitat loss**. This term describes the destruction of a particular type of habitat, such as decline of biodiversity in the North American natural plains, beginning in the nineteenth century.

Evolution can also be considered a direct mode of extinction. Taxonomic boundaries are sometimes very arbitrary, meaning that the distinction between groups is unclear. The lines between groups are drawn using evidence about the organism's habitat, body shape (or morphology), and living habits; most often, however, only the morphology can be relied upon. Some species in the fossil record show gradual change in morphology over evolutionary time. Paleontologists, scientists who research extinct organisms, must sometimes examine a progression from one body type to another

Event	Species Included in Great Extinction	Probable Cause of Great Extinction
Cambrian mass extinction	Trilobites; brachiopods; conodonts	Global Cooling Events
Ordovician mass extinction	Trilobites; archaeocyathids	
Devonian mass extinction	Stromatoporoids; corals; brachiopods; trilobites; conodonts; acritarchs; all jawless fishes; placoderms	
Permian mass extinction	Trilobites; corals; blastoids; acanthodians; placoderms; pelycosaurs	
End-Cretaceous mass extinction	Pterosaurs; belemnoids; many plant species; marine reptiles; mollusks; echinoids; fishes	Volcanic Activity or Meteorite Impacts

Five great extinction events.

and determine at what point the original species can be called a new species. Nonetheless, the original species can no longer exist when the new species begins, and this in itself is a kind of extinction.

Factors that Can Contribute to Extinction

Several factors influence the likelihood that an organism will go extinct. Some species have a very small range, so that they are very susceptible to small-scale changes in the environment. This is an extremely common explanation for the extinction of subspecies. Subspecies sometimes evolve when isolated populations of a species living at the boundaries of its natural range develop distinct behaviors and appearances that distinguish them from the parent species. Given a long enough period of separation from the parent species, these subspecies would develop into an entirely novel organism. Despite this, they often are subject to extinction because their small population size and range cause them to either die out or to be reassimilated into the parent species.

A particular type of feeding pattern is another extinction factor. Whereas generalist feeders, which rely on many sources of nutrition, can switch to a different diet if their food source were to disappear, specialist feeders, which consume only one particular food source, cannot and are therefore highly susceptible to extinction.

Some organisms can be said to have a very delicate niche dynamic for a combination of the above reasons. For example, olive ridley sea turtles return to the same beach year after year to lay eggs. The eggs are highly predated by local animals, and the beaches are often brightly lit and filled with human tourists, factors that decrease the fitness of the mothers and the young. The turtles, however, seem physiologically incapable of choosing other sites for nesting because of their dependence on a particular sort of fine-grained sand and on particular temperature patterns at the chosen beaches.

Once species numbers decline to a small amount of individuals, extinction speed is increased by a factor known as **inbreeding depression**.

inbreeding depression loss of fitness due to breeding with close relatives

In 2000, the population of California condors had climbed to eighty-seven, from a low of thirty in 1967. But of that number only 3 lived in the wild.

This occurs when so few individuals remain in a species that they are forced to mate with members of their own families out of necessity. The smaller gene pool causes increased incidence of genetic disorders, general poor health, and increased susceptibility to disease, all of which increase the species' decline.

Difficulties Determining When an Extinction Has Occurred

Extinctions are not always easy to pinpoint or determine. When a fossil organism stops appearing in the fossil record, this may be explained by a variety of reasons. It may be that environmental conditions during the following period did not favor fossil formation, so that the species survived but was no longer fossilized. Another possibility is that only a small population of a widely dispersed species may live in the region that allows fossilization; if this local population goes extinct, the entire species will disappear from the fossil record, but that does not necessarily mean that the entire species has also gone extinct. Another explanation is that the species may have merely migrated from a fossil-friendly environment to a fossil-unfriendly habitat, or perhaps to a region for which the fossil bed has not yet been found. A confounding factor in determining extinction can be as simple as researcher bias. Organisms seem to go extinct at the boundaries between geological periods of Earth's history, but this may be due to a quirk of the field of paleontology: Paleontologists often study only one period in the rock strata. They categorize all organisms that appear at the beginning of their period, and may not realize that the scientists researching an earlier period have already named the same species. Thus although it appears that an organism has become extinct, in reality it has just been mistakenly renamed.

Paleontologists try to account for all of these sources of error through thorough study and the use of probability equations, but the fossil record is irregular and difficult to interpret. For example, in the mid-twentieth century, the coelacanth, a species of bony fish that scientists had falsely declared extinct, was rediscovered as a living species. Coelacanths were thought to have gone extinct 70 million years ago because they disappeared from the fossil record. This mistake was remedied in 1938 when a fisherman caught a living coelacanth off the coast of southeastern Africa.

Reasons for Preventing Extinctions

Although extinction is a natural occurrence, there are many reasons to actively protect existing species from extinction. More and more, ecosystems are viewed as integrated modules, so that the extinction of one species in the ecosystem can disrupt all of the other species' population dynamics. If humans ignore the extinction of a seemingly uninteresting species, this could cause widespread extinctions in many other organisms. In general, biodiversity (the presence of a high number of species in an environment) is equated with a healthy ecosystem, and high extinction rates decrease biodiversity. Often, an environment of low biodiversity reveals what humans consider to be pests. These are merely organisms that are able to survive in an ecosystem reduced and dominated by humans. People naturally prefer a healthier ecosystem, with clean breathing air, green surroundings, and a wide variety of species. There is a value to the beauty of the environment, which is damaged by high extinctions. Furthermore, humans directly depend on some species for medical benefits, such as medicine, tissue and organ donations, and animal models of human disease. Organisms that go extinct can no longer be researched as possible cures for human ailments or be studied by engineers as models for building computers, machinery, and vehicles.

Preventing extinction is a political as well as a biological priority. The needs of humans often overshadow the decline of endangered species. For example, the economy of many Third World countries depends on agriculture. If natural ecosystems such as rain forests must be destroyed to support the agricultural needs of these nations, many species are put at risk and forced into extinction. Without that source of income, however, the peoples of these countries could languish and starve. A balance between preserving the rain forest habitat and ensuring the well-being of the humans must be sought.

CALIFORNIA CONDOR

California condors are the largest birds in North America, weighing up to 11.5 kilograms (25 pounds), with a wingspan of more than 2.7 meters (9 feet). In 1967 condors had declined to approximately thirty individuals. In 2000, eighty-seven condors were living, but only three were in the wild. While captive breeding programs have improved the outlook for condors, their future now depends entirely on human intervention.

Methods of Preventing Extinction

There are several contemporary means of preserving a particular species. Active breeding programs at nature reserves and at zoos attempt to maintain a sizable population of individuals to avoid inbreeding depression. When animals such as cheetahs are the victims of inbreeding depression, specialized veterinarians and behaviorists monitor their health and attempt to circumvent the danger of disease. Hunting and fishing regulations attempt to predict population flux and disallow overharvesting of game animals. Specialized herbariums and eco-landscaping firms are working to restore lost habitats within depleted landscapes.

Despite these endeavors, there is still an acute danger that many of the world's habitats will be thrown into disarray by human intervention. The shrinkage and parceling of natural habitats is especially damaging to animals with large ranges, such as Siberian tigers, bald eagles, and buffalo. Nature preserves are under constant study to improve the efficiency of the surroundings in order to prevent extinction. SEE ALSO Feeding Strategies; Fossil Record; Habitat Loss; Habitat Restoration; Hunting; Paleontology; Zoological Parks.

Rebecca M. Steinberg

Bibliography

Courtillot, Vincent. *Evolutionary Catastrophes: The Science of Mass Extinction.* Cambridge, U.K.: Cambridge University Press, 1999.

Glen, William, ed. *The Mass-Extinction Debates: How Science Works in a Crisis.* Stanford, CA: Stanford University Press, 1994.

Hallam, Anthony, and Paul B. Wignall. *Mass Extinctions and Their Aftermath.* Oxford, U.K.: Oxford University Press, 1997.

Raup, David M. *Extinction: Bad Genes or Bad Luck?* New York: Norton, 1992.

Schneiderman, Jill S. *The Earth Around Us: Maintaining a Livable Planet.* New York: W. H. Freeman, 2000.

Snyder, Noel F., and Helen Snyder. *The California Condor: A Saga of Natural History and Conservation.* San Diego: Academic Press, 2000.

Weinberg, Samantha. *A Fish Caught in Time: The Search for the Coelacanth.* New York: Harper Collins, 2000.

Extremophile

Most animals live in conditions where the temperature is between 4°C and 40°C (39°F–104°F), the pH (which measures acidity and alkalinity) is between 5 and 9, and oxygen is abundant. Some animals, called extremophiles, live in conditions that are outside these ranges. The term "extremophile" is given to micro-organisms that live in extreme environments. These environments range from hot springs to sea ice to brine lakes to deep-ocean hydrothermal (hot water) vents. Each of these environments has conditions that are considered punishing or even unbearable for most animals. However, extremophiles thrive under these conditions. Extremophiles may also provide a glimpse of what the earliest forms of life looked like.

Archae an ancient linage of prokaryotes that live in extreme environments

Extremophiles are part of a new kingdom of animals called **Archae**. The members of this kingdom look like bacteria and were considered a phylum in the Kingdom Monera. In the late-twentieth century, however, scientists separated the Archae from other bacteria based on their genetic and biochemical makeup.

Extremophiles are loosely grouped into categories on the basis of where they live. Thermophiles are found living in temperature extremes. Some thermophiles are found in hot springs with water temperatures that approach boiling. The hydrothermal vents along the **midoceanic ridges** support extremophiles that not only tolerate high temperatures and **acidic** conditions but also metabolize, or process, hydrogen sulfide, which is poisonous to most animals. At the other extreme, some extremophiles thrive in very cold conditions. These are found in sea ice and on glaciers.

These iceworms in a snowfield pollen feeder are examples of extremophiles, or the ability of animals to live in extraordinary climates.

Other examples of extreme environments include natural salt lakes such as the Dead Sea and Great Salt Lake. The extremophiles living there are called halophiles. Still other extremophiles live in highly acidic or highly **alkaline** environments. Acidophiles thrive in environments with a pH less than 5 while alkaliphiles live in environments with a pH greater than 9. Acidophiles are found in places such as hydrothermal vents while alkaliphiles are found in soda lakes such as are found in Egypt and the western United States. A final major group of extremophiles are the methanogens. They are found living in places with little oxygen, such as swamps and the intestinal tracts of animals. Methanogens do not use oxygen to metabolize their food and they produce methane gas as a waste product.

midoceanic ridges long chains of mountains found on the ocean floor where tectonic plates are pulling apart

acidic having the properties of an acid

alkaline having the properties of a base

Scientists have known about extremophiles for more than forty years. Most scientists considered them curiosities in the animal kingdom. Scientists became interested in extremophiles because of their enzymes. Because extremophiles live in extreme conditions, their enzymes must also work under these conditions. Enzymes extracted from extremophiles have grown into a multibillion dollar industry. The enzymes are used in industrial and medical applications that range from making stone-washed jeans to creating artificial sweeteners to conducting genetic tests.

The enzyme-based process known as PCR is used to amplify DNA for genetic identification or genetic testing for disease and conditions. The enzyme reactions used in the procedure occur slowly at room temperatures. By using enzymes from a thermophile, the reactions are performed at a much higher temperature and so at a faster rate.

In recent years, scientists have began searching extreme environments on earth in hope of discovering clues for finding extraterrestrial life. As scientists searched extreme environments, they found more and more kinds of extremophiles. Many environments that scientists had in the past considered sterile were discovered to be the home of many different organisms. Some scientists came to believe that the total mass of all extremophiles on Earth exceeded the mass of all humans on Earth. SEE ALSO ADAPTATIONS, BIOLOGICAL EVOLUTION, KINGDOMS OF LIFE.

Allan B. Cobb

Bibliography

Taylor, Michael Ray. *Dark Life.* New York: Scribners, 1999.

Internet Resources

Madigan, Michael T., and Barry L. Marrs. "Extremophiles." *Scientific American.* <http://www.sciam.com/ 0497issue/0497marrs.html>.

Farmer

Farmers make a living by managing or operating farms, places where plants (crops) or animals (livestock) are raised to be sold to others. Crops include grains such as wheat, vegetables, fruits; fibers such as cotton; nuts; flowers; and landscaping plants. The type of crop grown on a particular farm depends on the climate, soil, and layout of the land, whether it is low-lying or mountainous, for example. There are livestock, dairy, and poultry farmers, as well as farmers that raise bees and fish.

Farming is financially a risky business, with success depending on weather conditions, plant and animal diseases, insect problems, prices of fuel and other expenses, and market demand. Farmers may work on large commercial farms or on smaller farms which may be family owned. The work is very demanding physically and takes place mostly outdoors. During the growing season, farmers may work almost constantly, seven days a week. Animals must be cared for every day. Farmers must have both labor and management skills. They decide which crops to plant and which fertilizers to use. They need to know how to care for their livestock and keep the barns, pens, and other farm buildings in good condition. Farmers work with tools and machinery and maintain equipment and facilities. They must have good financial skills, including keeping records of expenses, taxes, and loans. Also, farmers must understand the various laws that apply to their business. Computers have become increasingly more important in farming to keep track of finances, manage inventory data, and track schedules for applying pesticides or breeding livestock.

Becoming a farmer does not generally require formal training or education. The enormous knowledge that is necessary for this profession is often acquired by a person raised on a farm. In grade and high school, it is good training to participate in agricultural programs run by organizations such as 4-H. However, even a person raised on a farm can benefit from getting an education at a university. A bachelor's degree in agricultural sciences, which include courses in farming, producing crops, and raising livestock, can be helpful, along with courses in crop, dairy, and animal sciences. Business courses such as economics, accounting, and marketing are also useful. SEE ALSO APICULTURE; AQUACULTURE; FARMING.

Denise Prendergast

Bibliography

Kircher, Harry B., Donald L. Wallace, and Dorothy J. Gore. *Our Natural Resources and Their Conservation*, 7th ed. Danville, IL: Interstate Publishers, Inc., 1992.

Internet Resources

Occupational Outlook Handbook 2000–01. U.S. Government. <http://stats.bls.gov/ ocohome. htm>.

Farming

Farming, or agriculture, is the science or art of cultivating the soil, growing and harvesting crops, and the raising of animals. Beginning some 10,000 years ago, people in various places around the world began to grow plants

This farmer in Sri Lanka uses two oxen to plow through a muddy rice paddy. Many farmers around the world still utilize ancient farming and cultivation methods.

and domesticate animals. Slowly and over time, farming made living in one place possible, encouraged innovations in tools, and allowed a dramatic increase in population. All civilizations, from the earliest we know about down to our own, have evolved from this ability intentionally to grow plants and raise animals for larger groups of people.

Ancient stories and the oldest oral traditions speak of the origins of plants and animals. In the classic mythologies of all world cultures, agriculture came as a divine gift. In most stories a god or goddess came to instruct the people in the arts of growing plants and raising animals. In the Mediterranean region instruction came from a goddess, Isis in Egypt, Demeter in Greece, Ceres in Rome. From cuneiform tablets we learn that the source for agriculture for the Babylonians, and Chaldeans was a god named Oannes, who appeared to these people of the Persian Gulf coast and taught them to grow crops and raise animals. In Chinese mythology P'a Ku separated the heavens and Earth, created the sun, moon, and stars, and produced plants and animals. The Aztec and Mayan people thought that corn was on Earth before humans. In all of the myths and stories about the origin of agriculture, knowledge is gratefully received as a blessing from the gods or goddesses.

From Hunting and Gathering to Farming

Our modern scientific stories suggest that, for several million years or more, our human ancestors survived by hunting wild animals and gathering wild plants. Then, from about 10,000 and to about 4,500 years ago, hunter-gatherer societies in at least seven regions of the world independently domesticated selected species of plants and animals. This time period is often referred to as the Neolithic Revolution. This development toward farming and the domestication of animals in the Middle East, southeast Asia, northern China, Africa, southern Mexico, Guatemala, and Peru profoundly altered the direction of humankind.

As these new agricultural systems emerged, they allowed human populations to increase, as well as setting the stage for the creation of complex human societies far beyond what had developed in hunting and gathering times. Large farming villages appeared as people gathered and settled in permanent villages. Villages turned into towns and cities, and eventually into city-states that dictated the production of food. These changes eventually led to the industrial and technological world that we live in today.

The question of why and how agriculture or farming became important in human societies continues to be investigated. One notable theory suggests that farming of some kind was practiced by hunters and gathering peoples all along. This "proto" farming encouraged certain plants and animals and resulted in increasing available foods. Other theories speculate that farming was less costly and safer than hunting and gathering or that climatic changes reduced the number of big game animals and made farming necessary to support a larger number of people. Farming may have allowed people to live in less hospitable environments such as semideserts and mountainous regions. Still other theories propose that changing climatic conditions eventually encouraged people to move into fertile riverine environments or people living in more marginal habitats encouraged the growth of certain plants that led to the deliberate planting of seeds and the cultivation of certain plants.

The Domestication of Plants and Animals

As people made the shift to farming they experimented with domesticating useful and familiar plants and animals. Perhaps this process started with a wild plant that people liked and used as an important food crop. Observation and experimentation resulted in plants that could be cultivated and relied upon. The big seeded grasses of the Middle East, rice in Asia, and the *zea* grasses that became corn in the Americas fulfilled this role. South Americans cultivated the potato, chocolate, and tomatoes.

Many early farmers domesticated animals as well as plants. People observed animals in the wild that were not solitary and not too large, fierce, or migratory. Many mammals can be tamed easily by capturing young animals and raising them in captivity. The domestication process requires rearing many animals over many generations and eventually altering the gene structure.

For example, in the Middle East we find species of goats and sheep that were domesticated from wild animals. In the wild they are relatively slow and docile, and both species lived in social groups ruled by a strong leader. Over time, these once-wild sheep and goats have undergone a reduction in size, a complete loss of horns in the female sheep, and **mutations** for wool. In goats, twisted horns and long hair called mohair appeared. Breeds of cattle appeared with long horns, short horns, crumpled horns, or humps. The earliest South American farmers found and domesticated llamas and alpacas. Other animals that lived on the outskirts of human settlements, such as dogs and pigs, developed relationships with humans before people settled as farmers. Small animals such as rabbits, turkeys, and guinea pigs were probably caught and enclosed.

mutations abrupt changes in the genes of an organism

Humans rely on other animal and plant species to produce food. Farming eventually succeeded because people figured out ways to coax more food from the environment than would otherwise be possible. The adoption of farming enabled human population to rise from an estimated 8 million present 10,000 years ago, to between 100 million and 300 million at the time of Christ, to 6 billion in the year 2000.

Biodiversity

Biodiversity is the vast and varied combination of habitats and the many species of plants and animals that thrive in combination with each other. One of the serious environmental problems humankind faces today is the loss of that biodiversity. Scientists feel that this is the direct result of the transformation of natural landscapes by people for farming and grazing uses. These lands include breaking up and clearing large tracts of wild lands and wetlands. The logging and clearing of tropical and temperate forests have contributed to the loss and decline of many species of plants and animals along with their genetic and ecological complexity. This biodiversity is lost when tens, hundreds, and thousands of farmers clear land to increase yield, when loggers clear forests to provide lumber for houses and furniture, and when city dwellers need more land for homes, schools, and factories. Cutting old-growth forests to make room for cultivated fields has encouraged erosion on slopes and mountains. Swamps have been drained and rivers damned and diverted to provide water for irrigation. Overgrazing of grasslands and the use of toxic fertilizers and pesticides have polluted lakes, rivers, and streams.

The accumulated actions of all of these people over time have led to a massive extinction of species of plants and animals. Although this process has been going on since humans began to farm, the pace of change has accelerated since the seventeenth and eighteenth centuries because of the industrial and agricultural revolutions. Innovations in machinery and genetics allowed for more crops to be grown with less labor and allowed people to do different kinds of work and move into cities. In the twenty-first century, increasing population, the global economy, and modern farming practices have created additional stresses on the environment.

Twenty-first century farming practices encourage cultivation of large-scale monoculture crops and single breeds of animals. Approximately eighty plant crops provide about 90 percent of the world's food sources. A little

over fifty animal species account for most of the domestic animal production used for food and fiber. Many scientists believe that this overdependence on a small number of genetically similar plants and animals could have devastating consequences if weather or pests take a toll on large monocrops. Thousands of other plants could be cultivated to prevent such a scenario. In addition, tens of thousands of plants are known to have edible parts that could be used.

Hundreds of thousands of animal species, many of them insects, are needed for pollination and protection of crops. Tens of thousands of microbial species, most of them living in soil or on plants, provide nutrients, act as agents of decomposition, and contribute to the success of living communities of plants and animals. Without this biodiversity many of the fundamental ecological processes that are necessary for all living things to thrive will have a devastating effect on humankind's ability to feed, house, and sustain itself.

The Future

In spite of all the changes in land use and agricultural practices, farming on the modern scale is productive and holds the promise of solving many of the world's food problems. However, its impact must now be considered alongside maintaining or increasing the natural biodiversity necessary for the maintenance of natural systems that sustain all life on Earth.

Scientists and commercial farmers are realizing that greater diversity leads to greater productivity. Research and experimentation is being conducted in areas such as rotations of grasslands for dairy and beef cattle production, precise matching of soil conditions with specific plant species, and the maintenance of seed banks to help protect genetic diversity and increase the number of plants that can be used.

Genetic diversity has also been lost in animals used for food and fiber. The number of breeds used by humankind has declined by nearly thirty since the mid-twentieth century. Scientists and breeders are working together to protect the genetic diversity of rare endangered breeds along with their wild relatives in hopes of maintaining diversity in the available supply of milk, meat, and fibers that people throughout the world depend on.

In addition, scientists are acknowledging that a significant portion of the world's biodiversity is in the hands of small indigenous farmers throughout the world who practice age-old farming and ecological practices. This body of specialized knowledge is invaluable and in danger of being lost unless these individuals can pass their knowledge on to people who can make use of it.

Along with preserving local knowledge, some scientists believe that rural and agricultural landscapes, if properly designed and managed, can help preserve a significant number of plant and animal species. The conservation of local biodiversity depends on how agricultural lands are used and also on the protection of wild lands. Farmers around the world can help maintain the biodiversity needed to maintain all kinds of life on Earth as well as taking care of our expanding human needs. SEE ALSO Apiculture; Aquaculture; Farmer; Hunter-Gatherers.

Leslie Hutchinson

Bibliography

Harlan, Jack. *The Living Fields: Our Agricultural Heritage.* New York: Cambridge University Press, 1995.

Nazarea, Virginia D. *Cultural Memory and Biodiversity.* Tucson: University of Arizona Press, 1998.

Smith, Bruce D. *The Emergence of Agriculture.* Washington, D.C.: Scientific American Library, 1995.

Solbrig, Otto T., and Dorothy J. Solbrig. *So Shall You Reap: Farming and Crops in Human Affairs.* New York: Island Press and Shearwater Press, 1994.

Tudge, Colin. *Neanderthals, Bandits and Farmers: How Agriculture Really Began.* New Haven, CT: Yale University Press, 1998.

Fausto-Sterling, Anne

American Professor of Biology and Women's Studies
1944–

Dr. Anne Fausto-Sterling is a Professor of Biology and Women's Studies at Brown University in Providence, Rhode Island. She teaches in the Department of Molecular and Cell Biology and Biochemistry. Her scholarly interests include developmental genetics, intersexuality (the study of people born with atypical sexual anatomy), and the interplay between science and gender. Her laboratory at Brown researches the evolution of sexual reproduction and **regeneration** in flatworms of the genus *Planaria*.

regeneration regrowing body parts that are lost due to injury

Fausto-Sterling is best known for her work on race, gender roles, and human sexuality. In addition to her teaching and research at Brown University, she has given lectures and held workshops on many campuses across the United States. The message she conveys to her audience is that gender plays an important role in how science is carried out and reported, and that science influences the perception of gender differences. Fausto-Sterling urges students of feminist scholarship to seek a broad understanding of scientific practices and knowledge.

Fausto-Sterling has been a faculty member at Brown for more than twenty-five years and has written a number of influential books on gender, development, and biology. These controversial but popular works (controversial because she criticizes the research practices of her colleagues) examine how race and gender have structured scientific practices and knowledge. In *Myths of Gender: Biological Theories About Men and Women*, Fausto-Sterling evaluates the scientific merit of studies on the biological basis of behavioral differences between men and women. She cautions the public to accept the results of these studies with skepticism, arguing that many theories set forth by this line of research are poorly supported by scientific evidence. In *Sexing the Body: Gender Politics and the Construction of Sexuality*, Fausto-Sterling discusses how human society influences the formation and dissemination of biological knowledge about animal and human sexuality.

Fausto-Sterling has received numerous honors and awards and has been elected to the membership of several prestigious scientific societies. Her honors come from the fields of science and the humanities. She received an honorable mention in *The Best American Essays of 1994* for a piece on

intersexuality entitled "The Five Sexes." In 1995 she received a Women of Distinction Award from the City University of New York. Her biography was also profiled in *No Universal Constants: Journeys of Women in Science and Engineering*. Fausto-Sterling is a Fellow of the American Council of Learned Societies and the Dibner Institute for the History of Science and Technology at the Massachusetts Institute of Technology.

Judy P. Sheen

Bibliography

Ambrose, Susan A., Kristin L. Dunkle, Barbara B. Lazarus, Indira Nair, and Deborah A. Harkus. *Journeys of Women in Science and Engineering: No Universal Constants.* Philadelphia: Temple University Press, 1997.

Fausto-Sterling, Anne. *Myths of Gender: Biological Theories About Men and Women.* New York: Basic Books, 1992.

———. *Sexing the Body: Gender Politics and the Construction of Sexuality.* New York: Basic Books, 2000.

Feeding

autotrophs organisms that make their own food

heterotrophs organisms that do not make their own food

photosynthesis the combination of chemical compounds in the presence of sunlight

chemosynthesis obtaining energy and making food from inorganic molecules

frugivores fruit-eating animals

Organisms that live on Earth are either **autotrophs** or **heterotrophs**. Autotrophs obtain energy directly from their physical environment through **photosynthesis** or **chemosynthesis**. Heterotrophs must obtain their energy by eating autotrophs or by eating other heterotrophs. Plants are autotrophs, but all animals are heterotrophs. Animals that feed on living organisms or parts of living organisms can be classified into three general groups based on feeding behavior: herbivores, carnivores, and omnivores.

A herbivore is an animal that eats the tissues of green plants and only plants. Herbivores consume many different parts of plants. This group of animals can be further subdivided into such categories as folivores (eaters of leaves), **frugivores** (eaters of fruit), and granivores (seed eaters). Herbivores have special adaptations that allow them to extract sufficient energy and nutrients from plants. For example, herbivores have large stomachs, allowing them to eat a large amount of material. Some herbivores have two stomachs. Food stored in the first stomach is partially broken down by bacteria through a process similar to fermentation. Then the material is regurgitated, chewed some more, swallowed again, and passed to the second stomach. Herbivores have also evolved special teeth adapted for cutting and grinding plant tissue. Herbivores include such animals as grasshoppers, caterpillars, cattle, and antelope.

Carnivores eat other animals. The animals eaten by carnivores may be herbivores, omnivores, or other carnivores. Since animal tissue is more densely packed with nutrients than plant tissue, carnivores have relatively shorter digestive tracts. They have also evolved special teeth suitable for tearing flesh. Some members of order Carnivora, such as cats, have all fanglike teeth ideally suited for cutting or tearing through animal tissue.

Carnivores are all predators. They are generally larger than their prey (but not always; for example, wolves prey on moose and caribou). Predators pursue and capture their prey, so they require a large amount of calories.

They therefore must catch and eat many individual prey items during their lives.

Cattle graze at the Simplon Pass in the Switzerland Alps. Cattle are herbivorous, eating only plants and the tissues of green plants.

Carnivores are generally very important to the ecosystems they inhabit. Since carnivores eat other animals and must eat a large number of prey individuals, they almost always act as a check on populations of herbivores. Carnivores include animals such as cats, wolves, shrews, and polar bears. Wolves are classified as carnivores but most of the Canids (which also include foxes, coyotes, and domestic dogs) will eat fruit and berries or other plant tissue when they are hungry and the fruit is available.

Omnivores obtain energy by eating both plant and animal tissue. Some omnivores hunt, pursue, and catch other animals, just as predators do. Most omnivores will readily eat the eggs of other animals. Many omnivores are also **scavengers**. Omnivores eat plants, but not all plants and not all parts of the plants they do eat. Omnivores can eat fruits and tubers. Some grains can be eaten by omnivores.

scavengers animals that feed on the remains of animals that they did not kill

Humans are omnivores who have expanded their food choices by discovering fire and inventing cooking. Cooking animal or plant tissue tends to break down complex molecules, making more nutrients and calories available. Since omnivores eat both plant and animal tissue, they have evolved several different kinds of teeth, including incisors for shearing plant and animal tissue, canines and bicuspids for tearing and crushing meat, and molars for grinding seeds and other plant tissues. Omnivores include black bears, humans, many apes, cockroaches, chickens, and raccoons.

detritus dead organic matter

Detrivores are a group of organisms that get energy from dead or decaying plant and animal matter. Detrivores can be classified as **detritus** feeders or decomposers. There are no animals that act as decomposers, so animal detrivores are all detritus feeders. Animal detrivores can be considered omnivores that eat the dead remains of other organisms. Earthworms are typical detrivores.

The sun is the source of all energy for life on Earth. Plants harvest sunlight and store the energy in the chemical bonds of carbohydrates, fats, and proteins. Animals obtain their energy from plants. Herbivores obtain solar energy directly by eating plants. Carnivores obtain solar energy indirectly by eating other animals. All animals have evolved feeding behaviors that allow them to obtain sufficient energy and essential nutrients to live, grow, and reproduce. Some animals (herbivores) eat vast quantities of food with low nutritional value. Other animals (carnivores) consume smaller amounts of food with higher nutritional content, but they have to work harder to get it. Still other animals (omnivores) eat a variety of foods allowing them to use whatever food sources are available at any given time.

producers organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

consumers animals that do not make their own food but instead eat other organisms

A trophic level is a group of organisms that all consume the same general types of food in a food web or a food chain. In a typical food web, all **producers** (autotrophs) belong to the first trophic level and all herbivores (primary **consumers**) belong to the second trophic level.

The second trophic level in a grassland ecosystem would be all of the herbivores that eat the grass. This group can include a wide variety of organisms. For example, in the original grasslands of the central United States, the second trophic level included grasshoppers, rabbits, voles and other small rodents, prairie dogs, and American bison (*Bison bison*). Since all of these creatures eat the same grass, they are all at the same trophic level, despite their differences in size, reproductive habits, or any other factors.

The third trophic level includes primary carnivores, such as wolves and warblers. Primary carnivores prey on herbivores. Secondary carnivores, such as falcons and killer whales, prey on primary carnivores as well as herbivores. Omnivores, such as humans, are able to feed at several different trophic levels. SEE ALSO Feeding Strategies; Foraging Strategies.

Elliot Richmond

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Leatherwood, Stephen L., and Randall R. Reeves. *The Sierra Club Handbook of Whales and Dolphins.* San Francisco: Sierra Club Books, 1983.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth, 1990.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer, 1987.

Feeding Strategies

All animals must eat to live. Animals obtain energy and essential nutrients from the things that they eat. Since animals cannot harvest energy directly from the sun, they obtain energy to grow, move, and reproduce by consuming other organisms. Herbivores obtain solar energy by eating plants. Carnivores prey on other animals. Omnivores, such as humans, obtain energy by eating both plants and other animals.

Some animals consume enormous quantities of food with little nutritional value. Grazers, for example, eat large quantities of grass and other plants that have a low energy content and nutritional value. These animals have evolved special adaptations, such as two stomachs, that allow them to obtain sufficient energy from grass.

Some predators have developed special adaptations that allow them to consume large quantities of food at one time. Large snakes may catch and consume prey only three or four times a year. Lions and other large cats have adaptations that allow them to gorge on large amounts of meat at one time, then go without eating for several days or weeks.

Other predators take a different approach. The blue whale (*Balaenoptera musculus*), the largest animal that has ever lived, primarily feeds on small, shrimp-like crustaceans called **krill**. Vast quantities of krill must be consumed for the whale to obtain sufficient energy and nutrients. A blue whale may consume four tons of krill per day. The whale shark (*Rhincodon typus*), the largest living fish, feeds mainly on tiny plankton, anchovies, and sardines that it filters from the water.

krill an order of crustaceans that serves as a food source for many fish, whales, and birds

Foraging

Feeding and searching for food take up most of an animal's time. Foraging behavior requires some sort of system for distinguishing food from nonfood and for recognizing desirable food. Omnivores that consume a variety of different foods must learn which foods are good to eat. Sampling is risky, because many possible food items can be poisonous.

Rats need to consume forty different kinds of material including water, amino acids, fatty acids, vitamins, and minerals. The food available at any given time may lack some essential part, requiring the rat to spend extra time searching for foods that contain the missing element. In one study, rats were provided with a variety of foods, including yeast, a source of B-complex vitamins. When the yeast was removed from their diets, they immediately began to consume feces, another good source of B-vitamins. When yeast was reintroduced, they stopped consuming feces.

Humans are the ultimate foragers, regularly consuming an amazing variety of different foods. Yet people are generally cautious about trying new foods. Human cultures are easily identified by the food they eat. Food choices embody the accumulated wisdom of a culture about what is good to eat. However, humans do not seem to make food choices based on the need for essential vitamins and minerals. For example, a craving for fresh fruit does not appear to develop in people suffering from vitamin C deficiency. British sailors had to be required to eat limes in order to counteract scurvy

African wild dogs surround their prey, a wildebeest, on the Serengetti Plains of Tanzania.

caused by vitamin C deficiency. Humans also crave and eat far more fat and salt than is necessary for good health.

Foraging behaviors are learned and are adapted to an animal's lifestyle. Nervous systems are organized to enable animals to make associations between toxic effects and foods ingested hours earlier. Most people have experienced a strong aversion to the kind of food consumed right before an illness that caused nausea and vomiting, even when the food had nothing to do with the illness.

Grazers and Herbivores

frugivores fruit-eating animals

Herbivores consume many different parts of plants. This group of animals can be subdivided into folivores (eaters of leaves), **frugivores** (eaters of fruit), and granivores (seed eaters).

Caterpillars are probably the most familiar example of folivores. Caterpillars must eat large quantities of leaves in order to store enough fat and protein to undergo metamorphosis. However, some plants have developed a defense against caterpillars. In Finland, caterpillars of the moth *Oporinia autumnata* eat leaves of the birch tree. Caterpillars that feed on leaves from trees that were heavily damaged the previous year grow more slowly than caterpillars that feed on lightly damaged trees. Apparently the birch tree has developed chemicals that make the damaged leaves hard to digest.

Species of milkweed have evolved a highly toxic sap that prevents most caterpillars from consuming their leaves. However, the caterpillar of the monarch butterfly has evolved a tolerance for the toxin in milkweed sap and readily consumes it. Toxins from the sap are incorporated into the tissue of the caterpillars, making the caterpillars unpalatable to most predators. However, certain species of orioles have evolved a tolerance for this toxin and readily consume the insect.

Mammalian grazers generally consume a variety of different plants during a day. Only a few, such as the koala of Australia, eat only one type. Large species of grazers tend to be less selective than smaller species. In East Africa, communities of grazing animals have developed a commensal relationship. Elephants and buffalo first eat the tall, coarse grasses and then move on. They are able to consume large quantities of this low-nutrition food source. Zebras follow along behind the elephants, reducing the plant biomass even more. The zebras are followed by still smaller wildebeest, who select among the lower-growing plants that remain after the zebras have fed. Finally the smallest grazers such as Thompson's gazelles are able to reach the young, protein-rich sprouts of grass missed by the wildebeest.

Filter Feeders

Filter feeders are found in many different animal phyla, including **brachiopods**, mollusks, various worms, and chordates. They are indiscriminate eaters. They feed on prey much smaller than themselves that are suspended in water or air. Each filter feeder has some sort of apparatus with which it filters prey from the medium of air or water. The structure of this apparatus determines the size of prey. Filter feeders also have an apparatus for moving the air or water relative to the filter. This can be done by moving the filter. Barnacles wave feather-like fronds through the water, periodically drawing in whatever happens to have been caught. Other animals, such as oysters, pump water through a filter, thus moving the medium. Sometimes the filter feeder is passive and depends on wave action to move the medium. More often the filter feeder expends energy to move the medium through the filter. For example, the blue whale and the whale shark swim through the ocean with gaping mouths. The blue whale is able to gulp an enormous quantity of water because its throat has special pleated folds that allow it to expand to several times its original volume. Then the whale closes its mouth, forcing the water back through a specialized structure known as **baleen**. The whale shark has special structures in its gills that filter small organisms and other debris from the water passing through the gills. Sponges have specialized cells with flagella that keep a constant flow of water through the sponge. Once the energy has been expended to capture the prey, the filter feeder rarely rejects it, thus being indiscriminate eaters.

brachiopods a phylum of marine bivalve mollusks

baleen fringed filter plates that hang from the roof of a whale's mouth

Carnivores

Carnivores are animals that eat other animals. Carnivores can be found in most of the animal phyla. Some mollusks prey on other mollusks; praying mantids eat other insects and anything else they can catch; hawks and eagles eat small mammals, large insects, fish, and other birds. Roadrunners catch and eat large insects, lizards, and small snakes. Many species of fish prey on other fish. Some species of fish that live in the deep ocean, where other animal life is scarce, have jaws so huge they can swallow another fish substantially larger than themselves. All of these animals obtain energy and essential nutrients by eating other animals.

Mammals in the order Carnivora are highly specialized to prey on other animals. They have specialized digestive systems that are inefficient at digesting plants. This order includes dogs, cats, bears, weasels, and seals. Within this group, the cats, family *Felidae*, have evolved to prey almost exclusively on other mammals. Lions have evolved specialized behaviors, teeth, and digestive systems that allow them to pursue and kill much larger mammalian herbivores. They are able to consume huge amounts of meat by gorging on the kill, which they slowly digest. This specialized behavior is necessary because lions may go several days or longer between kills. Cheetahs are even more specialized. They have evolved speed at the expense of strength and are now so specialized that their diet consists almost exclusively of the small gazelles that graze the African plains. Grazers and filter feeders eat vast quantities of food with low nutritional value. Carnivores consume smaller amounts of food with higher nutritional content, but they have to work harder to get it. SEE ALSO FORAGING STRATEGIES.

Elliot Richmond

Bibliography

Clark, E. "Gentle Monsters of the Deep: Whale Sharks." *National Geographic* 182 (1992):6.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Leatherwood, Stephen L., and Randall R. Reeves. *The Sierra Club Handbook of Whales and Dolphins.* San Francisco: Sierra Club Books, 1983.

Miller, G. Tyler Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth Publishing Company, 1990.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates Inc., 1987.

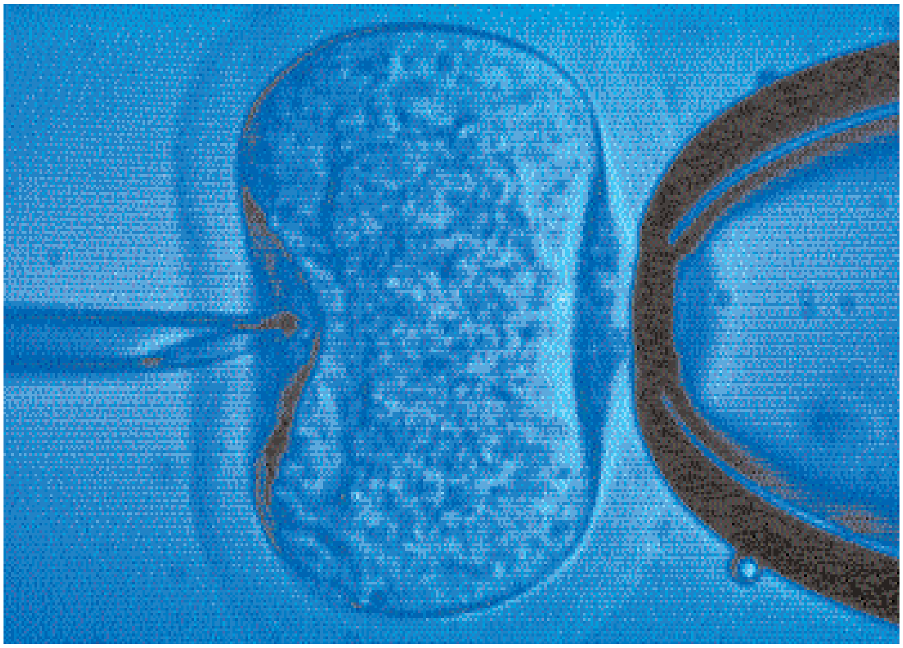
Fertilization

Life can persist in one of two ways. First, living things can spurn death in the hope of living forever. This is usually not possible, because death by predation or other unintentional causes is virtually inevitable. Second, living things can make copies of themselves, or reproduce, as a means of "hedging their bets" against death. Then, all that is required for life to persist is for at least one of the copies, or offspring, to remain alive at any one time. Thus, all living things reproduce.

How does reproduction occur? Some organisms reproduce asexually. The single-celled prokaryotes undergo binary fission, meaning literally "to split in half." Binary fission occurs after the cell has doubled the amount of its cellular constituents. The single circular chromosome is replicated from a single initiation point, the replication fork moving bidirectionally around the chromosome. Finally, inward growth of the plasma membrane separates the large cell into two equal halves. Some multicellular organisms reproduce asexually through budding. For example, in hydra, a relative of the jellyfish, a mass of mitotically dividing cells grows on the parent's side and eventually detaches as a small copy of the parent. However, most multicellular organisms reproduce sexually. Sexual reproduction takes place after the production of special reproductive cells termed **gametes**. Gametes are typically labeled as being of one sex or the other, male or female, with the female gamete being the larger of the two types. Fertilization is the union of a male and a female gamete to form a **zygote**, the developing offspring. There are many ways in which fertilization can occur in nature.

gametes reproductive cells that only have one set of chromosomes

zygote a fertilized egg



This microscopic image demonstrates in vitro fertilization. The needle (at right) injects sperm cells into a human egg (center).

The sexual organs of animals are called gonads. Gametes are made in the gonads—the female gonads produce eggs, the male gonads produce sperm. Human males produce millions of sperm every day. Females produce one mature egg in each menstrual cycle. When a sperm and an egg fuse during fertilization, a diploid zygote is formed. This zygote divides mitotically until it is an adult organism. Animals are unique in that they have a special type of cells called **germ cells**, in the gonads. The sole function of these cells is to undergo meiosis to form the **precursors** of eggs and sperm, oocytes and spermatocytes, which differentiate into the mature gametes necessary for reproduction. One can think of animal bodies, which are made of **somatic** cells derived from the original germ cells, as the machines that germ cells use to ensure their successful passage to the next generation.

germ cells egg or sperm cells, gametes

precursors a substance that give rise to a useful substance

somatic having to do with the body

Animals may release gametes into the external environment to be fertilized, or the male may deposit gametes into the female, allowing fertilization to take place inside the female reproductive tract. External fertilization occurs only in aquatic or moist habitats where gametes will not dry out. **Sessile** animals such as corals often release millions of gametes into the water at one time ensuring that at least some will be fertilized. In such cases, fertilization does not require that members of the opposite sex be near each other, although it is necessary that both males and females release their mature gametes at the same times. They do this by responding to species-specific environmental cues such as light cycles or temperature.

sessile immobile, attached

Some animals, including fish and amphibians, use external fertilization but do so only with a particular mate. When a female is receptive to a particular male, she will lay her clutch of eggs in the water and the male will distribute his sperm over them. In this form of external fertilization, unlike internal fertilization in which the female can store and use sperm from many males, the male is assured of paternity and is therefore much more likely to take care of the offspring.

Internal fertilization requires that the male introduce his sperm directly into the female, so there is a much greater probability that any particular gamete will be fertilized. Furthermore, animals are no longer dependent on water for fertilization and may become completely terrestrial. Animals with internal fertilization, especially females who incur most of the cost of reproduction, are selected to be extremely choosy with whom they mate. If they do not pick healthy mates they may spend precious energy and time raising an offspring that cannot compete with the offspring of choosier parents. There are usually species-specific behaviors, courtship displays, and other physical cues that allow females to pick healthy mates of their own species, a phenomenon known as sexual selection.

glycoprotein an organic molecule that contains a carbohydrate and a protein

At the cellular level, a mammalian sperm must undergo several steps before it can fertilize the egg. The first step is termed the acrosomal reaction, in which enzymes from the sperm cap, or acrosome, are released. These enzymes serve to break down the barrier of follicle cells that surround the egg, as well as the zona pellucida, a **glycoprotein** envelope that encases the egg. The sperm can tunnel through the zona pellucida only if the acrosomal enzymes recognize species-specific molecules of the female's egg. Eventually the sperm gains access to the egg itself, and the sperm and egg plasma membranes fuse. At this stage the egg becomes activated and initiates a rapid sequence of events.

First, the activated egg blocks entry to other sperm, as polyspermy (the fertilization of an egg by more than one sperm) is generally lethal to the developing embryo. When the first sperm fuses with the egg plasma membrane, the egg begins to increase its concentration of positively charged sodium ions from the surrounding environment of the female oviduct. The change in the electric potential across the plasma membrane (the excess positive charge inside the egg) prevents further sperm/egg fusions. Next, development processes begin; the egg increases oxygen consumption and begins protein synthesis. Eventually the nuclei of the sperm and egg fuse to form the diploid nucleus of the new zygote. SEE ALSO REPRODUCTION, ASEXUAL AND SEXUAL.

Todd A. Schlenke

Bibliography

Austin, C. R., and R. V. Short, eds. *The Evolution of Reproduction.* Cambridge, U.K.: Cambridge University Press, 1976.

Dale, Brian, ed. *Mechanism of Fertilization: Plants to Humans.* New York: Springer-Verlag, 1990.

Gwatkin, Ralph B. L. *Fertilization Mechanisms in Man and Mammals.* New York: Plenum Press, 1977.

Longo, Frank J. *Fertilization*, 2nd ed. New York: Chapman and Hall, 1997.

Fitness

Fitness is a central concept of evolutionary biology. We will consider individual fitness, followed by fitness as applied to alleles or genotypes.

direct fitness fitness gained through personal reproduction

The **direct fitness** of an individual is related to the number of offspring that that individual produces. Specifically, it is one-half of the number of offspring produced, because in sexual species, only half of an offspring's genes come from either parent. That proportion, one-half, represents the **degree of relatedness**, or proportion of genes shared, between parent and offspring.

degree of relatedness how closely related members of a population are

Indirect fitness derives from shared genes with kin other than the direct offspring of an individual. This might include cousins, nieces, nephews, siblings, and so on. The indirect fitness of an individual is calculated by adding the relations of that individual multiplied by the degree of relatedness. Inclusive fitness represents the sum of direct and indirect fitness.

indirect fitness fitness gained through aiding the survival of non-descendant kin

The concept of indirect fitness was developed by the evolutionary biologist W. D. Hamilton. The idea originated with attempts to explain **altruistic behavior** in animals. Altruistic behavior is defined as behavior that harms the actor yet benefits the recipient, and includes such actions as alarm calling, which may draw the attention of the predator to the caller.

altruistic behavior the aiding of another individual at one's own risk or expense

According to natural selection theory, altruistic behavior should be eliminated from populations because it hampers individual survival and reproduction. However, Hamilton noted that if altruistic behavior benefits the kin of the actor, that behavior can nonetheless be selected for. This is because kin share genes with the actor. **Hamilton's Rule** dictates when altruistic behavior is beneficial: Altruism is selected for if the cost of a behavior to the actor is less than the benefit to the recipient, multiplied by the recipient's degree of relatedness to the actor. Thus, altruistic acts are more likely if they benefit close kin rather than distant kin, or unrelated individuals.

Hamilton's Rule individuals show less aggression to closely related kin than to more distantly related kin

Kin selection explains a wide variety of altruistic behavior. It also explains the evolution of social systems in which some individuals forego reproduction in order to help parents raise siblings. This is the situation in many pack species, such as wolves. In wolves, packs are often made up of two parents and their offspring from several mating seasons. Only the parents, which are the dominant individuals in the pack, reproduce.

Kin selection also explains more extreme examples of social behavior, such as that found in **eusocial** insects (species in which there are non-reproductive individuals. The primary groups of eusocial insects are the Hymenoptera (ants and bees) and the termites. Both groups have evolved special genetic systems in order to make kin selection more powerful. The Hymenoptera are characterized by **haplodiploidy**, a genetic system in which the males are haploid and females are diploid.

eusocial animals that show a true social organization

haplodiploidy sharing of half the chromosomes between a parent and an offspring

One consequence of haplodiploidy is that females (who are the crucial players in the colony) share a greater proportion of genes with their sisters than they would with their own offspring. It therefore benefits females to care for sisters in the colony rather than try to reproduce on their own. Termites are not haplodiploid, but they do go through repeated cycles of inbreeding, which also results in individuals sharing an unusually large proportion of their genes.

Kin selection is more complicated in the real world than Hamilton's Rule suggests because the expected reproductive success of individuals must also be factored in. For example, even though an offspring only shares half its genes with a parent, the parent may protect an offspring more vigorously than expected because reproductive success of the younger offspring may be greater than that of the more aged parent.

So far, this discussion has focused on individual fitness. Fitness can also be defined for alleles or for genotypes rather than for individuals. Allelic or genotypic fitness describes the relative contribution of one allele or genotype to the next generation as compared to that of possible alternate alleles or genotypes. These forms of fitness are central to population genetics.

Genotypes and alleles with higher fitness are selected for in the next generation, and make up a greater proportion of the total gene pool than other genotypes and alleles. All else being equal, alleles with greater fitness will eliminate and replace alleles of lower fitness. However, the fitness of particular alleles or genotypes may depend on numerous external factors, and changes in the relative fitnesses of alternate alleles/genotypes may help maintain **polymorphisms** in populations, situations in which a population has multiple alleles for a given locus.

polymorphisms having two or more distinct forms in the same population

One external factor determining the fitness of alleles and genotypes is the specific environment in which they are found. One well-studied example is that of the sickle-cell **anemia** allele. This allele is normally disadvantageous because individuals who are homozygous for the allele (that is, carrying two copies of it) have sickle-cell anemia. However, in malaria-prone areas, it has been shown that individuals who are heterozygous (carrying one sickle-cell allele and one normal allele) are more resistant than individuals who have two normal alleles. So, in areas where malaria occurs, the fitness of the sickle-cell allele is higher than in malaria-free areas.

anemia a condition that results from a decreased number of red blood cells

Another external factor determining the fitness of a particular allele or genotype is the alleles an individual possesses for other genes. This is called **epistasis**.

epistasis a phenomenon in which one gene alters the expression of another gene that is independently inherited

Yet an additional external factor that may determine the fitness of an allele or genotype is its frequency in the population. This is known as **frequency-dependent selection**. Frequency-dependent selection is known to operate in mimicry systems, in which there are poisonous individuals as well as non-poisonous individuals of the same species that mimic the appearance of poisonous individuals. The fitness of either type depends on the relative frequencies of poisonous and nonpoisonous individuals in the population.

frequency-dependent selection a decline in the reproductive success of a particular body type due to that body type becoming common in the population

Jennifer Yeh

Bibliography

Alcock, John. *Animal Behavior*, 4th ed. Sunderland, MA: Sinauer Associates, 1989.

Futuyma, Douglas J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, 1998.

Ridley, Mark. *Evolution.* Boston: Basil Blackwell Scientific, 1993.

Fishes

See Osteicthyes.

Flight

Three different groups of animals—insects, birds, and mammals—include species that have evolved the ability to fly. This ability developed independently in each group through separate evolutionary processes. Recent research has shown that a fourth group of animals, the now-extinct winged reptiles known as Pterosaurs, were probably capable of true flight as well. Whereas the aerodynamics of flight apply equally to all types of flying animals, the mechanical details of flight vary significantly among the groups.

All insects, birds, and mammals that fly move themselves forward by flapping their wings. They do not depend exclusively on gliding and soaring to remain aloft. However, many species of birds combine extensive gliding and soaring with episodes of true flight to conserve energy.

Forward flight is produced in all true flying animals in a similar way. Each animal moves its wings up and down in a circle or figure-eight pattern. The wings are moved downward and backward, producing forward thrust and lift. Then the wings are rotated and moved back to the original position to start a new stroke.

Insects

Insects have two pairs of wings, but one pair may be small and degenerate or modified into wing covers. So insects may use either one or two pairs of wings in flight. In insects with one pair of wings, such as flies, mosquitoes, wasps, and bees, the tip of the wing moves in an oval path. On the down stroke, the wing is held parallel to the body and is moved forward and down. On the upstroke, the wing is turned perpendicular to the body plane.

Wing movement in insects with two pairs of wings, such as dragon flies, is similar, but the front and rear wings move alternately, one wing moving down while the other moves up. Because of the **exoskeleton** anatomical structure of insects, muscles are not attached directly to the wings. Instead, the wings are attached to the thorax (chest area). Four sets of muscles inside the thorax cause it to flex and twist, thus moving the wings.

exoskeleton hard outer protective covering common in invertebrates such as insects

Bats and Birds

Some people think that bats are birds because both fly. Bats and birds do have some common features, such as very lightweight skeletons, but bats are mammals, not birds. The bones of a bat's wing are quite distinct from a bird's. The long bones of a bat's wings are actually finger bones with a thin, leathery membrane stretched between. Only the thumbs of the bat remain as useful digits. The thumbs have strong claws that the bat can use for climbing.

In birds and bats, the muscles that control wing movement are attached directly to the wing bones. Birds have large chest muscles that are attached to a deep, keel-like sternum (breastbone). The depth of the sternum gives the wing muscles additional leverage, allowing for strong flapping motion. Smaller muscles return the wing to the upper position. Pterosaurs also had deep, keel-like sternums.

Birds also have specially designed wing feathers to aid flight. These feathers flatten out, overlap, and lock together on the down stroke to produce lift. As the wing is drawn back up, the individual feathers separate and rotate. This allows air to flow between the feathers, reducing drag. The downward movement of the wing propels the bird forward and provides lift. In forward flight, the body does not remain stationary in the air, so the wing

Because of their very small wings, hummingbirds are barely able to glide at all. Some hummingbirds flap their wings over 100 times per second to manuever.

always moves forward relative to the air. From the viewpoint of the bird, the tip of the wing moves in an oval or figure-eight path, with the wing tip moving forward and downward on the "power" stroke then upward and backward on the return stroke.

Most birds and all bats spend their time in the air in forward flight. Birds fly by flapping or gliding. Bats do not glide efficiently, so they flap continuously. Flapping consumes large amounts of energy. To conserve energy while staying aloft, many birds alternate flapping and gliding. Birds such as woodpeckers and many sparrows flap furiously, then fold their wings and glide through the air like little guided missiles. This produces an undulating motion to their flight path: they move up and forward while flapping, then move down and forward while gliding.

The long wings of many larger birds allow for extended periods of soaring and gliding. In contrast, the short, tiny wings of a hummingbird must be flapped constantly to keep the bird hovering in the air. Not surprisingly, hummingbirds must consume an enormous number of calories each day to provide the energy for their constant flapping.

Hovering is a specialized form of flight that is characteristic of, but not unique to, hummingbirds. Kestrels and kingfishers often hover when hunting. Other birds hover occasionally as well. However, hovering requires large energy expenditures, so it is common only among hummingbirds, whose body mass is very small.

In flight, hummingbirds can move forward, backward, up, or down. Hovering allows hummingbirds to hang motionless while drawing calorie-rich nectar from the blooms of plants. This allows hummingbirds to obtain nectar that would otherwise be out of reach. Hummingbirds have specialized shoulder joints that allow the wing to be rotated completely around to an upside-down position. By rotating the wing this way, the hummingbird is able to gain lift from both the forward and backward strokes of its wing. The wing tip follows a figure-eight pattern as in other birds, but the specialized shoulder joint allows the figure eight to be turned sideways. While performing these adjustments, it is not unusual for hummingbirds to reach a flapping frequency of up to 100 times per second.

Energy Requirements of Birds

The expression "eats like a bird" is often used to describe someone who eats a very small amount of food, but this is not an accurate description. Relative to their body weight, birds eat an enormous amount of food. An active hummingbird may eat three or four times its own body weight in food every day. This would be like an 80 kilogram (180 pound) person eating 240 kilograms (530 pounds) of food each day. Hummingbirds (and other birds) eat so much food because sustained flight requires that their large muscles work constantly, and this expenditure of energy must be replenished continually.

The metabolic rate is the rate at which a bird, or any animal, converts food calories into available energy. Flight takes a large amount of energy, so a high metabolic rate is necessary. To maintain the high metabolic rate necessary to provide energy for flight, birds must consume foods with the greatest possible energy content.

Carbohydrates, fats, and proteins all provide energy. Birds can use as much as 90 percent of the energy found in these foods. The diet of birds varies according to species, but common sources of carbohydrates include seeds, fruit, and flower nectar. Protein comes from such sources as insects, worms, fish, and small mammals, depending on the species, size, and habitat of a bird.

Seeds are rich in carbohydrates and fats, both of which are good sources of calories. Most fruit contains sugar, but fruit is not very high in calories compared to seeds and nuts. That is why fruit-eating birds need to spend long periods of their day feeding to get enough food. Flower nectar, which provides a rapidly metabolized, high-energy source, is mostly sugar dissolved in water. Twenty percent of all bird species utilize this energy source at least part of the time. Although nectar is good for quick energy, it contains little protein or fat. So birds supplement their nectar diet with other sources.

Insects are an excellent food source for birds. Insects are high in protein and fats and therefore contain a lot of energy-producing calories. Most people are surprised to learn that insects provide as much as 50 percent of the calories in a hummingbird's diet! Unfortunately for birds, insects are not always available. Although they are common in spring and summer, they die off during the colder months. Insect-eaters must switch to other foods or move to warmer areas where insects are more common. Birds of prey, including owls and hawks, rely on small mammals and fish as sources of protein.

How Birds Conserve Energy

Because flight requires so much energy, bird species have evolved various energy-saving techniques. Geese, cranes, pelicans, and other large birds often fly in formation. This is an energy saving technique. Each bird's downward wing stroke creates an updraft. By flying in formation, each bird is able to use the updrafts produced by the bird just in front of it. This provides extra lift and saves energy over long distances. The lead bird does not get any benefit, so birds take turns leading the formation. Energy saving formations include the familiar "V" of geese and swans and the ragged diagonal line in which brown pelicans often fly.

Gliding and soaring are two other energy saving techniques. Gliding is "coasting" on the wind in a straight line or gentle curve while gradually losing altitude. Soaring is using air currents to gain altitude.

The long, slender wings of albatrosses and shearwaters are ideal for gliding. Using a combination of gliding and soaring, an albatross can fly over hundreds of kilometers of ocean surface in search of food without flapping. The glide path starts high above the ocean waves with the bird headed downwind and slowly losing altitude in a long, straight glide. Close to the ocean surface, the wind speed is less because of friction between the air and ocean surface. As it gets close to the water surface, the albatross turns into the slower wind and, using its momentum, soars back up to the original altitude, never flapping its wings unless absolutely necessary. It then turns back downwind and repeats the process.

Gulls, hawks, and many other birds soar to take advantage of updrafts created when wind encounters an obstacle such as a cliff or mountain. Birds can soar on these updrafts for long periods of time with little effort.

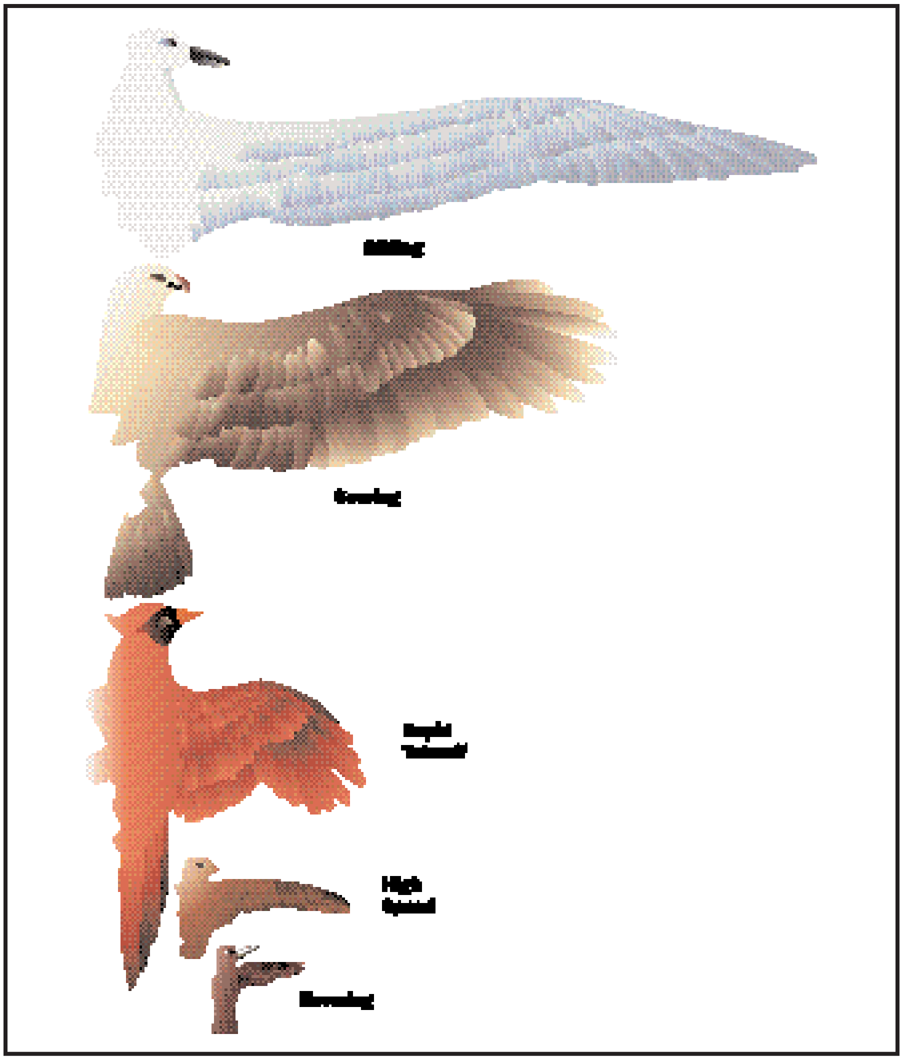
Other species, such as eagles and vultures, take advantage of rising columns of heated air called *thermals* to soar with little effort to great altitudes, from which they glide downward to the next thermal. Their long, broad wing shape allows them to take advantage of these upward air currents. Thermals occur because warm air is less dense than cold air. Denser cold air forces the less dense warm air to move upward as the cold air flows in to replace the warm air. Thermals are often found over plowed fields and darkly colored parking lots. Most birds whose flight patterns rely on thermals are searching for prey or carrion. Some birds, including storks, use thermals to migrate, climbing within one thermal, then gliding downward to the next.

Wing Shape and Flight Behavior

Each different kind of bird has a unique wing shape specially adapted to that bird's flight behavior and habitat. Birds that skim the surface of large bodies of water have glider-like wings that are long but slender and tapered to take advantage of the aerodynamic conditions of their environment. The narrow wings of birds of this type, such as the albatross, minimize drag, whereas the spectacular length of their wings (over 3.3 meters in the Wandering Albatross) provides sufficient lift.

Eagles, vultures, and hawks have wings that are both long and wide. This combination of length and width produces a large wing surface area that is ideal for soaring. These birds also have other specialized adaptations for soaring. For example, at the tips of their wings, each flight feather operates separately and independently of the others. This reduces drag due to turbulence, helps prevent air from spilling over to the top of the wing (which would reduce lift), and increases the bird's ability to make the small flight adjustments necessary for optimal soaring.

Just as the flight patterns of ground-dwelling birds differ from those of sea birds, such as the albatross, or high-altitude birds, such as hawks and eagles, so do their wing shapes. Ground-dwelling birds, including pheasants and turkeys, need to be able to fly rapidly for short distances. Their typical behavior is to remain motionless for as long as possible until a preda-



Wing shapes at various points of flight. Redrawn from *The Bird Site*, 2001.

tor approaches too closely, then explode into flight with much noise, thus distracting and confusing the predator. This kind of flight requires a short, broad wing attached to powerful chest muscles. This wing design also allows the bird to change direction rapidly. However, such a short, rounded wing is not suitable for extended flight. Although they are not ground-dwelling birds, parrots and other tree-dwelling birds also exhibit this type of wing. Because they do not need to fly great distances, their rounded wings enable them to maneuver quickly through the many trees of their forest homes.

High-speed birds, including falcons and swallows, have slender, tapered wings that can be flapped rapidly and efficiently to produce high-speed flight. All birds capable of high-speed flight exhibit this wing shape that produces little drag. Peregrine falcons are widely reported to have the fastest flight of all birds. One falcon overtook an airplane flying at 175 mph. However, this was in a dive. The highest speed ever reported for a bird in level flight was 218 mph for a spine tailed swift, *Hirandapus caudacutus*, in the Cachar Hills of India. This speed was recorded by timing the flight of the bird between two known points using a stopwatch.

It would seem that flight gives enormous evolutionary advantages. The Pterosaurs inhabited a wide variety of different habitats and survived for 140 million years. Bats occur in every part of the world except the Arctic and Antarctic. Worldwide, there are thousands of different species of birds, with 1,700 different species found in North America alone, inhabiting a wide variety of ecological niches. However, the insects are the real success story of flight. Nearly one million insects have been identified, and many entomologists estimate there at least that many more. Insects were the first to evolve the ability to fly, and they have made the most of it! SEE ALSO Gliding and Parachuting; Locomotion.

Elliot Richmond

Bibliography

Audubon Nature Encyclopedia. Philadelphia: Curtis Publishing Company, 1971.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishers, 1989.

Wetmore, Alexander. *Song and Garden Birds of North America.* Washington, D.C.: National Geographic Society, 1975.

Internet Resources

"Flight Mechanics." *The Bird Site.* <http://www.nhm.org/birds/guide/ pg018.html>.

Flatworms *See Platyhelmithes.*

Food Web

All organisms, dead or alive, are potential food sources for other organisms. A caterpillar eats a leaf, a robin eats the caterpillar, a hawk eats the robin. Eventually, the tree and the hawk also die and are consumed by decomposers.

Organisms in an ecological community are related to each other through their dependence on other organisms for food. In a food chain a producer is eaten by a herbivore that is in turn eaten by a carnivore. Eventually, the carnivore dies and is eaten by a decomposer. For example, in a lake, phytoplankton are eaten by zooplankton and zooplankton are eaten by small fish. The small fish are eaten by large fish. The large fish eventually die and decompose. Nothing goes to waste. Food chains are channels for the one-way flow of solar energy captured by photosynthesis through the living components of ecosystems. Food chains are also pathways for the recycling of nutrients from producers, through herbivores, carnivores, omnivores, and decomposers, finally returning to the producers.

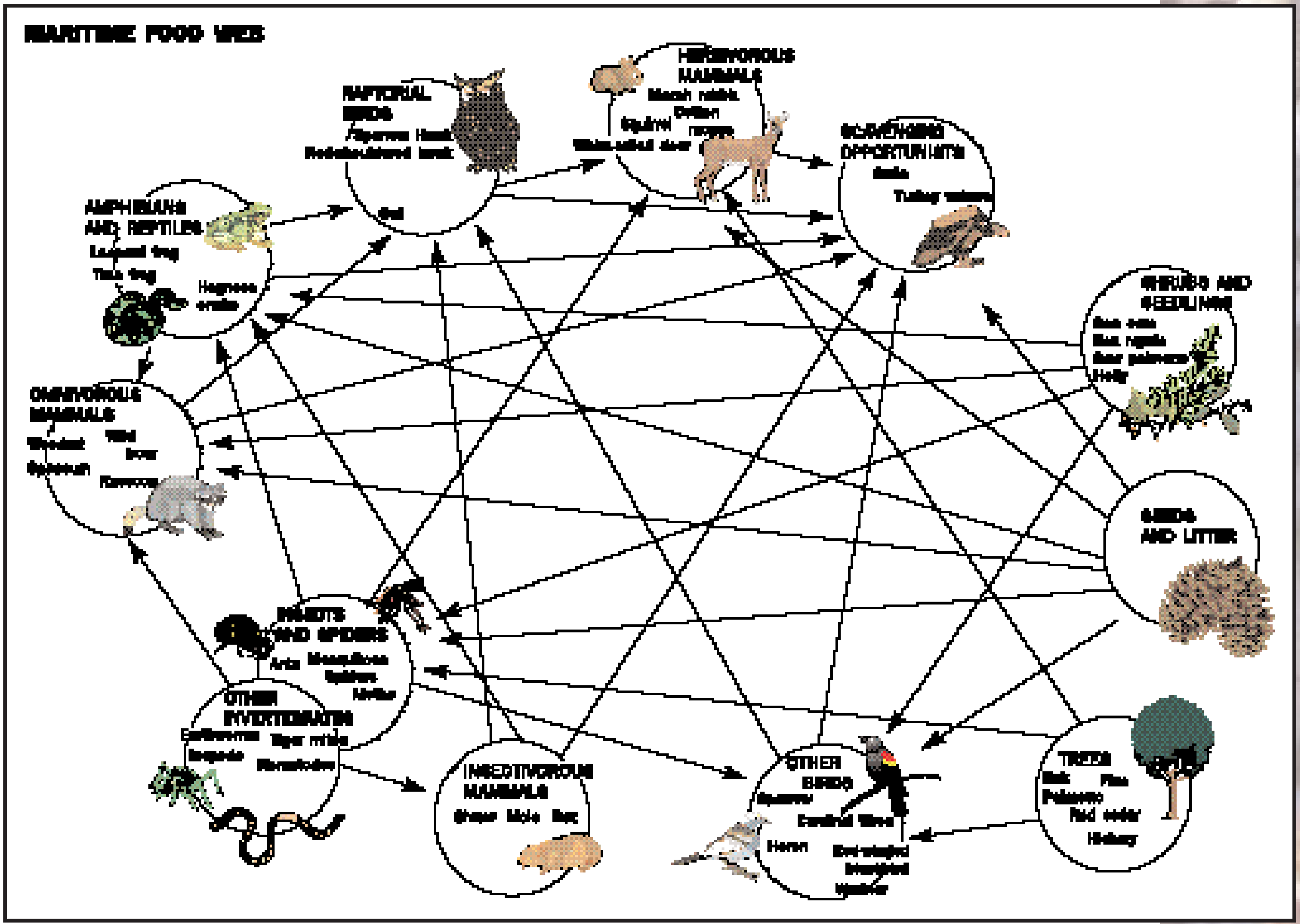
The perfectly linear relations represented by food chains are almost never found in natural ecosystems. Although all organisms have somewhat specialized diets, most can eat a variety of different foods. Thus, each **trophic level** appears as part of several different interconnected food chains. These food chains combine into highly complex food webs.

As with food chains, a food web's source of energy is the sun. The solar energy is harvested by producers such as green plants or algae. These producers are known as **autotrophs** or **photosynthesizing autotrophs**. Al-

trophic level division of species in an ecosystem by their main source of nutrition

autotrophs organisms that make their own food

photosynthesizing autotrophs animals that produce their own food by using sunlight to convert other substances to food



most all other organisms obtain their energy, directly or indirectly, from the sun. The exceptions are the communities found around deep ocean thermal vents, which are supported by various bacteria that convert heat energy into stored chemical energy. These bacteria are known as **chemotrophs** or **chemosynthetic autotrophs**.

This maritime food web demonstrates how the different elements of an ecosystem depend upon one another.

Autotrophs are always found at the first trophic level. In an ecosystem this trophic level may include monerans, protists, and several different phyla of plants. They can all be placed at the first trophic level because they all have the same source of energy, and the entire food web depends on the energy harvested by them. For example, in a grazing food web, a herbivore eats living plant tissue and is eaten in turn by an array of carnivores and omnivores. Herbivores and the carnivores that prey on them are known as **heterotrophs**. In contrast, a detrivore (also a heterotroph) harvests energy from dead organic material and provides energy for a separate food chain.

Each step in a food web or food chain involves a transfer of matter and energy (in the form of chemical bonds stored in food) from organism to organism. Thus food webs are energy webs because the relationships represented by connections in the web represent the flow of energy from a group of organisms at one trophic level to another group of organisms at a different level. Because energy is lost (as waste heat) at each step, food chains rarely involve more than four or five steps or trophic levels.

chemotrophs animals that make energy and produce food by breaking down inorganic molecules

chemosynthetic autotrophs an organism that uses carbon dioxide as a carbon source but obtains energy by oxidizing inorganic substances

heterotrophs organisms that do not make their own food

At each level the organisms waste much energy in the form of heat generated by normal activity. Only a fraction is stored as food or used for growth. Only about 10 percent of the food entering a link is available for the next organism in the chain. After about five links, there is insufficient energy to support a population of organisms (other than decomposers). For example, in the food chain starting with diatoms and ending with killer whales, only about 0.01 percent of the initial energy stored by the diatoms is delivered to the killer whales.

Energy flow through a food web depends greatly on the nature of the producers at the first trophic level. These are usually photosynthetic plants, phytoplankton, or algae. In forest ecosystems, trees are the largest and most abundant organism. They determine the physical structure of the ecosystem, and they can be eaten directly by small or even very large animals. However, much of the matter and energy harvested by the trees goes to build a supporting structure. These supporting structures are composed of cellulose and other wood fibers that are poor sources of energy (although they may be good sources of valuable minerals and other nutrients).

In contrast, grasses do not invest much energy in supporting structures, so more energy is available per kilogram of plant material present to the grazers that obtain energy from plants. Consequently, all of the aboveground parts of the grass plants are eaten by herbivores.

detritus dead organic matter

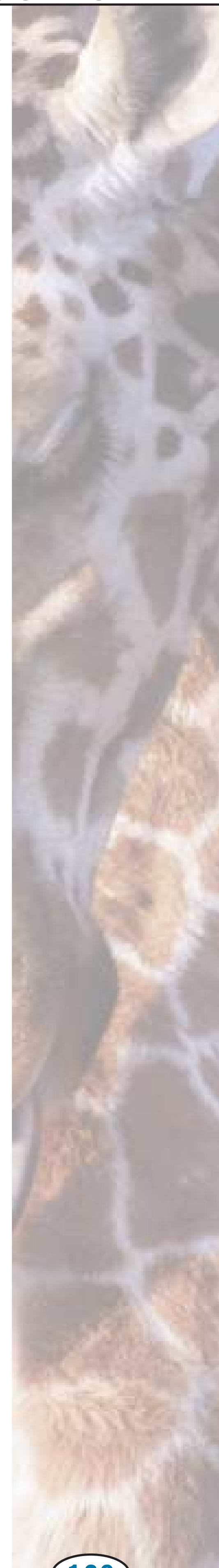
Energy spreads out through the food web, from the lowest trophic level to the highest. At the "top of the food chain," large carnivores harvest the remaining energy. However, all things eventually die, no matter where they are in the food web, and the dead organic matter accumulates in the soil, lake bottom, or forest floor. This **detritus** becomes the basis for a completely different ecosystem, the detritus food web.

Detritus feeders and decomposers harvest solar energy from the detritus by breaking down the organic material into simpler organic compounds and inorganic compounds. By this process, the matter is recycled and made available for reuse by plants. The detritus food web is vitally important to all ecosystems on Earth. Without it, dead organic matter would accumulate and bury everything.

Humans are omnivores. They can operate on several trophic levels, eating plants, insects, mammals, birds, fish, mollusks, and many other organisms. Humans can also shorten the food chain when resources are scarce. In areas of the world where the population may be straining resources, people commonly increase the total food supply by eliminating one or more steps in the food chain. For example, to obtain more energy humans can switch from eating herbivores that obtain their energy from cereal grains to eating the cereal grains themselves.

keystone species a species that controls the environment and thereby determines the other species that can survive in its presence

The food web does not tell us everything there is to know about the complex biological communities called ecosystems. Not all relationships are equally important in these dynamic, evolving communities. Food webs contain both strong and weak links. Weak links can often be broken with little impact on the community. On the other hand, some species have a disproportionately large effect on the community in which they occur. Called **keystone species**, they help to maintain diversity by controlling populations of



species that would otherwise come to dominate the community. Or they may provide critical resources for a wide range of species.

For example, in the intertidal communities of the Northwest Pacific coast of North America, the starfish *Pisaster ochraceus* feeds on the small mussel *Mytilus californius.* Experiments have shown that when the starfish is artificially removed, the population of mussels explodes, soon covering all available space. Other species are crowded out. The interaction between *Pisaster* and *Mytilus* helps to maintain the species diversity of these intertidal communities.

Research has shown that ecological communities with complex feeding relationships have greater long-term stability and are less affected by external stresses. This suggests an evolutionary basis for the diverse and complex ecological relationships found in many communities of organisms. However, humans often violate this sound ecological principle in order to increase agricultural productivity by creating artificial ecosystems that contain only one plant, such as corn. These systems are called **monocultures**. While greater agricultural productivity is possible with monoculture crops, they are very unstable ecosystems. Disease, drought, or a new insect pest can easily destroy an entire year's harvest. SEE ALSO BIOMASS; FEEDING; FEEDING STRATEGIES; TROPHIC LEVEL.

monocultures cultivation of single crops over large areas

Elliot Richmond

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth, 1989.

Miller G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth, 1990.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology*. Sunderland, MA: Sinauer Associates, 1987.

Foraging Strategies

The term "forage" means to wander in search of food. Every animal has a particular method of locating food, whether they smell it, find it by sight, or detect it by chemical means. Animals seek out food both individually and in groups.

Collecting food as efficiently as possible allows a species to propagate its genes more effectively. The optimal foraging theory, developed by Robert H. MacArthur and E. R. Pianka, states that food gatherers that do a better job of increasing the benefits and of decreasing the costs of foraging should procreate more effectively than those whose feeding activities yield lower net benefits. Foraging decisions are, in effect, cost-benefit problems that animals have to solve.

Food, whether animal or vegetable, provides stimuli that predators can detect. Waste products of animals give off olfactory signals that help predators locate their next meal. For example, when dung-eating beetles smell far-off feces, they quickly take to the air and forge their way along the odor trail leading straight to their primary food source. A more highly specialized adaptation involves the urine and dung of the vole, a small rodent, which does more than release olfactory signals. The waste products of the vole reflect a certain amount of ultraviolet radiation that is invisible to the

This garden dormouse forages for a pear. Animals have a wide variety of foraging methods that are dictated by sight, sense, and smell.

human eye but is clearly evident to the kestrel, a small hawk. From the air the kestrel can detect the ultraviolet markings left by the vole, which increases the kestrel's hunting success.

Foragers do not always work alone. Sometimes their companions inform them of food locations. Social insects such as bees, wasps, ants, and termites have evolved incredible techniques for transferring this kind of information. Probably the most fascinating is the complex dance of the honeybee. It is performed when a forager has found pollen or nectar and has returned to the hive. Depending on the distance and direction of the food source in relation to the sun, the honeybee will perform either a waggle dance or a round dance. The round dance informs other worker bees that a food site is located within fifty meters of the hive. The waggle dance, depending on the number of abdomen waggles and direction faced when waggling, illustrates both the distance and the direction of a food source in relation to the hive. Karl von Frisch spent twenty years experimenting with bees that he had trained to visit particular feeding stations. By studying their dances he determined that their behavior changed significantly depending on the distance and direction of a food source's location.

What about solitary animals who go unaided in the search for prey? Some rely on deceitful measures to catch their dinner. One ingenious method is used by the bolas spider (*Mastophora dizzydeani*), which releases a scent identical to the sex pheromone of certain female moths. When the male moth of the species goes in search of a mate, he may encounter instead a bolas spider armed with a sticky globule attached to a long, silken thread. The spider throws the blob, hits the moth, and then feasts on the captured prey. By employing the deceptive scent, the bolas spider lures insects within attack range. This maximizes the spider's success rate while reducing its energy output.

fauna animals

Because of potentially toxic foods, predators must pay attention to warning coloration and behavior of **fauna** prey and carefully avoid more difficult-to-detect toxins in flora. Herbivores must be able to determine whether the plant they have selected to eat has low concentrations of toxic terpenoids—poisons that many plants incorporate into their tissues to repel consumers.

A study of the **herbivorous** Costa Rican howler monkeys illustrates how some animals deal with this problem. Foraging very carefully, these monkeys avoid toxic leaves and those low in nutritional value. Although the choices they make in selecting particular leaves may raise the costs of foraging, they ingest fewer poisons and more usable proteins. For example, howlers tend to avoid foraging in common tree species, opting instead to eat the leaves from scarcer species. These preferred tree species, it turns out, have lower levels of alkaloids and tannins. Alkaloids are poisonous to howlers, and tannins make leaves harder to digest. Also, the monkeys tend to feed on only the petiole—the leaf part lowest in toxins—while discarding the more toxic leaf blade.

herbivorous describes animals who eat plants

The optimality theory does not always work in a clear-cut fashion. Some animals must balance the cost of consuming more food per unit of foraging time against the risk of becoming food themselves. For instance, the hoary marmot, a relative of the groundhog, stays close to its burrow on rocky slopes and feeds primarily on the heavily grazed margin of meadow located nearby rather than venturing further into greener pastures. This reduces its risk of becoming prey for an eagle or coyote. Thus, it spends more time looking out for food than for danger. Although this may compromise foraging efficiency in caloric or nutritional terms, it keeps them alive. Whirligig beetles behave in much the same way, restricting their movements to the dense cluster of beetles that form on the water's surface. In this way, they steer clear of being eaten yet sacrifice foraging opportunities that exist beyond the safety of numbers. SEE ALSO FEEDING; FEEDING STRATEGIES.

Ann Guidry

Bibliography

Alcock, John. *Animal Behavior*, 6th ed. Sunderland, MA: Sinauer Associates, 1998.

Alexander, R. McNeill, ed. *Encyclopedia of Animal Biology*. New York: Facts on File, 1987.

Burton, Robert, ed. *Animal Life*. New York: Oxford University Press, 1991.

Whitfield, Philip, ed. *Macmillan Illustrated Animal Encyclopedia*. New York: Macmillan, 1984.

Fossey, Dian

American Primatologist
1932–1985

Dian Fossey, born in 1932, was a celebrated mountain gorilla researcher. Fossey initially dreamed of becoming a veterinarian, but her science grades prevented her from pursuing that goal. A fairly antisocial person, she got along well with children and animals as an occupational therapy intern before making her way to Africa at the age of thirty-one. There she was immediately captivated, and she became acquainted with renowned anthropologist Louis Leakey, who was engaged in research. Impressed with her attitude, Leakey sent her to eastern Congo in 1966, and Africa became the setting of her life's work.

Scientist Dian Fossey was well-known for her pioneering work with gorillas.

Fossey enjoyed working in Africa despite horrifying conditions. Shortly after her arrival in the Republic of Congo (later Zaire), the country became embroiled in civil war, and she later escaped to Rwanda. Despite the tense political situation and other extreme difficulties (poachers, disease, lack of funding, and so on), Fossey vigorously protected her subjects of choice, mountain gorillas. She quickly got closer to them than other researchers and managed to become accepted among them. Although some critics argued that her methodology was unscientific, saying it was unquantifiable, Fossey logged thousands of contact hours and observations, frequently finding new groups of animals to work with.

Louis Leakey believed women were better suited than men to observe and note animal behavior because he thought women were more patient.

Fossey also worked to keep the gorillas' habitat intact. Frequent invasions by poachers and cattle herdsmen destroyed what little mountain gorilla habitat remained. Fiercely independent, she was unwilling to compromise her activities or research methods despite the conflicting opinions of others.

In 1973, Fossey left Africa to begin her graduate studies at Cambridge. After earning her Ph.D in 1976, she was a visiting professor at Cornell University from 1980 to 1982. She also took this time to write *Gorillas in the Mist*, a firsthand account of her experiences. It became an enormously popular book although it was less well received by other primatologists. She returned to Africa in 1983, convinced that her methods of **poaching** prevention would best serve the gorilla population.

poaching hunting outside of hunting season or by using illegal means

In 1985, Fossey was murdered, most likely by poachers. Since her death, there have been few poaching incidents and the mountain gorilla population has been growing. Fossey brought the plight of the mountain gorilla to public consciousness and left behind the Dian Fossey Gorilla Fund for their protection. SEE ALSO Primates.

Ian Quigley

Bibliography

Hayes, Harold T. P. *The Dark Romance of Dian Fossey.* New York: Simon and Schuster, 1990.

Fossey, Dian. *Gorillas in the Mist.* Boston: Houghton Mifflin, 1983.

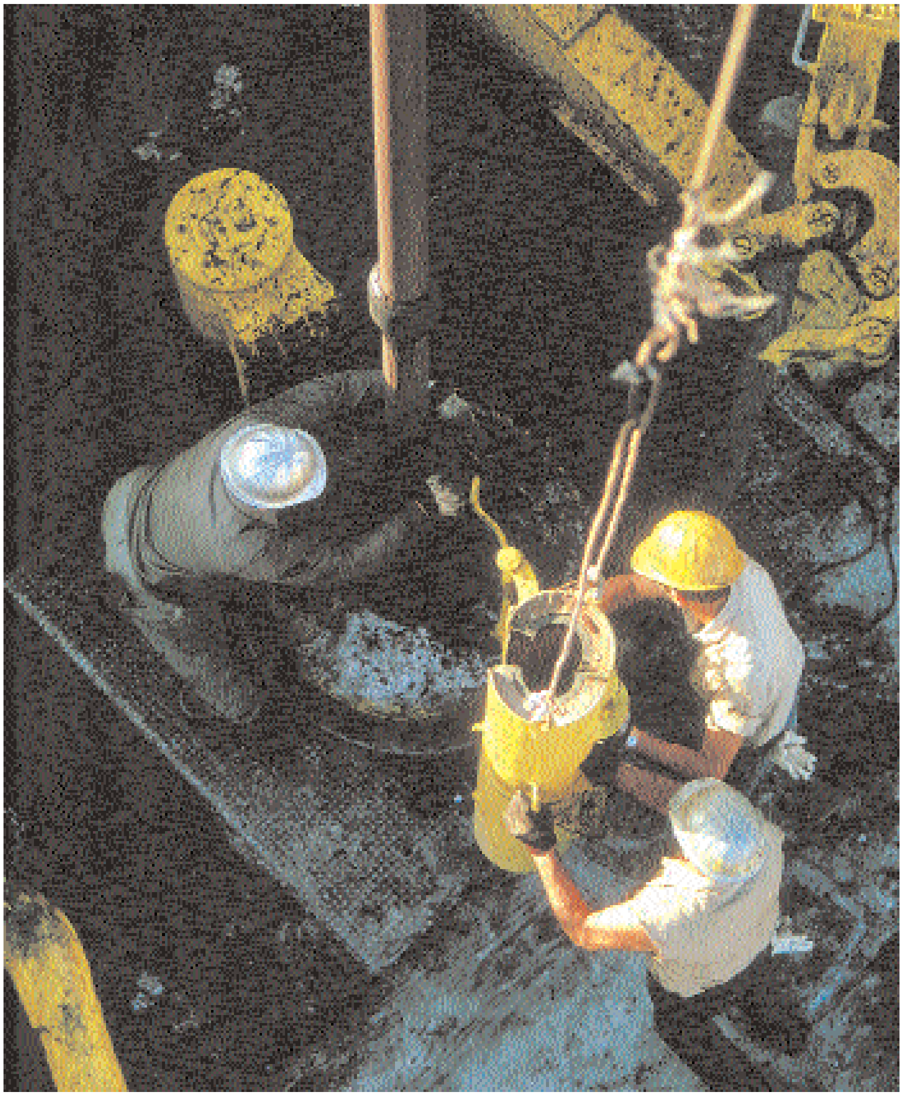
Internet Resources

The Dian Fossey Gorilla Fund International. <http://www.gorillafund.org>.

Fossil Fuels

Fossil fuels are buried deposits of plants and animals that have been converted to coal, petroleum, natural gas, or tar by exposure to heat and pressure in the Earth's crust over hundreds of millions of years. The energy in fossil fuels comes from sunlight, either directly or indirectly.

Coal comes primarily from the remains of plants that were buried in anaerobic conditions (without oxygen). Coal ranges from 55 percent to 90 percent carbon mixed with water and other substances including compounds of nitrogen and oxygen. Coal is graded according to hardness and carbon content. The lowest grade, lignite, is soft and brown in color. The hardest, anthracite, is nearly pure carbon. It is so hard it can be polished like a gemstone.



Workers drilling for gas. Natural gas is usually found in varying amounts, along with crude oil and with coal.

Petroleum (crude oil) is a liquid containing primarily hydrocarbon compounds along with small amounts of compounds containing oxygen, sulfur, and nitrogen. Crude oil originates with the buried remains of various types of plankton, primarily diatoms. It varies in consistency from a thin liquid the color of port wine to a thick, black, tarlike substance that must be heated before it will flow. Crude oil is the source of gasoline, jet fuel, diesel, heating oil, bunker oil, plastics, and other compounds.

Natural gas is usually found in varying amounts along with crude oil and with coal. It is also found by itself. Natural gas consists of a mixture of methane (CH_4) and other hydrocarbons such as ethane (C_2H_6), propane (C_3H_8), and butane (C_4H_{10}). Methane is a natural byproduct of the anaerobic decomposition of organic remains.

Oil and Natural Gas

Petroleum ranges in quality from a relatively thin, free-flowing liquid called light or sweet crude to a thick, gooey black liquid with high sulfur content called heavy or sour crude. Because sweet crude is cleaner to burn and easier to transport, it is more valuable. Some oil flows naturally to the surface but most must be pumped. After primary recovery, hot water, steam, or high-pressure carbon dioxide can be injected into adjacent wells to force out some additional wells. Only about one-third of the oil can be extracted in primary and secondary recovery.

Oil, a useful fuel that can power automobiles, trucks, and airplanes, is a relatively inexpensive energy source. It has a high energy content and is easily transported. However, most experts expect little of the world's original oil reserves to remain by the middle of the twenty-first century. If world oil consumption increases at a rate of 2 percent per year, 80 percent of the world's supply will be used up by 2037.

When natural gas deposits are tapped, the gas is pressurized, which causes the propane and heavier hydrocarbons to liquefy. This liquefied petroleum gas (LPG) is stored in pressurized tanks and used in rural areas where natural gas supplies are not available. The remaining gas, mostly methane, is dried, cleaned of hydrogen sulfide, and distributed through pressurized pipelines.

Natural gas is a very clean-burning substance. If the gas is properly treated to remove sulfur and other contaminants, combustion products consist of water and carbon dioxide. Natural gas burns hotter and produces less pollution than any other fossil fuel.

The U.S. Department of Energy has estimated that all known and unknown reserves of natural gas will last until 2045 at present levels of consumption. If consumption rises by 2 percent per year, natural gas reserves will be depleted by 2022.

Coal

Coal is the world's most abundant fossil fuel. The United States, China, and Russia contain about two-thirds of known and estimated undiscovered coal reserves. Much of that coal contains large amounts of sulfur. When coal containing sulfur is burned, sulfur dioxide is created. Sulfur dioxide is one of the primary components of acid rain, so it is a pollutant. It is very difficult to remove the sulfur before the coal is burned, so the sulfur must be removed from the stack gases. Removing the sulfur is costly, although part of the cost can be recovered by selling the byproduct, sulfuric acid. World reserves of coal will last 220 years at current consumption rates and 65 years if consumption rates increase by 2 percent per year. Identified coal reserves in the United States will last about 300 years at current consumption rates.

Coal must be extracted by mining, the most environmentally destructive and expensive form of extraction. The least expensive form of mining is strip mining. The layer of rock and soil over the coal is removed by heavy machines, the coal is extracted by other heavy machines, and the rock and soil are replaced. Existing laws require that strip-mined land be returned to its original contour and replanted in suitable ground cover. When properly done, this restoration leaves the land in good condition.

Unfortunately, much of the land that was strip-mined before the laws were passed has not been restored. This results in erosion and pollution. Much of the coal that can be strip-mined in the United States is in the arid west, where restoration is more difficult and expensive. These requirements have made coal more expensive. Since natural gas is cheaper and burns cleaner, most new electric power plants being built are gas-fired.

Carbon Dioxide

All fossil fuels represent millions of years of stored solar energy. Plants remove carbon dioxide from the air and use the energy of sunlight to separate the carbon from the oxygen. The oxygen is released and the carbon is used to build carbohydrates, fats, and proteins. The carbon stored in fossil fuels is the result of this process. When fossil fuels are burned, this process is reversed. Oxygen from the air combines with carbon in the fossil fuels to form carbon dioxide, which is released into the atmosphere. Carbon dioxide levels in the atmosphere have been increasing steadily since the beginning of the industrial revolution. Most scientists now think that these increasing levels of carbon dioxide in the atmosphere are contributing to **global warming** through a process known as the **greenhouse effect**. SEE ALSO Global Warming.

global warming a slow and steady increase in the global temperature

greenhouse effect a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

Elliot Richmond

Bibliography

Miller G. Tyler, Jr. *Living in the Environment.* 6th ed. Belmont, CA: Wadsworth, 1990.

Fossil Record

Geologists and other scientists use fossils to correlate the ages of different rock strata (thin layers or beds of rock that differ in some way from adjacent layers) in different places on Earth. If two different rock strata contain the same set of fossil species, then the two different rock strata were probably deposited about the same time. Fossils also can give clues about the environment of Earth in the past. For example, certain fossils are only found in the ocean. When these fossils are found in a rock strata, it is a sure sign that the rock strata was deposited in an ocean even if it is now on top of a high mountain.

Fossils can also help to establish the relative ages of rocks (which rocks are older and which are younger). If a fossil species can be assigned an absolute date by radioactive dating, then that same fossil species can be used to help determine the absolute dates of other rocks that contain it. The fossil record also gives clues as to how life has evolved.

A fossil is any preserved remains of ancient life. There are several different categories of fossils. Trace fossils include such things as tracks, burrows, and coprolites (fossilized excrement). Body parts or whole bodies of organisms can be preserved by a process known as mineralization, in which minerals gradually replace the organic remains and the fossil is turned to stone.

Molds, casts, and imprints make up another category of fossils. They are formed when the sediment has solidified about an organic object and the object is subsequently dissolved, leaving a hole in the rock—a mold. Deposition of mineral matter from underground solutions may fill the hole, producing a cast. Molds of thin objects (such as leaves of ferns often found in coal) are called imprints.

Organisms with hard tissues are more likely to be preserved. Organisms that are more abundant are more likely to be preserved. Organisms that live in swamps or near water are less likely to decay when they die and are more likely to be preserved. All these factors make the fossil record somewhat incomplete. Nevertheless, the fossil record extends back at least 3.5 billion years. During this immense span of time, tens of millions of different species have lived on Earth.

superposition the order in which sedimentary layers are found with the youngest being on top

sedimentary rock rock that forms when sediments are compacted and cemented together

The fossil record can also be used to determine the ages of rocks. The geological principle of **superposition** states that if rock layers are undisturbed, older rock layers are found below younger layers. If the rock layers contain fossils, then the relative ages of those fossils can be determined from the relative ages of the rock in which they were found. Then those same fossils can be used to help determine the relative ages of rocks found elsewhere. A bed of **sedimentary rock** can be identified by its fossils.

Using these ideas, geologists working in the first part of the nineteenth century at many different places gradually developed a theory of the history of life on Earth. This life history is now known as the geological time scale. Although the early researchers dramatically underestimated the age of Earth, they did establish the principle of determining the age of rocks by looking at the fossils found in those rocks.

Even a superficial examination of the fossil record shows that many species existed in the distant past that no longer exist today. Likewise, even an incomplete fossil record reveals that species living today did not exist in the distant past. Thus the fossil record and the geological time scale provided the background for Charles Darwin and other scientists to develop their theories of evolution. SEE ALSO BIOLOGICAL EVOLUTION; GEOLOGICAL TIME SCALE; MORPHOLOGICAL EVOLUTION IN WHALES; TETRAPODS—FROM WATER TO LAND.

Elliot Richmond

Bibliography

Dott, Robert H., Jr., and Roger L. Batten. *Evolution of the Earth*, 3rd ed. New York: McGraw-Hill, 1994.

Faul, Henry, and Carol Faul. *It Began with a Stone: A History of Geology from the Stone Age to the Age of Plate Tectonics.* New York: John Wiley & Sons, Inc., 1983.

Foster, Robert. *Geology*, 3rd ed. Columbus, OH: Charles E. Merrill, 1976.

Schneer, Cecil J. "The Rise of Historical Geology in the 17th Century." *Isis.* 45, no. 141 (1954):256–268.

Stanley, Stephen. *Earth and Life through Time.* New York: W. H. Freeman & Co., 1989.

Toulmin, Stephen, and June Goodfield. *The Discovery of Time.* New York: Harper & Row, 1965.

Fruit Fly *See Drosophila.*

Functional Morphologist

Functional morphology is a relatively new field in biology. Morphology is the study of the size, shape, and structure of animals, plants, and microorganisms, and the relationships of their internal parts. Unlike anatomy, morphology is not just simple description. It also involves the principles according to which form are related. The organizing principles used by morphology include evolutionary relations, function, and development.

The functional morphologist studies how the shape, or morphology, of an organism or some part of an organism relates to its function. For example, there is a relationship between the shape of a tree and how it is affected by wind. Tall trees grow in protected valleys and can shelter each other. Bristlecone pines, which tend to be small and sturdy, grow where the soil is thin and the wind blows constantly. The form of a bird's wing is related to the speed and manner of its flight. Swifts and falcons are unrelated birds, but both have narrow, sharply pointed wings, ideally suited for rapid flight.

Peregrine falcons have long, slender and pointy wings. Functional morphologists have deduced that the shape of their wings evolved to their present shape to allow the birds to fly quickly.

Functional morphologists study motion, support structures, energetics of motion, neural control of locomotion, and motion occurring at the cellular and molecular levels. Fluid flow in cardiovascular systems, fluid flow in respiration, and feeding strategies are all part of functional morphology. Research in functional morphology is multidisciplinary and has applications in ecology, evolution, and medicine.

A functional morphologist will usually have studied biology with a heavy emphasis in anatomy courses as an undergraduate student. Some physics or even engineering courses are also useful. At the graduate level, courses in biomechanics, comparative vertebrate anatomy, comparative physiology, mathematical and computer modeling, and advanced mechanics are necessary preparation for functional morphology, and the student will also specialize in an area, such as fish feeding behaviors or the mechanics of shark movement.

Elliot Richmond

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates Inc., 1987.

Functional Morphology

Functional morphology involves the study of relationships between the structure of an organism and the function of the various parts of an organism. The old adage "form follows function" is a guiding principle of functional morphology. The function of an organ, appendage, tissue, or other body part dictates its form. Furthermore, the function can often be deduced from the form. The idea of relating form and function originated with the French naturalist Georges Cuvier (1769–1832).

The primary task of functional morphology is observing living organisms to see how they live and function. From observations of living organisms, scientists also attempt to discern principles that will allow them to determine function from the forms of fossils, such as bones, shells, or whatever happens to be preserved from organisms that no longer exist.

Theoretical morphology tries to determine the limits of form; not every conceivable form could actually exist in nature.

Functional morphology studies the ways in which structures such as muscles, tendons, and bones can be used to produce a wide variety of different behaviors, including moving, feeding, fighting, and reproducing. Functional morphology integrates concepts from physiology, evolution, development, anatomy, and the physical sciences, and synthesizes the diverse ways that biological and physical factors interact in the lives of organisms. Functional morphology and biomechanics allow scientists to observe and quantify not only how animal skeletons and joints move and how muscles work but also how these things relate to the diversity of animal behaviors.

Functional morphology helps to understand the form of modern animals. For example, even casual observation reveals that elephants have very thick legs relative to their body size when compared with smaller animals such as antelope or horses. This is not just a fluke of nature's design; elephants need thick legs to hold up their body mass. But why are the legs of an elephant proportionately thicker than the legs of smaller animals?

The mass of an object is related to its volume. Imagine an animal, an elk for example, scaled up to be twice as tall (about the height of an elephant) while keeping all proportions the same. An animal twice as tall as another animal of a similar shape will have much more than twice the volume. Because it is also twice as long and twice as wide, the scaled-up elk will have eight times as much volume as the normal-sized elk. Assuming bone and muscle density remain about the same, the scaled-up elk will also have eight times as much mass. However, the legs of the larger elk will only have four times the area of the legs of the normal-sized elk.

According to the principles of engineering, the strength of a column of bone and muscle is proportional to its cross-sectional area. Legs with only four times the cross-sectional area will not be strong enough to hold up eight times the weight. To hold up the scaled-up elk, its legs must be proportionately thicker than the legs of the normal-sized elk. Consequently, in order to attain the great size they have, elephants had to evolve legs proportionately much thicker than those of smaller animals.

Elephants also have large ears. Functional morphology helps to understand this feature as well. As elephants evolved to larger body size, the area of their skin did not increase as rapidly as their volume. Thus, the elephant's skin could not dissipate enough heat to keep the elephant cool. The elephant's relatively large ears, however, significantly increase its ability to give off heat. Forest elephants live in somewhat cooler environments, so their ears are not as large as elephants that spend more time in the sun.

Functional morphology also helps to understand the limits on the size of cells. If a spherical bacterial cell grows to twice its original size, it has eight times the volume but only four times the surface area. Because the cell absorbs nourishment through its surface, it must sustain eight times as much mass with only four times as much nourishment. At some point, a cell will become so large that it cannot absorb enough materials to sustain its mass, and it will then divide. SEE ALSO ALLOMETRY.

Elliot Richmond

FUNCTIONAL MORPHOLOGY

A couple walk hand in hand along the beach. Suddenly an ant appears at the top of a sand dune, scaring the wits out of the couple. This is no ordinary ant, this is a *giant* ant the size of an elephant! Since ants are extremely strong for such small animals, this gigantic ant must be unbelievably strong, able to throw automobiles around like toys, right? Actually, no. As an object increases in size, its weight grows much faster than its strength. When an object doubles in size, it becomes four times as strong, but eight times as heavy. The thin legs of the ant are strong enough to support several times its own weight. However, if the ant were scaled up to be as tall as an elephant, its legs would be too flimsy to hold up its own weight.

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Cuvier, Georges. *Memoirs on Fossil Elephants and on Reconstruction of the Genera* Palaeotherium *and* Anoplotherium. New York: Arno Press, 1980.

Gould, Stephen J. *The Panda's Thumb.* New York: Norton, 1980.

Huxley, Julian S. *Problems of Relative Growth*. New York: Dial Press, 1932.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates Inc., 1987.

Thompson, D'Arcy W. *On Growth and Form.* Cambridge: Cambridge University Press, 1942.

Genes

A common feature of organisms is that offspring tend to look like their parents. For example, tall, brown-eyed parents tend to have tall, brown-eyed children. The mechanism by which parents pass on particular traits to their offspring is termed **heredity**. The focus of the following entry will be to explore the role of genes in heredity.

heredity the passing on of characteristics from parents to offspring

What Is a Gene?

Originally, most biologists believed in "blending inheritance," where the joining of a sperm from the father and an egg from the mother yields offspring which have characteristics that are a blend of the characteristics of the two parents. However, Austrian botanist Gregor Mendel's (1822–1884) pioneering work with inheritance in pea plants largely disproved this theory. Mendel showed that for many traits, when a pea plant with one trait (e.g., green pods) is bred to a pea plant with another trait (e.g., yellow pods), the offspring always look like one of the parental types, never a mixing of both (e.g., yellow-green pods are never seen). Mendel proposed that traits are inherited in a "particulate" manner. Parents transmit individual hereditary units to their offspring, and the particular combination of these units in an offspring controls how that offspring will look. These hereditary units are now known as genes. Thus the science of heredity is termed **genetics** and the overall genetic makeup of an organism is termed its **genotype**. The genotype determines the types of traits an organism will have, otherwise known as the organism's **phenotype**.

genetics the branch of biology that studies heredity

genotype the genetic makeup of an organism

phenotype the physical and physiological traits of an animal

Most organisms are diploid, that is, they have two copies of every gene. Different forms of a particular gene are known as **alleles**. In the example above, the gene for pod color had two alleles, green and yellow. Diploid parents make **haploid** eggs and sperm, meaning those gametes have only one copy of each gene. Thus when the egg and sperm fuse, the resulting offspring is a diploid, having one copy of each gene from both parents. An offspring with two copies of the same allele for a particular gene is called a **homozygote**, while an offspring with two different alleles for a particular gene is called a **heterozygote**.

alleles two or more alternate forms of a gene

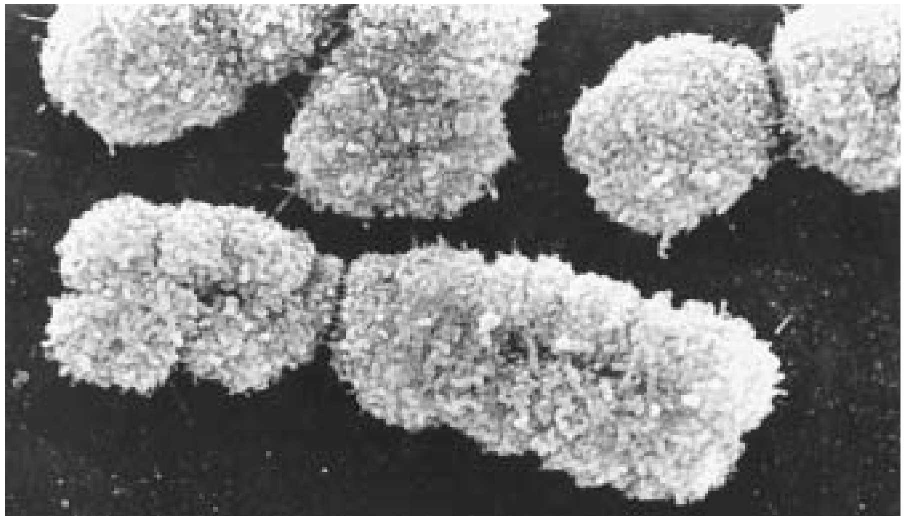
haploid cells with only one set of chromosomes

homozygote an animal with two identical alleles for one trait

heterozygote an organism whose chromosomes contain both genes of a contrasting pair

When an offspring receives different alleles of a particular gene from its parents (e.g., a yellow pod allele from its mother and a green pod allele from its father), one allele is typically **dominant** over the other. In our

dominant an allele that is always an expressed trait



Genes are passed through human reproductive chromosomes, such as these X-chromosomes.

example, green pod is dominant over yellow pod so that an individual with both color alleles will always have green pods. The nondominant allele is known as the **recessive** allele.

recessive a hidden trait that is masked by a dominant trait

Although uncommon, some pairs of alleles do not behave in a completely dominant or recessive manner. For example, the flowers of snapdragons typically come in two colors, red and white. Mating a red-flowered plant with a white-flowered plant yields pink-flowered offspring, which would be expected under the blending inheritance theory. To show that Mendel's laws still hold, a cross may be made between a pink-flowered plant and a white-flowered plant. A proponent of the blending inheritance theory would predict that all offspring from this cross would have light pink flowers, whereas in fact half the offspring have white flowers and the other half have the original pink. When the phenotype of the heterozygote is a combination of the phenotypes of homozygotes for those two alleles, the alleles are said to show **incomplete dominance**.

incomplete dominance a type of inheritance where the offspring have an intermediate appearance of a trait from the parents

codominance an equal expression of two alleles in an heterozygous organism

antigen foreign substances that stimulate the production of antibodies in the blood

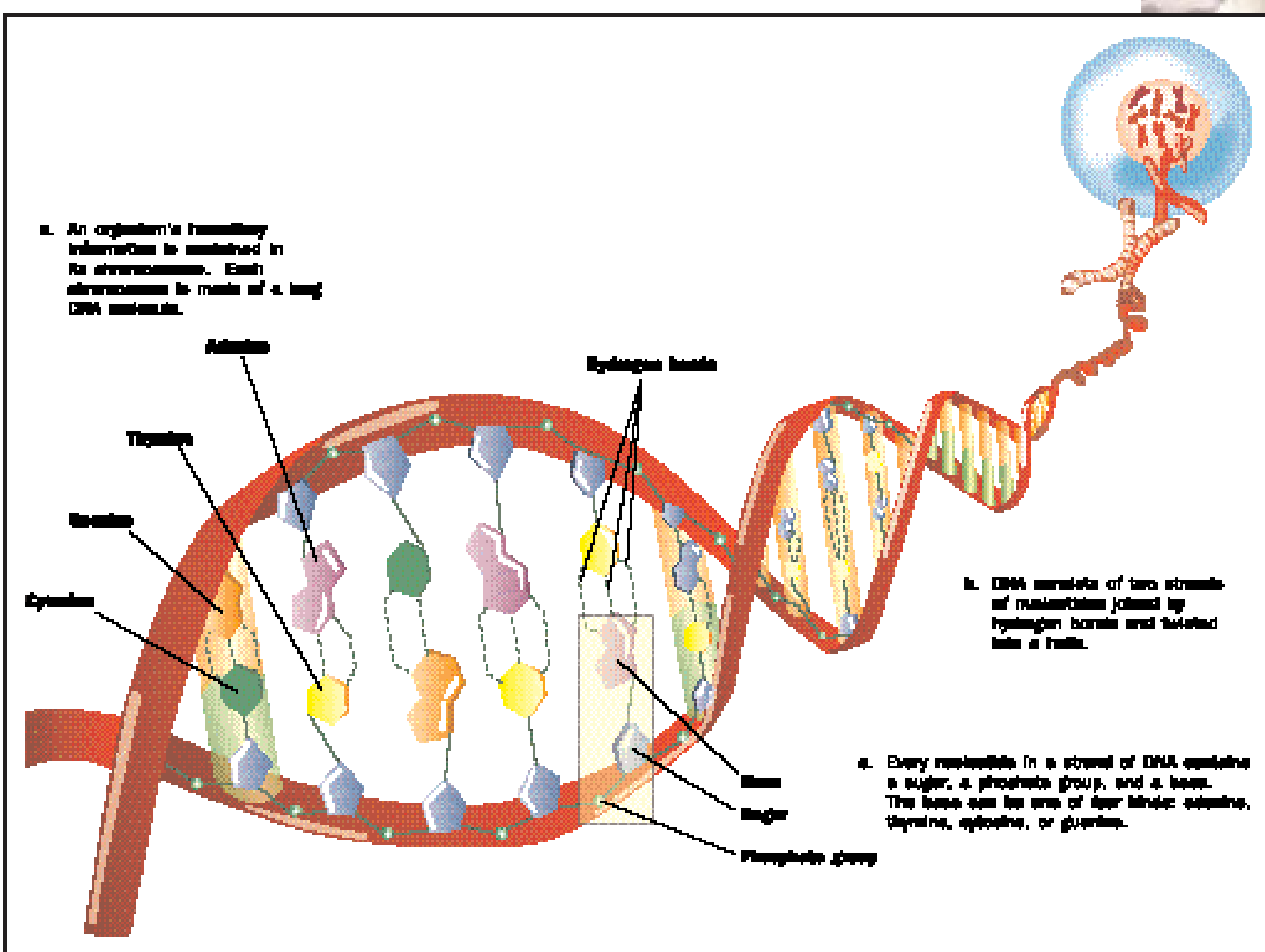
genome an organism's genetic material

Codominance occurs when a heterozygote expresses both of the homozygote phenotypes. Take for example the A and B blood groups of humans, which determine the type of **antigen** a blood cell will produce. If a homozygote for A (written AA) mates with a homozygote for B (BB), the offspring will be heterozygous (genotype AB), and will produce both A antigens and B antigens, not a blending between the two.

Other factors may affect whether a normally dominant allele expresses its phenotype. Siamese cats have a dominant black fur allele, but that allele only expresses its phenotype at colder temperatures. These cats tend to have dark ears, paws, and a dark tail but are light-colored in areas of the body closer to the body's warm core. Furthermore, other genes in the **genome**, such as genes that code for modifiers and suppressors, can affect how an allele at one particular gene is expressed.

DNA as the Genetic Material

Because genes control the structural and functional properties of organisms, it became increasingly important to biologists in the early twentieth century that they determine what type of molecules genes actually are. It was



Structure of DNA. Redrawn from Johnson, 1998.

tempting to believe that genes were proteins, as it had been established that proteins are an extremely diverse group of molecules that perform a wide variety of specific functions within cells. However, several lines of study eventually led to the conclusion that genes are made of deoxyribonucleic acid, or DNA.

When a diploid organism makes new cells, the new cells are also diploid and are exact copies of the old cells. The mechanism by which cells replicate is termed **mitosis**. However, when adult organisms mate, they make haploid gametes (eggs and sperm) through a process known as **meiosis**. Scientists worked out the steps by which **diploid cells** make diploid copies (mitosis) and haploid copies (meiosis) in the late 1800s. The difference between mitosis and meiosis lies largely in the sorting in the cell nucleus of chromosomes, condensed strands of DNA packaged with various proteins. Interestingly enough, chromosomes seem to move from one generation to the next in a way that mirrors the movement of genes across generations. In adult cells there are two copies of every chromosome, as there are two copies of every gene. Meiosis yields gametes with one copy of each chromosome, and fertilization of the egg by a sperm restores the chromosome number to its original state, paralleling the fact that one copy of each gene from both

mitosis a type of cell division that results in two identical daughter cells from a single parent cell

meiosis a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

diploid cells cells with two sets of chromosomes parents are fused into their diploid offspring. Thus genes appeared to be associated with chromosomes. Furthermore, later studies showed that particular genes could be mapped to precise locations within chromosomes.

bacterium a member of a large group of single-celled prokaryotes

In the 1920s, a British physician named Frederick Griffiths performed a number of experiments with the **bacterium** that causes pneumonia in humans, *Streptococcus pneumoniae.* Griffiths worked with two strains of the bacteria, one that was virulent and caused disease, and another that was avirulent (not virulent). Griffiths found that the avirulent bacteria, in the presence of extract from the virulent strain, could be transformed into a virulent form. This "transforming agent" was studied intensively by the American bacteriologist Oswald Avery and his colleagues over several years. They were able to destroy various chemicals found in the virulent strain extract so as to be able to test the significance each chemical had on virulence individually. In 1944 they concluded that DNA from the virulent strain extract was the transforming agent.

Further proof that DNA is the molecule of inheritance came in 1952 with the publication of a paper by Alfred Hershey and Martha Chase of the Carnegie Laboratory of Genetics. They studied the bacteriophage T2, a virus that infects bacteria such as *Escherichia coli (E. coli).* It was known that viruses were made almost entirely of protein and DNA, and that some viral component moved into the bacterial cells and caused the bacteria to use its cellular apparatus to make new viruses. Hershey and Chase were able to label the protein component of the virus and the DNA component of the virus in different ways so as to track which component was responsible for controlling the host cell. Their results confirmed that the viral DNA, not protein, was responsible for manipulating the bacterial host cells. It was finally apparent that the genetic material is made of DNA.

How Does the Genotype Determine the Phenotype?

George Beadle and Edward L. Tatum's work on the bread mold *Neurospora crassa* in the 1940s at the California Institute of Technology provided some of the first convincing evidence that the function of genes is to control the production of proteins. *Neurospora* can be grown in the lab on a medium made of a few simple nutrients. However, *Neurospora* mutants that required certain supplements in the medium to be able to grow were known to exist. In these mutants, **enzymes** (proteins that catalyze molecular reactions) that are necessary to the functioning of particular metabolic pathways do not perform properly. Beadle and Tatum irradiated *Neurospora* cells with x-rays to induce a wide variety of mutations that made the *Neurospora* unable to live on the minimal medium. Some of these mutations blocked different steps within the same metabolic pathway. Because the genes controlling different enzymatic steps from the same pathway were mapped to different chromosomal locations, it became clear that particular enzymes correspond to particular genes. In other words, each gene, which is made of DNA, is responsible for the production of one enzyme. It was later shown that genes can "code" for any kind of protein, including enzymes.

enzymes proteins that act as catalysts to start biochemical reactions

nucleotides the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

Biologists quickly focused on determining the structure of DNA to try to gain insight into the actual mechanism whereby genes control the production of proteins. DNA was found to be a double helix made primarily of the four **nucleotides**: adenine (A), cytosine (C), guanine (G), and thymine

(T). The structural makeup of DNA is shared among all living things, suggesting that the different forms of life have a single common ancestor. The process by which DNA specifies the type of protein to be made was labeled the "central dogma of molecular biology." Genes are first copied from DNA to RNA (ribonucleic acid) in a process termed **transcription**. This RNA, which is referred to as **messenger RNA** or mRNA, then specifies the formation of proteins in a process termed **translation**. Translation involves the breaking up of the DNA into **codons**, combinations of three nucleotides in a row. Each combination of three bases (e.g., ATG, TCA, ...) encodes a particular amino acid, the building blocks of proteins. So, despite the small number of nucleotide types that make up DNA, sequences of these nucleotides code for the wide variety of proteins found in organisms.

The Structure of Genes

In eukaryotes (organisms that possess membrane-bound **organelles** such as a nucleus), genes are typically made up of **exons** and **introns**. Exons are regions of the gene that code for protein (the codons), while introns are regions of the gene that are transcribed into mRNA but are spliced out before the translation stage. Introns are thought to have evolved to allow exon shuffling, the process whereby an exon from one allele of a gene in a heterozygote may "switch places" with the same exon from the second allele. This mixing and matching of exons in the two copies of a gene allows for rapid evolution of proteins. The exons are switched through a process known as recombination, the physical breaking and piecing together of **homologous** chromosomes. Having introns increases the probability that the locatio of the chromosomal breakpoints during recombination are not in coding DNA and so will not cause deleterious mutations.

There are several other types of noncoding regions within genes. For example, promoters are specific DNA sequences in front of the coding region which allow the RNA **polymerase** enzyme to bind and to start transcription of the gene. Other DNA sequences near the coding region of the gene allow for regulatory enzymes to bind and cause up-regulation (more or faster transcription) or down-regulation (less or slower transcription) of that gene. For example, if a host cell is being attached by a bacteria, enzymes in the host cell bind to and cause the up-regulation of genes coding for proteins that destroy bacterial cells.

transcription a process where enzymes are used to make an RNA copy of a strand of DNA

messenger RNA a type of RNA that carries protein synthesis information from the DNA in to the nucleus to the ribosomes

translation a process where the order of bases in messenger RNA codes for the order of amino acids in a protein

codons the genetic code for an amino acid that is represented by three nitrogen bases

organelles membrane-bound structures found within a cell

exons the coding region in a eukaryotic gene that is expressed

introns a non-coding sequence of base pairs in a chromosome

homologous similar but not identical

polymerase an enzyme that links together nucleotides to form nucleic acid

Gene Evolution

Genes control the phenotype, the structural and functional properties of an organism. Since it is clear that phenotypes have evolved and diversified over the history of life, it stands to reason that genes controlling the phenotype have evolved as well. How do genes evolve?

The ultimate cause of evolution is the accumulation of mutations in the DNA of an organism. Mutations can be caused by a number of factors, including errors made by DNA polymerase during replication of the genome, by reactive molecules in the cell, and by external factors such as x-rays. Eukaryotes utilize many mechanisms, including repair enzymes, to fix mutations when they occur, but inevitably some mutations are not corrected and are then passed on to future generations. The overwhelming majority of mutations are harmful or neutral with respect to the fitness of the organism possessing them. However, when advantageous mutations occur, natural selection tends to increase their frequency in a population.

Point mutations. The most common types of mutations are point mutations, mutations that occur within a single gene. Point mutations can be broken up into a number of classes. Because the genetic code is "degenerate," that is, different codons may code for the same amino acid, some mutations are silent. Often a change in the third base of a **codon** (e.g., ACA to ACG) does not change the amino acid that is coded for. Silent mutations have virtually no effect on the fitness of an organism. Missense mutations are mutations that change a codon and change the amino acid that is coded for. A protein with one altered amino acid may be nonfunctional but will more likely just be less efficient in its job than the original. Nonsense mutations are mutations that change a regular codon into a stop codon, prematurely terminating translation of the mRNA. These mutations generally have severe effects on the ability of the protein to perform its required function. Frameshift mutations do not cause base substitutions but instead delete or add nucleotides into a sequence. Imagine a frameshift mutation that adds one nucleotide into a coding sequence. Because the mRNA message is read three nucleotides (one codon) at a time, the one base insertion will cause all the downstream codons to be one base off and to be read wrong. These mutations are extremely disruptive to the genes they occur in.

codon the genetic code for an amino acid that is represented by three nitrogen bases

Gene duplication. Other than point mutation, another way in which a gene might gain a new function is through gene duplication. Occasionally, parts of chromosomes or even whole chromosomes are duplicated. If a gene is duplicated, then one of the duplicates is free to evolve in any direction since the other will continue to fulfill its duties. Gene duplication allows genes to acquire novel functions and to create novel phenotypes. Gene duplication may be extremely important in an evolutionary sense; for example, it appears that the great diversification of vertebrates was accompanied by several genome duplication events.

Although most new point mutations have harmful effects on fitness, the majority of mutations which become "fixed," that is, which reach 100 percent frequency in a population, are neutral or advantageous. This is because natural selection tends to weed out harmful mutations or keep them at extremely low frequencies. Thus when comparing the gene sequences from two closely related species, any differences in the DNA sequences can be attributed to the fixation of neutral or advantageous mutations that have arisen since the time when those species evolved away from their most recent common ancestor. There has been great debate in the scientific literature regarding what proportion of fixed differences between species were actually favored by natural selection. The Japanese geneticist Motoo Kimura, in his controversial 1983 book *The Neutral Theory of Molecular Evolution*, provided compelling evidence to suggest that much of the evolution that genes undergo over time is neutral, and that very few genetic differences between species were favored by selection. SEE ALSO Biological Evolution; Geneticist; Mendel, Gregor; Morphology.

Todd A. Schlenke

Bibliography

Adams, Mark D. "The Genome Sequence of *Drosophila melanogaster*." *Science* 287 (2000):2185–2195.

Dawkins, Richard. *The Selfish Gene.* Oxford, U.K.: Oxford University Press, 1989.

Griffiths, Anthony J. F., Jeffrey H. Miller, David T. Suzuki, Richard C. Lewontin, and William M. Gelbart. *An Introduction to Genetic Analysis*, 6th ed. USA: W. H. Freeman and Company, 1996.

Johnson, George B. *Biology: Visualizing Life*. New York: Holt, Rinehart and Winston Inc., 1998.

Kimura, Motoo. *The Neutral Theory of Molecular Evolution.* Cambridge: Cambridge University Press, 1983.

Lewin, Benjamin. *Genes IV.* Oxford, U.K.: Oxford University Press, 1990.

Li, Wen-Hsiung, and Dan Graur. *Fundamentals of Molecular Evolution.* Sunderland, MA: Sinauer Associates, Inc., 1991.

Smith, John Maynard. *Evolutionary Genetics.* Oxford: Oxford University Press, 1989.

Stern, Curt, and Eva R. Sherwood, eds. *The Origin of Genetics: A Mendel Source Book.* San Francisco: W. H. Freeman, 1966.

Genetic Engineering

Genetic engineering is the altering of an organism's deoxyribonucleic acid (DNA) to create a desired effect. Genetic engineers follow a set of techniques that allows them to remove genetic material from two or more species, recombine the genetic material (to create **recombinant DNA**), and integrate it into a host's genome, or genetic material. Genetic engineering is used for a variety of scientific, agricultural, and medical purposes.

recombinant DNA DNA that is formed when a fragment of DNA is incorporated into the DNA of a plasmid or virus

Restriction Enzymes

All recombinant DNA technology requires the use of **restriction enzymes**. These enzymes are naturally occurring in bacteria that fight phage, or virus, DNA, but geneticists can use restriction enzymes as tools to cut DNA into manageable fragments.

restriction enzymes bacterial proteins that cut DNA at specific points in the nucleotide sequence

Restriction enzymes recognize specific sequences along the DNA where it can be cut. These sequences contain four or more bases and occur randomly, and each enzyme cuts at a different sequence. Most restriction enzymes cut double-stranded DNA in a staggered fashion, so that a single strand extends from each end. These complementary "sticky" ends tend to bond to each other in solution.

Geneticists often need to isolate specific DNA molecules from a mixture. Restriction enzymes cut DNA into many small fragments. These fragments can be run through an electrophoretic gel, which distributes them according to size. In a technique known as Southern blotting, an absorbent membrane is then placed on the gel, transferring the ordered DNA fragments. Finally, a radioactive DNA probe is applied to the membrane, binding to any complementary DNA sequences and thereby labeling them.

Restriction enzymes can also be used to map genes. Restriction sites often vary by one or more nucleotides within a species. Genetic variation at a restriction site can produce a change in the length of a DNA sequence, also known as restriction fragment length polymorphism (RFLP). RFLP can then be measured, what is often called "DNA fingerprinting." Any genetic variation that is correlated with the RFLP is likely to be in the same part

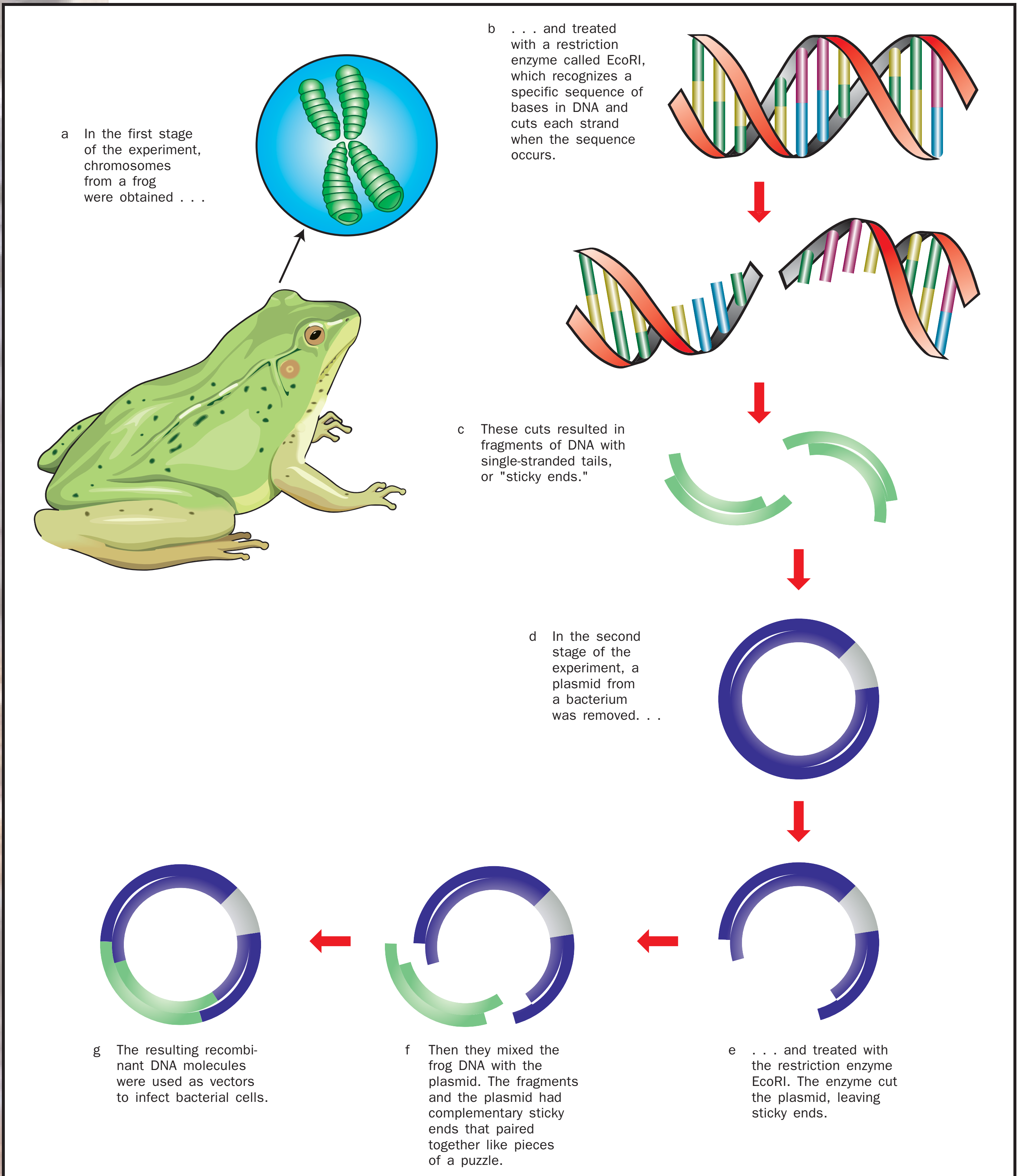
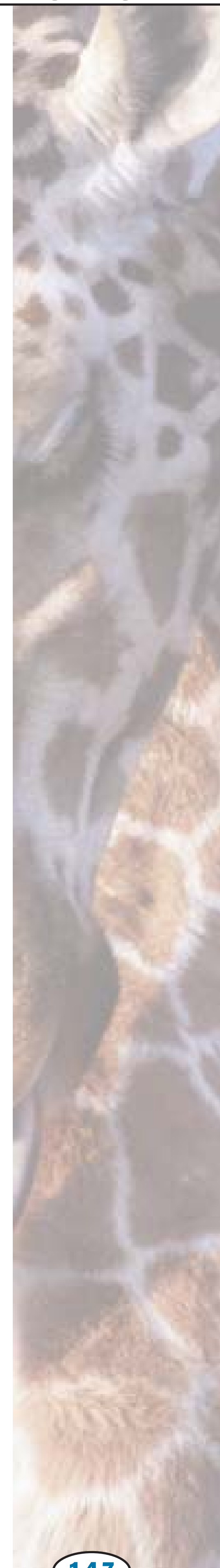


Illustration of plasmids being inserted into a vector. Redrawn from Johnson, 1998.

of the genetic material because correlations between distant genetic locations (loci) tend to break down over time as a result of recombination between chromosomes.



Recombinant DNA

Making recombinant DNA requires isolating the DNA that will be cut, donor DNA, and the DNA into which the donor DNA will be inserted, vector DNA. The combination of donor DNA and vector DNA is recombinant DNA.

A vector is a small piece of DNA that carries the donor DNA into host cells. A common vector is a plasmid, a small ring of bacterial DNA that replicates independently of the main chromosome. Plasmids are useful vectors because they easily enter bacterial cells. A plasmid vector must first be removed from the rest of the bacterial genome. The DNA is removed and centrifuged so that the smaller plasmids sink farther than the larger chromosomes. Alternatively, an alkaline pH degrades genomic DNA but not plasmids, and the genomic DNA can be precipitated out of the solution.

Donor DNA and vector DNA must be digested with a restriction enzyme so that they can be spliced together. Some sticky ends will anneal (bind) vector DNA to donor DNA. Although their initial bonding is temporary, adding DNA ligase creates stronger bonds between the joined ends to make a continuous molecule.

To improve the efficiency of this procedure, annealing between two vector molecules or two donor molecules can be prevented by adding complementary nucleotides to one strand of each molecule, for example, As to the donor molecules and Ts to the vector molecules. Furthermore, two different restriction enzymes may be used for donors and vectors, allowing greater flexibility in choosing splice sites.

Cloning

Plasmid vectors are introduced into bacteria by transformation. The plasmid replicates within each **bacterium**, and the bacteria divide many times. Consequently, a single DNA donor molecule can be amplified into billions of copies. This set of copies is referred to as a clone.

bacterium a member of a large group of single-celled prokaryotes

Most plasmids used to make recombinant DNA carry genes for drug resistance. This feature allows geneticists to apply an antibiotic to select bacteria that have been transformed by the recombinant plasmid. The antibiotics destroy bacteria that do not carry the plasmid. Plasmids also have particular restriction target sites that tailor them to the use of certain restriction enzymes. Vectors can have two different drug resistance genes, one of which contains the restriction site. If an insertion of donor DNA occurs, drug resistance is lost, and application of the drug will destroy all bacteria carrying the insert. In this way bacterial colonies carrying the desired gene can be identified and allowed to grow.

Lambda phage, a bacterial virus, can also be used as a cloning vector. Phage heads selectively package chromosomes about fifty kilobases in length. If a piece of phage DNA is removed and replaced by a donor DNA fragment of approximately the same size, the recombinant DNA can still be packaged. However, if the insertion is not successful, the phage head will not form and the DNA cannot be injected into bacteria. Successful transfection of donor DNA into a bacterial colony can be detected as a plaque indicative of infection.

There are several other types of vectors. Cosmids are hybrids of lambda phages and plasmids. Because they are larger than either phages or plasmids, they are capable of inserting larger DNA fragments. Expression vectors allow foreign genes produce proteins in a bacterium. Yeast artificial chromosomes (YAC) can carry very large inserts into yeast cells for replication. Bacterial artificial chromosomes (BAC) are capable of carrying large inserts into bacteria.

DNA Libraries

One goal of cloning genetic material is to develop a DNA library. A library is a collection of clones covering part or all of the genome of interest. It may consist of phage, bacteria, or yeast, depending on the vector used. A library may be genomic or cDNA. A cDNA library contains only coding DNA because it is synthesized from messenger RNA, which is the template from which proteins are made. A cDNA library is useful to researchers interested in genes that are expressed in particular tissues, from which they can obtain mRNA. Because the donor cDNA encodes protein, what is known as a cDNA expression library can also transcribe and translate genes into proteins.

Once a library is created, it can be screened with a probe to find a gene of interest. A probe is a piece of single-stranded DNA or an antibody that is radioactively labeled. A DNA probe will bind to a complementary strand of DNA in the library, whereas an antibody probe will bind to a protein. cDNA probes can be synthesized as an oligonucleotide, a short piece of synthetic DNA, from the amino acid sequence of the protein of interest. Because of the redundancy of the genetic code, many different cDNA's can code for the same protein. Therefore, a cocktail is often made of many different cDNA oligonucleotides.

Positional cloning is a process of using information about the location of a gene so as to clone it more efficiently. Clones can be ordered by their positions along a chromosome by doing a chromosome walk. A chromosome walk uses the ends of each clone to probe the rest of the library for overlapping clones. If another gene is closely linked to the gene of interest and its position is known, only the clones near the first gene need be probed to find the gene of interest.

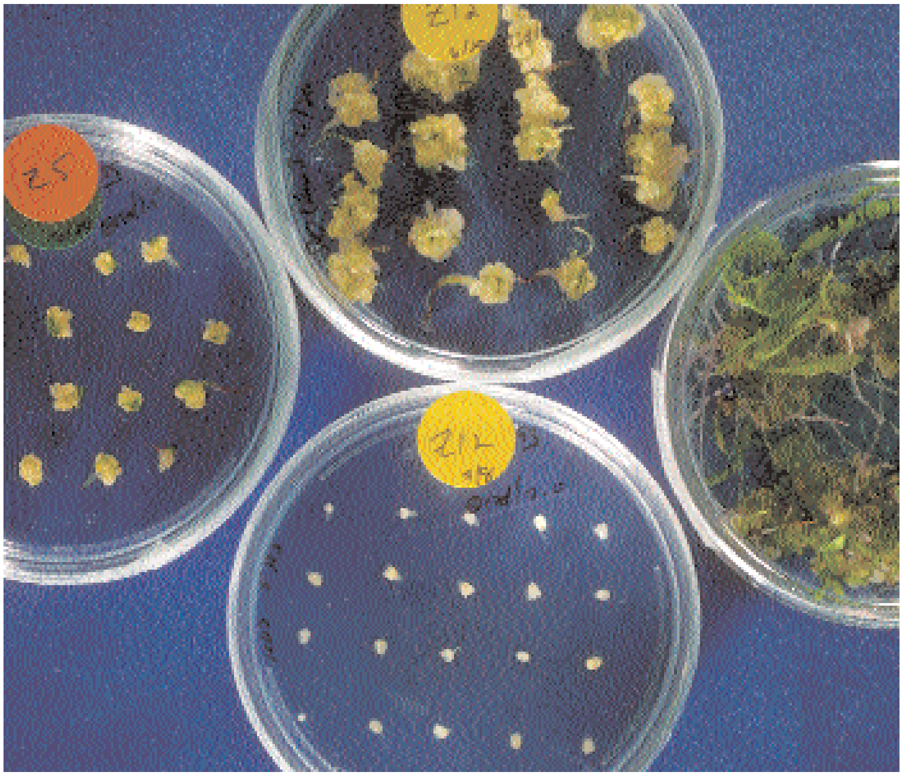
Tagging is a process in which a known DNA sequence (tag) is allowed to insert at random places in a genome. If by chance an insertion occurs in the gene of interest, it will likely cause a mutation that limits the functioning of the gene's product. Mutant lines are selected and used to construct a genomic library, which is then tested with the tag as a probe to identify the gene of interest.

DNA Sequencing

polymerase an enzyme that links together nucleotides to form nucleic acid

primer short preexisting polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase

Once a gene is cloned, its DNA sequence can be determined. First, the gene of interest is copied with a **polymerase** enzyme, a **primer** to direct the polymerase to the gene, and nucleotides. The nucleotides are not all the same, however. Some are missing an oxygen atom, which prevents them from adding another nucleotide to the end. Thus, the sequencing reaction results in an array of partial copies of the gene. If the reaction is performed with some deoxygenated thymine, then all of the copies will end in thymine. A



Corn tissues are used by geneticists in an attempt to produce desired traits.

different sequencing reaction can be performed for each deoxygenated base to generate four different sets of partial copies. The next step is to separate the partial copies according to size. Larger fragments travel more slowly through a gel, and mobility through an acrylamide gel is extremely sensitive to size. If one were to run two sets of fragments differing by just one base in size, the difference would be evident as two distinct bands on an acrylamide gel. Thus the products of a sequencing reaction will show up as an array of bands on an acrylamide gel, with each band representing the position of the deoxygenated nucleotide used in the sequencing reaction. Alternatively, just one sequencing reaction may be done with some of each nucleotide deoxygenated if each is labeled with a unique fluorescent dye, resulting in color-coded bands.

If the precise location of a gene is not known, sequencing can reveal its location. A functional gene usually appears as an open reading frame (ORF), which is a sequence of DNA uninterrupted by a stop signal. A sequence can be analyzed by a computer program, which examines all three possible reading frames on each strand. Unusually long ORFs indicate the presence of a gene, because otherwise stop codons are expected to appear at random.

If a gene has been cloned and sequenced, it can be copied from any individual in a population by polymerase chain reaction (PCR). Primers, short oligonucleotides that attach to complementary DNA and act as targets for the polymerase enzyme, are designed from the gene sequence. The strands of DNA are separated at a high temperature. The temperature is lowered again, one primer attaches to each strand of DNA, and the polymerase extends each one in opposite directions. This process is repeated many times by a machine, providing billions of copies of the gene in a few hours. PCR is useful for quickly amplifying DNA from many individuals in a population.

Gene Alteration and Expression

All of the above recombinant techniques allow geneticists to identify and describe genes. Once a gene has been sufficiently characterized, it can be manipulated to produce a desired outcome. In vitro mutagenesis can change a single target nucleotide to another nucleotide. First the gene is cloned into a single-stranded phage vector. An oligonucleotide primer is constructed from the gene's DNA sequence. The primer is complementary to the gene with the exception of the target site, which is changed to the desired nucleotide. (Although not completely complementary to the template DNA, hybridization occurs under certain conditions.) The phage is allowed to replicate so that its copy incorporates the new nucleotide. Continued copying will produce mostly mutant genes, which can be identified with the mutant primer as a probe under conditions that prevent hybridization with nonmutants.

Synthetic oligonucleotides can also be used to construct entire genes up to sixty bases in length. The automated reaction adds bases one at a time to the growing oligonucleotide, which is embedded in a resin. Overlapping oligonucleotides can be pieced together to synthesize longer sequences. Herbert Boyer's lab synthesized the gene for somatostatin, a human growth hormone, in this manner. The scientists added a restriction site to each end of the gene and a methionine codon to one end. Restriction enzymes were used to insert the gene into a bacterial plasmid that carried the same restriction sites. The insertion occurred in the middle of a bacterial beta-galactosidase gene, which the bacteria transcribed and translated. The resulting protein was a chimera (of genetically diverse tissue) of somatostatin and beta-galactosidase, separated by a methionine residue. Cyanogen bromide was used to cleave the protein at the methionine residue and recover the somatostatin.

There are other ways to produce eukaryotic (non-bacterial) gene products in bacteria. For example, phage T7 contains promoters that generate a large amount of protein during a late stage of infection. First, a gene is inserted next to a T7 promoter. The promoter interacts with T7 RNA polymerase, which is synthesized in the presence of lactose. Therefore, the addition of lactose to bacteria carrying the recombinant T7 will produce large quantities of the gene product. Insulin, somatostatin, and many pharmaceutical drugs are now produced with engineered bacteria and fungi.

transgenic an organism that contains genes from another species

Genetic engineering is not restricted to placing eukaryotic genes in bacteria. Eukaryotic cells can be altered by inserting foreign DNA into their genomes. An organism derived from such a cell is referred to as **transgenic**. There are several ways to produce transgenic organisms. For example, the gene of interest (the transgene) can be paired with a eukaryotic promoter in a vector and injected into the nucleus of the organism's gamete. The promoter will cause the gene to be expressed whenever the promoter's natural gene is expressed. This may be useful in determining the expression pattern of the natural gene if the product is not as easily detectable as that of the transgene. Or, the transgene's product alone may be valuable. For example, crops can be endowed with genes for pesticides or metabolizing nitrogen.

Unfortunately, the ecological consequences of introducing transgenic organisms into nature are unknown.

Gene Therapy and Screening

Gene therapy is the insertion of a normal gene into a chromosome carrying a defective copy of the gene. The first case of gene therapy in a mammal was the cure of a growth hormone deficiency in mice. A gene was inserted into the ova of mice carrying two defective promoters for the gene. The gene was paired with a promoter-regulator for the metallothionein gene, which activates in the presence of heavy metals. Offspring carrying the transgene showed higher growth rates in the presence of heavy metals than did those without the transgene, indicating that a functional metallothionein promoter had taken control of the growth hormone gene.

gene therapy a process where normal genes are inserted into DNA to correct a genetic disorder

Human gene therapy can be either germinal or somatic. Germinal gene therapy introduces transgenes into both somatic cells and germ line cells of the early embryo. This therapy has been performed on mice but not humans. Somatic gene therapy inserts transgenes only into affected tissues using a viral vector. This form of therapy has proven successful in treating severe combined immunodeficiency disease and atherosclerosis. Because most transgene vectors insert randomly throughout the genome, one potential side effect of gene therapy is a mutation caused by insertion into a healthy gene.

Although gene therapy for humans remains highly experimental, genetic screening for diseases is already being applied. Embryonic cells are collected from the amniotic fluid or the **placenta**. Some genetic abnormalities can be detected by their effects on restriction sites. A probe constructed from the cDNA of the gene of interest is used to identify fragments of DNA carrying the gene. These fragments are digested by a restriction enzyme whose target site contains the deleterious mutation. Mutant genes will not be cleaved by the restriction enzyme, whereas normal genes will. This can be detected as two different banding patterns on an electrophoretic gel. A related technique takes advantage of the often tight linkage between mutant genes and restriction fragment length polymorphisms (RFLP), which can serve as indicators for the presence of mutant genes.

placenta the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

PCR can also be used to amplify DNA for sequencing or another form of testing. SEE ALSO Genes; Genetically Engineered Foods; Genetics.

Brian R. West

Bibliography

Griffiths, Anthony J. F., et al. *An Introduction to Genetic Analysis*, 6th ed. New York: W. H. Freeman, 1996. Chapters 14 and 15.

Johnson, George B. *Biology: Visualizing Life*. New York: Holt, Rinehart and Winston, Inc., 1998.

Genetic Variation in a Population

Genetic variation in a population describes the existence in that population of different alleles, or alternative forms, for a given gene. The presence of genetic variation implies that individuals of the population vary in the alleles they possess, meaning that individuals differ in genotype. Genetic loci for which there are multiple alleles are described as **polymorphic**. Humans, for example, are polymorphic for traits such as eye color and blood type.

polymorphic referring to a population with two or more distinct forms present

phenotypic variation the differences in physical and physiological traits within a population

Genetic variation is one facet of the more general concept of **phenotypic variation**. Phenotypic variation describes differences in the characteristics of individuals of a population. Phenotypic variation is of interest to biologists because it is what natural selection acts upon: different phenotypes may have different fitnesses, and selection results in fitter phenotypes leaving more descendants.

Phenotypic variation arises from either of two sources: genetic variation and environmental variation. However, only differences that arise from genetic variation can be passed on to future generations. Furthermore, only a fraction of the genetic component of variation, the additive genetic variation, is actually heritable. The additive genetic variation divided by the total phenotypic variation yields the **heritability**, which describes how much offspring resemble their parents.

heritability the ability to pass characteristics from a parent to the offspring

The Amount of Genetic Variation

In the 1960s there was considerable debate regarding how much genetic variation actually exists in populations. The common view was that polymorphic loci are fairly rare. Then, the development of the technique of gel electrophoresis allowed biologists to examine patterns of protein variation across populations and to quantify genetic variation.

Biologists detected surprisingly large amounts of genetic variation. In most vertebrate species, for example, approximately 30 percent of genes were found to be polymorphic. Studies in the 1970s in humans showed that genetic variation occurs at approximately the same levels as in other animal species. The studies in humans also revealed, famously, that so-called human races are not real biological groupings. It was found that there is considerably more genetic variation within races than between them.

Since then it has been the absence of genetic variation that is considered anomalous. Absence of genetic variation in populations generally suggests that there was a population bottleneck in the recent history of the group, a time when the population size became very small. The result of a population bottleneck is that all members of the current population are descended from a small number of individuals, and therefore have only limited genetic variation. Genetic variation is expected to build up over time in these populations as new mutations appear.

How Genetic Variation Is Maintained

The discovery of large amounts of genetic variation in nearly all populations led to the formulation of a different question: How is genetic variation maintained? In many cases, after all, natural selection removes genetic variation by eliminating genotypes that are less fit.

Many factors act to increase or maintain the amount of genetic variation in a population. One of these is **mutation**, which is in fact the ultimate source of all variation. However, mutations do not occur very frequently, only at a rate of approximately one mutation per 100,000 to 1,000,000 genetic loci per generation. This rate is too slow to account for most of the

mutation an abrupt change in the genes of an organism

A group of stallions, mares, and foals graze in the Black Hills of South Dakota. The population's genetic variations resulted in the different hair color evident between the horses.

polymorphisms seen in natural populations. However, mutation probably does explain some of the very rare phenotypes seen occasionally, such as albinism in humans and other mammals.

A second factor contributing to genetic variation in natural populations is selective neutrality. Selective neutrality describes situations in which alternate alleles for a gene differ little in fitness. Because small fitness differences result in only weak natural selection, selection may be overpowered by the random force of genetic drift. Alleles whose frequencies are governed by genetic drift rather than by natural selection are said to be selectively neutral. Under neutrality, allele frequencies vary over time, increasing or decreasing randomly. Over long periods of time, random fluctuations in the relative frequencies of different alleles may result in some being eliminated from the population. However, genetic polymorphisms are long-lived, and novel neutral alleles may arise continually through mutation.

polymorphisms having two or more distinct forms in the same population

Finally, several forms of natural selection act to maintain genetic variation rather than to eliminate it. These include balancing selection, frequency-dependent selection, and changing patterns of natural selection over time and space.

Balancing selection occurs when there is **heterozygote advantage** at a locus, a situation in which the heterozygous genotype (one including two different alleles) has greater fitness than either of the two homozygous genotypes (one including two of the same allele). Under heterozygote advantage, both alleles involved will be maintained in a population.

heterozygote advantage a condition where a heterozygous individual has a reproductive advantage over a homozygous individual

A classic example of heterozygote advantage concerns the allele for sickle-cell **anemia**. Individuals who are homozygous for the sickle-cell allele have sickle-cell anemia, which causes the red blood cells to become

anemia a condition that results from a decreased number of red blood cells

> One well-studied example of genetic variation in populations is that of *Biston betularia,* the peppered moth.
>
> There are three color morphs in the peppered moth: a light morph, a dark or melanistic morph, and an intermediate morph. Before the Industrial Revolution, the light morph was the most common form, although melanistic moths were also seen occasionally. However, by the end of the nineteenth century, the melanistic morph had become much more common, and had practically replaced the light morph in certain areas.
>
> Biologists traced this shift to industrial pollution in urban areas. Without camouflaged resting places, the light moths became easy targets for bird predators. This explained both the prevalence of melanistic moths in polluted urban environments, and of light moths in comparatively pristine country habitats.
>
> The puzzling aspect of the peppered moth story is that genetic variation was not entirely eliminated in populations. In urban areas, for example, melanistic moths make up only from 90 to 100 percent of the total population, despite very strong selection. Apparently there are forces other than predation pressure at work. It was hypothesized briefly that heterozygote advantage might be the explanation, but that theory was ultimately rejected. It is now believed that gene flow between country and urban areas, and frequency-dependent selection are viable alternatives. However, much work remains to be done on this historic system.

sickle-shaped when they release oxygen. These sickle-shaped cells become caught in narrow blood vessels, blocking blood flow. Prior to the development of modern treatments, the disease was associated with very low fitness, since individuals usually died before reproductive age.

Heterozygotes, however, have normal, donut-shaped blood cells and do not suffer from sickle-cell anemia. In addition, they enjoy a benefit of the sickle-cell allele, which offers protection from malaria. Consequently, heterozygous individuals have greater fitness than individuals who have two copies of the normal allele. Heterozygote advantage in this system is believed to have played a critical role in allowing a disease as harmful as sickle-cell anemia to persist in human populations. Evidence for this comes from an examination of the distribution of the sickle-cell allele, which is only found in places where malaria is a danger.

Another form of natural selection that maintains genetic variation in populations is frequency-dependent selection. Under frequency-dependent selection, the fitness of a genotype depends on its relative frequency within the population, with less-common genotypes being more fit than genotypes that occur at high frequency.

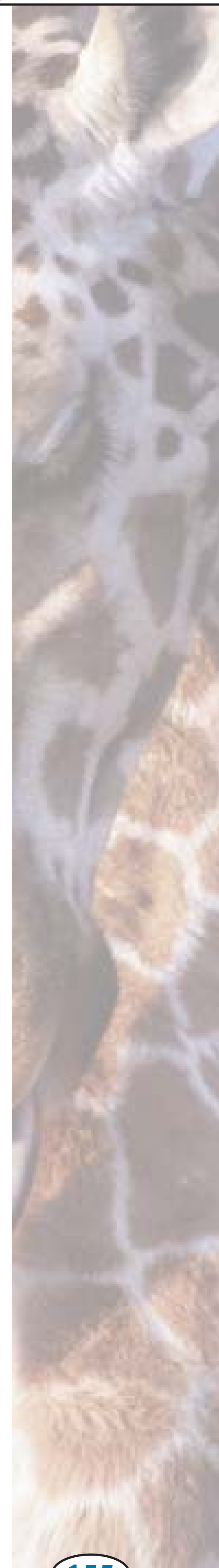
Frequency-dependent selection is believed to be fairly common in natural populations. For example, in situations where there is competition for resources, individuals with rare preferences may enjoy greater fitness than those who have more common preferences. Frequency-dependent selection may also play a role in predation: if predators form a search image for more common prey types, focusing on capturing those, less common phenotypes may enjoy better survival.

Finally, changing patterns of selection over time or space can help to maintain genetic variation in a population. If selection patterns fluctuate over time, different alleles or genotypes may enjoy greater fitness at different times. The overall effect may be that both alleles persist in a population. Changing selection pressures over time are encountered by a species of grasshopper characterized by two color morphs, a brown morph and a green morph. Earlier in the year, when the habitat is more brown, the better-camouflaged brown grasshoppers enjoy greater protection from predators. Later in the season, however, the environment is greener and the green grasshoppers have higher fitness.

Another possibility is that selection patterns vary from one place to another as a result of differences in habitat and environment. The prevalence of different genotypes in different habitats, combined with gene flow between habitats, can result in the maintenance of multiple alleles in a population.

One example comes from the allele for resistance to copper toxicity in species of grass. Copper-tolerant alleles are common in areas adjacent to copper mines, where the soil is contaminated. They are not expected in uncontaminated areas, however, where they are less fit than normal alleles. However, because grass species are wind pollinated, gametes can travel considerable distances, and copper-tolerant alleles are often found in areas where they are at a selective disadvantage. SEE ALSO GENES; GENETICS; PEPPERED MOTH; SELECTIVE BREEDING.

Jennifer Yeh



Bibliography

Curtis, Helena. *Biology.* New York: Worth Publishers, 1989.

Futuyma, Douglas J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, 1998.

Gould, James L., and William T. Keeton, with Carol Grant Gould. *Biological Science*, 6th ed. New York: W. W. Norton & Company, 1996.

Patterson, Colin. *Evolution*, 2nd ed. Ithaca, NY: Comstock, 1999.

Ridley, Mark. *Evolution.* Boston: Blackwell Scientific, 1993.

Genetically Engineered Foods

Through genetic engineering, scientists are able to alter, add, or remove specific genes from animals. Scientists are even able to add genes from a plant or animal to another plant or animal. The new genetic material in the plant or animal creates what is called a **transgenic** organism. A transgenic organism is one that contains genetic material from two different organisms.

transgenic an organism that contains genes from another species

Genetic engineering is attractive to agriculture because transgenic organisms can be designed with specific characteristics. Transgenic animals may grow faster, produce different proteins, resist disease, eat different foods, or gain weight faster. Transgenic plants may resist freezing, tolerate droughts or excess water, grow in poor soil conditions, resist pests, and resist pesticides. Transgenic plants or animals hold the promise of increasing production with less work and expense. While transgenic organisms may be the key to feeding the rapidly expanding human population, there are potential risks. Eating foods from transgenic organisms may cause allergic reactions or other interactions. Genes from transgenic organisms may find their way into "wild" populations of plants or animals, thereby affecting the genes of that population.

The first genetically engineered food introduced to the market was the Flavr Savr tomato in 1994. The Flavr Savr tomato was not a transgenic organism because new genetic material was not added. Instead, one of the genes in the tomato was altered to slow down the ripening process. The Flavr Savr tomato was engineered to ripen after being picked green and to slow down the chemical reactions that cause spoiling. The result was a tomato that can be picked green, ripen on the shelf on the way to the grocery store, and then remain fresh on the shelf. This type of genetically engineered food is probably safe because no new genetic material was inserted into the tomato plant.

Foods based on transgenic organisms have a higher risk for problems. In 1996 scientists created a transgenic soybean plant which had been altered to include a gene from the Brazil nut to increase its nutritional content. However, it was found that the soybeans from this transgenic plant produced some of the same proteins as Brazil nuts. One of these proteins was one to which some people are allergic. As a result, someone with allergies to Brazil nuts would also have an allergic reaction to the soybeans.

Not all transgenic organisms cause trouble. One of the first food uses for transgenic organisms was in the production of cheese. Cheese is made from milk. One of the first steps in making cheese is to separate the milk into curds (solids) and whey (liquid). This is done with an enzyme called **rennin**. Rennin has traditionally been extracted from the stomachs of slaughtered cows.

rennin an enzyme used in coagulating cheese, is obtained from milk-fed calves

A lab technician picks away corn embryos that will be grown in controlled conditions for a specific result.

In 1990, scientists used genetic engineering to splice the gene from cows that stimulated the production of rennin into yeast cells. The result was yeast cells that produce rennin. The rennin produced by the yeast cells is identical to the rennin produced by cows. The only difference is that the rennin from the yeast cells does not need to be extracted. This has lowered the price and increased the amount of rennin available. As a result, cheese is easier and cheaper to make. Transgenic rennin was approved for use in 1990; there have been no reports of problems and its use continues in about 65 percent of cheese production.

When genetically engineered organisms are used for food, it is easy to see where problems may develop. However, genetically engineered organisms could also pose problems with the environment. Crop pests such as insects damage a large percentage of crops each year. To combat pests, farmers use chemical pesticides. Sometimes these pesticides can cause problems with people who eat the crop or to animals living near the fields. Scientists have started using genetic engineering to make plants that resist crop pests. One way of making corn pest resistant is by inserting a gene from a bacterium, *Bacillus thuringiensis*. The resulting transgenic plant then produces a toxin originally produced by the bacteria. This toxin, *Bt* toxin, is poisonous to the corn borer, a common pest insect. Now, the corn plant itself produces its own pesticide. This means that farmers do not need to use pesticides on their fields, resulting in higher yields and fewer pesticides in the environment. At first glance, this seems like an excellent solution for increasing profits.

Unfortunately, corn borers, like other insects, reproduce quickly. Some of the corn borers were actually resistant to the *Bt* toxin. The corn borers that survived because of their resistance were able to pass the resistance on to their offspring. Now, just like with so many other pesticides, the pests were developing resistance. Scientists believed that this would be a minimal problem, and with limited use of other pesticides, these insects could be controlled. However, when farmers started growing transgenic corn that produced *Bt* toxin, they found an unexpected result.

Corn reproduces by pollen being carried from one plant to another. Unlike many plants, corn pollen is carried by the wind. Cornfields produce incredible amounts of pollen and the pollen often coats everything surrounding the fields. Scientists soon discovered that caterpillars of Monarch butterflies were being killed. The caterpillars eat a plant called milkweed, not corn plants. However, the transgenic corn pollen was deposited on the milkweed and the caterpillars were eating it along with the milkweed. The *Bt* toxin in the pollen was enough to kill the caterpillars.

Because of the benefits that genetically modified organisms provide, their use will probably continue to grow. No one knows how widespread the use of genetically modified organisms is in the United States. In 2000, the amount of transgenic crops was 52 percent of soybeans, 19 percent of corn, and 48 percent of cotton. The U.S. Food and Drug Administration has been working with scientists to devise ways of testing and even labeling foods that are transgenic or are derived from transgenic materials. The debate over genetically engineered foods and products will no doubt continue. SEE ALSO Bioethics; Farming; Genes; Genetic Engineering; Genetics.

Allan B. Cobb

Bibliography

Cobb, Allan B. *Scientifically Engineered Foods: The Debate Over What's On Your Plate.* Rosen Publishing Group, 2000.

Marshall, Elizabeth L. *Hight-Tech Harvest: A Look at Genetically Engineered Foods.* Danbury, CT: Franklin Watts, 1999.

Silver, Lee M. *Remaking Eden: How Genetic Engineering and Cloning Will Transform the American Family.* New York: Avon Books, 1998.

Geneticist

Geneticists, or genetic scientists, study heredity. Heredity is the process by which certain characteristics of an organism are handed down from parent to offspring. Geneticists study plants and animals, including humans. Geneticists work in three broad fields: biology, medicine, and agriculture. They attempt to increase knowledge about biology in order to understand and cure genetic diseases. Also, they counsel families at risk for genetic diseases or disorders. Geneticists breed new crop plants and livestock that are disease resistant or have other desirable properties. The rapidly growing biotechnology field uses genetics to produce everything from medicines to microchips. Sensitive genetic tests are being increasingly used in criminal cases to identify persons. At the turn of the twenty-first century, geneticists are involved in very important work known as the **Human Genome Project**. This international research program aims to construct detailed maps of the human genome, determine the complete sequence of the 3 billion bits of genetic information, and find the location of the approximately 30,000 human genes. Its results will have major impacts on biology and medicine, especially in relation to the approximately three thousand to four thousand hereditary diseases of humans.

Human Genome Project a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

There are four main types of geneticists: those performing basic research; those working in specialized laboratories; genetic counselors; and clinical geneticists. Geneticists in basic research must generally have a doctoral or Ph.D. degree and from two to four years of postdoctoral training. They might hold a faculty position at a university or work at a private research institute or biotechnology firm. Laboratory geneticists apply genetics to agriculture, legal or police work, drug development, and clinical medicine. Depending on the position held at the laboratory, this type of geneticist is required to have a bachelor's, master's, doctoral, or medical (M.D.) degree. Genetic counselors have specialized graduate degrees in medical genetics and counseling. They assist families at risk for genetic diseases. Their work can include speaking with the family, interpreting information about genetic conditions, and conducting research. Clinical geneticists must usually have a medical degree. Many work at university medical centers or large hospitals. They work to identify genetic disorders and birth defects and arrange for proper treatment of the patient. Also, they help the patient and family cope with the disorder.

At the high school level, persons interested in becoming a geneticist should study math, chemistry, physics, biology, English, writing, and computer studies. In college, persons wishing to conduct basic research generally major in biology or genetics. Also, they take math, chemistry, and physics courses. A doctoral degree in genetics is generally required to conduct basic research. Clinical geneticists must obtain medical degrees. Genetic counselors usually obtain specialized graduate degrees. Their curriculum consists of two years of master's-level programs with courses and field training in medical genetics and counseling. SEE ALSO BIOLOGICAL EVOLUTION; GENES; GENETICS; MENDEL, GREGOR.

Denise Prendergast

Bibliography

Cosgrove, Holli R., ed. *Encyclopedia of Careers and Vocational Guidance*, 11th ed. Chicago: Ferguson Publishing Company, 2000.

Internet Resources

The Genetics Societies. <http://www.faseb.org/genetics/>.

The National Human Genome Project Research Institute. <http://www. nhgri.nih. gov/>.

Genetics

Genetics is the study of the mode and mechanism of the transmission of heritable information. **Heredity** is the passing of a trait from one generation to the next. The heritable information of an organism is contained in its DNA, and the DNA an organism has is called its genome. DNA passes from cell to cell by cell division and from parent to offspring by reproduction.

heredity the passing on of characteristics from parents to offspring

The actual unit of inheritance is the gene, a region of DNA that codes for one trait. The sequence of DNA makes up the **genotype** of an individual. A genotype can be for one single gene, for the entire genome of an individual, or anywhere in between. The physical location of a gene on a chromosome is called a locus. The particular copy of a gene at each locus is called an allele. For example, the gene for eye color occurs at one locus and has different alleles that code for blue or brown or green, etc. Diploid eukaryotes have pairs of chromosomes. Therefore, individuals have two copies of each gene, one copy on each chromosome in the pair. The genotype of a diploid organism for one single gene is the pair of alleles for that locus. So the genotype for eye color is composed of two alleles, one on each chromosome in the same location. Alleles interact with each other when they

genotype the genetic makeup of an organism are expressed. This interaction is referred to as dominance. Sometimes one allele hides the other allele. Other times the alleles are both expressed equally. There can also be complicated interactions between alleles and the environment in expressing a trait.

How a gene is actually manifested into a physical structure is the **phenotype** of an individual. The phenotype is the outward appearance of an organism, the reactivity of a digestive enzyme, or even the presence or absence of a disease. The phenotype of an individual is important because it is what natural selection works on. The genotype determines the phenotype of a trait. Since there are two alleles for each locus and alleles can interact, different combinations of alleles produce different traits, in other words, different genotypes produce different phenotypes. The genotype is the underlying genetic basis of a phenotype.

phenotype physical and physiological traits of an animal

Inheritance Through Reproduction Produces Genetic Variation

The difference among genotypes is referred to as genetic variation. There is genetic variation at one gene when different individuals have different combinations of alleles. Genetic variation also refers to the combination of alleles at different genes. Different phenotypes reflect underlying genetic variation. People with blonde hair and blue eyes have a different genotype and phenotype than people with brown hair and brown eyes. This difference is genetic variation.

In **asexual reproduction**, the parent and offspring have identical DNA. Mitosis is one form of cell division that produces daughter cells that are identical to the mother cell. Asexual reproduction results in clones, organisms that are identical to each other genetically.

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

sexual reproduction reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

Sexual reproduction produces offspring that are the combination of the genetic makeup of two individuals. In humans, a baby gets half of its genetic material from its mother and half from its father. Gametes, the sperm and egg, contain only half the genome of an individual; only one of the pair of chromosomes are in each gamete. Reducing the genetic material by half is accomplished through meiosis, cell division that produces gametes. Since gametes have only one copy of all chromosomes when they join to form a zygote, the zygote has two copies of each chromosome like its parents.

Organisms that are clones inherit the genotype of their parent since they are genetically identical. In sexually reproducing organisms, the identical genotype of an individual cannot be inherited since each offspring's DNA is made up from one half of the mother's DNA and one half of the father's. In the same way, a phenotype cannot be inherited because it is derived from the genotype. Only genes are inherited. When sexual reproduction occurs, genotypes are split up and new genotypes are formed, making sexual reproduction an important source of genetic variation for evolution.

In his pea experiments, Gregor Mendel observed that each gamete an individual makes is unique. The two processes that make gametes unique are the law of segregation and the independent assortment of homologous chromosomes. In normal meiosis, each gamete ends up with one copy of each chromosome. The law of segregation describes the process of the separation of the two alleles at the same locus on a pair of chromosomes into separate gametes. Independent assortment is when the two chromosomes in

These two calves in Japan were cloned from cells contained in a cow's milk called colostrum, produced in the first week after a cow has delivered.

a pair are randomly distributed during meiosis into the four gametes. Each time four haploid gametes are produced from one parent cell, each gamete has a different combination of one set of chromosomes. Independent assortment is another important source of genetic variation.

Recombination redistributes combinations of alleles of different genes. During meiosis, crossing over happens among the tetrad of chromatids during prophase I. Bits and pieces of homologous chromatids are swapped among chromatids at the chiasmata during crossing over. This means that different alleles for the same gene are being swapped. The result is that for different genes, different alleles are now being combined. For example, suppose the gene for pea-coat texture is on the same chromosome as the gene for pea-coat color. On one chromosome, the allele for round peas is present with the allele for yellow peas. On the homologous chromosome, the combination is the allele for wrinkled peas and for green peas. Recombination through crossing-over events can produce a gamete that has one chromosome with the allele for round peas with the allele for green peas. It could also produce a gamete that has a chromosome with an allele for wrinkled peas with an allele for yellow peas. Of course it is possible to get the parental combinations in gametes as well. Recombination is another very important source of genetic variation.

Genetic mutation is the ultimate source of genetic variation. When DNA is replicated during cell division, mistakes are made at very low levels in copying and dividing chromosomes. These mistakes can lead to changes in the DNA called genetic mutations. Mutations can be in the sequence of the DNA during replication. They can also occur when pieces of different chromosomes get mixed up during cell division, or when whole chromosomes are not divided equally among daughter cells during cell division. Mutations often have negative effects. A mutation in the DNA can produce a phenotype that is not normal. When natural selection acts against these abnormalities, the mutations are called deleterious mutations. Only very rarely does mutation produce a variant of a phenotype that is better than normal. If natural selection favors this phenotype, the mutation is a beneficial mutation and the trait that results from natural selection is an adaptation. Adaptations can spread throughout a population over a few generations.

Genetic Variation and Biological Evolution

Genes are the raw material for biological evolution. Genes are the only things that are inherited in sexually reproducing organisms. Combinations of different alleles for the same gene and different combinations of alleles at different genes make up genetic variation. Genetic variation comes from genetic mutation and from processes related to sexual reproduction, including recombination and independent assortment. Without genetic variation, biological evolution can not take place.

Evolution is a change in the frequency of a gene in a population over time. Natural selection, the most important of the five forces that cause biological evolution, selects on phenotypes of individuals. However the genes, not the genotype or the phenotype, are passed on to the next generation. The other forces that cause evolution do effect the genes. Nonrandom mating pairs up different combinations of genes in new individuals, or keeps existing combinations of genes together. Gene flow from other populations can introduce new genetic variation into a population. Mutation can change the genes directly during cell division and create new genes, both deleterious and beneficial, during reproduction. Random genetic drift can also change the gene frequency in a population. Random genetic drift is a subsampling of a population, for example, if there is a big die off from disease. When only a few individuals are left, only a few alleles are present for each gene, and the combinations that exist are just a few of the possible combinations. Random genetic drift can dramatically change the genetic variation and the gene frequencies of a population, causing much evolution.

Genetics and biological evolution are typically even more complicated. Most traits, such as how tall humans are, do not have categorical differences but vary continuously. For example, humans are not 1.5 to 1.8 meters (5–6 feet) tall, but instead are 5 feet 1 inch or 5 feet 2 inches, and height can be measured in even smaller increments. Quantitative traits such as height typically result from many genes; they are polygenic traits. Alleles at several **loci** interact to produce the overall height of an individual. The environment can interact with the genotype and affect the phenotype of an indi-

loci sites or location

vidual. For example, if a child does not have the proper nutrition growing up, he or she will be shorter as an adult than if well nourished.

Molecular genetics has changed how genetics is performed and what we can understand about the origin and diversity of animals. In April, 2000, Celera Genomics announced it had sequenced the entire genome of one human being. Being able to know the entire genetic sequence of not only one organism, but of several different organisms, will revolutionize genetics. Being able to compare whole genomic sequences of different organisms will provide a new understanding of how evolution created and maintains the diversity of organisms on Earth. SEE ALSO Biological Evolution; Genes; Geneticist; Mendel, Gregor; Morphology.

Laura A. Higgins

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

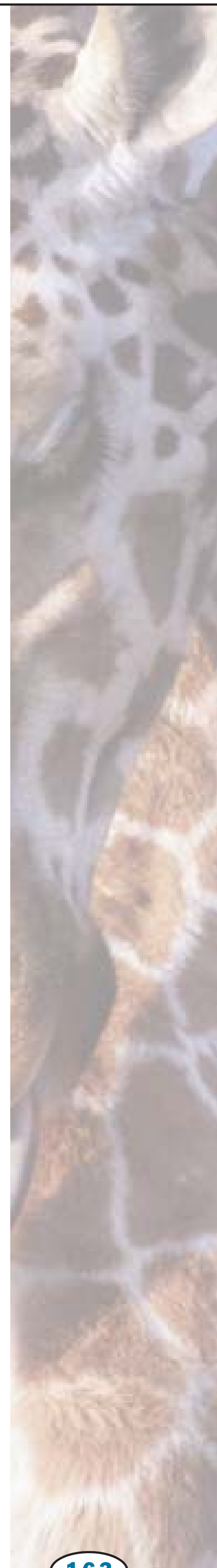
Griffiths, Anthony J. F., Jeffrey H. Miller, David T. Suzuki, Richard C. Lewontin, and William M. Gelbart. *An Introduction to Genetic Analysis*, 6th ed. New York: W. H. Freeman and Company, 1996.

Lewis, Ricki. *Human Genetics*, 2nd ed. Chicago: Wm. C. Brown Publishers, 1997.

Geological Time Scale

Geologic Time Scale

Era	Period	Epoch	Significant Events	Million Years Before Present
Cenozoic	Quartenary	Holocene	recorded human history, rise and fall of civilizations, global warming, habitat destruction, pollution mass extinction	0.01
		Pleistocene	*Homo sapiens*, ice ages	1.6
	Tertiary	Pliocene	global cooling, savannahs, grazing mammals	5.3
		Miocene	global warming, grasslands, *Chalicotherium*	24
		Oligocene		37
		Eocene	modern mammals flourish, ungulates	58
		Paleocene		66
Mesozoic	Cretaceous		last of age of dinosaurs, modern mammals appear, flowering plants, insects	144
	Jurassic		huge plant-eating dinosaurs, carnivorous dinosaurs, first birds, breakup of Pangea	208
	Triassic		lycophytes, glossopterids, and dicynodonts, and the dinosaurs	245
Paleozoic	Permian		Permian ends with largest mass extinction in history of Earth, most marine inverterbrates extinct	286
	Pennsylvanian		vast coal swamps, evolution of amniote egg allowing exploitation of land	320
	Missipian		shallow seas cover most of Earth	360
	Devonian		vascular plants, the first tetrapods, wingless insects, arachnids, brachiopods, corals, and ammonite were also common, many new kinds of fish appeared	408
	Silurian		Coral reefs, rapid spread of jawless fish, first freshwater fish, first fish with jaws, first good evidence of life on land, including relatives of spiders and centipedes	438
	Ordovician		most dry land collected into Gondwana, many marine invertebrates, including graptolites, trilobites, brachiopods, and the conodonts (early vertebrates), red and green algae, primitive fish, cephalopods, corals, crinoids, and gastropods, possibly first land plants	505
	Cambrian		most major groups of animals first appear, Cambrian explosion	570
Proterozoic			stable continents first appear, first abundant fossils of living organisms, mostly bacteria and archeobacteria, first eukaryotes, first evidence of oxygen build-up	2500
Archean			atmosphere of methane, ammonia, rocks and continental plates began to form, oldest fossils consist of bacteria microfossils stromatolites, colonies of photosynthetic bacteria	3800
Hadean			pre-geologic time, Earth in formation	4500



Bibliography

Foster, Robert. *Geology.* 3rd ed. Columbus, OH: Charles E. Merrill, 1976.

Stanley, Stephen. *Earth and Life Through Time.* New York: W. H. Freeman, 1989.

Toulmin, Stephen and June Goodfield. *The Discovery of Time.* New York: Harper & Row, 1965.

Internet Resources

United States Geological Survey. <http://pubs.usgs.gov/gip/fossils/contents.html>.

Gills

Gills and lungs are the two structures commonly used by animals for respiration. Both are characterized by large amounts of surface area that function in gas exchange. The difference between them is that gills involve external extensions from the body surface, whereas lungs possess internal foldings. Gills have evolved independently several times in a variety of animal groups.

Among the **annelids**, certain species of terrestrial worms have long slender, branching gills which extend from the body. **Horseshoe crabs** possess structures known as book gills, which are actually modified appendages that function in gas exchange. **Crustaceans** also have gills that have been modified from **thoracic** or abdominal appendages.

Gill structures are highly diverse among crustaceans. Generally, the more aquatic crustaceans have more elaborate gills, while the more terrestrial species are characterized by simplified gills. That is a consequence of the greater availability of oxygen on land, from the air, than in water.

In **echinoderms**, the group that includes starfish, the large surface area provided by the many appendages and by the tube feet are used in gas exchange. However, some species supplement these with gills around the oral cavity. **Mollusks** possess gills within their **mantles**. These are oriented to face the water current. Vertebrates such as **salamanders** are also characterized by external gills, which in their case are filamentous structures that extend from the head region. In some species, only the aquatic larvae have gills. However, in many species that remain aquatic their entire lives, the gills may be retained into adulthood.

Fish also use gills in gas exchange. The gills of fish are supported by a series of bony **gill arches**. The gill arches lie between the gill clefts, through which oxygenated water flows. The gill arches support tissue that includes the tiny blood vessels which carry in deoxygenated blood and carry away oxygenated blood, as well as the **gill filaments**, where gas exchange actually occurs. The gill filaments each have numerous secondary gill lamellae that further increase the surface area available for gas exchange.

Fish that have high energy demands, such as those which swim quickly, have more surface area associated with their gills. The **operculum** of bony fishes is a covering that protects the entire gill area. It also covers the operculum chamber, which is essential to the process of pumping water over the gills.

annelids segmented worms

horseshoe crabs a "living fossil" in the class of arthropods

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

thoracic the chest area

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

mollusks large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

mantles tissues in mollusks that drape over the internal organs and may secrete the shell

salamanders a four-legged amphibian with an elongated body

gill arches arches of cartilage that support the gills of fishes and some amphibians

gill filaments the site of gas exchange in aquatic animals such as fish and some amphibians

operculum a flap covering an opening

Gills are used by fish for respiration. Over time, gill structure has evolved independently in several different animal groups to form other skeletal elements.

Gas exchange across the gills occurs in what is described as a counter current fashion. This is a very efficient mode of gas exchange because water flows in one direction and blood flows in the other. The consequence of countercurrent flow is that well-oxygenated blood encounters well-oxygenated water, and is able to pull more oxygen from the water, while less-oxygenated blood encounters less-oxygenated water. Oxygenation thus occurs along the entire pathway where the water and blood are juxtaposed.

Fish push oxygen-rich water across their gills by one of two methods. In ram ventilation, fast-swimming species such as sharks swim with their mouths open. Water is forced into the mouth and out over the gills.

buccal mouth

Most bony fish species, however, employ a second method, **buccal** and opercular pumping. In this method, serial expansions and contractions of the mouth cavity and the opercular cavity occur, resulting in the continuous flow of water over the gills. First, the mouth, or buccal, cavity expands, drawing water in. Then, the mouth closes and the buccal cavity contracts. This forces water to flow over the gills into the opercular cavity. At the same time, the opercular cavity expands, which draws more water in from the buccal cavity. Water exits through the operculum.

Some fish will use buccal and opercular pumping while swimming slowly and ram ventilation when swimming faster. Ram ventilation is essential in some species, which suffocate if they are not able to swim fast enough.

The gill arches have played a crucial role in vertebrate evolution. Over evolutionary time, they have been modified to form other essential skeletal structures. The vertebrate jaw, which characterizes all vertebrates aside from lamprey and hagfish, was modified from a single pair of gill arches.

incus one of three small bones in the inner ear

In mammals there has been a further modification of this pair of gill arches. Mammals have evolved a "new jaw," and the original bones of the jaw joint now function as middle-ear bones in mammals. The **incus** and

malleus are both homologous to the jaw bones in other vertebrates, which are homologous to gill arches in primitive fish groups. The middle-ear bones are involved in conducting sound between the eardrum and the inner ear, where neural processing occurs. The third mammalian middle-ear bone, the **stapes**, occurs in all terrestrial vertebrates, and is also derived from the gill arches. SEE ALSO BLOOD; RESPIRATORY SYSTEM.

malleus outermost of the three inner ear bones

stapes innermost of the three bones found in the inner ear

Jennifer Yeh

Bibliography

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Hildebrand, Milton, and Viola Hildebrand. *Analysis of Vertebrate Structure*. New York: John Wiley, 1994.

Withers, Philip C. *Comparative Animal Physiology*. Fort Worth, TX: Saunders College Pub., 1992.

Gliding and Parachuting

Many vertebrates have independently evolved the ability to glide. In spite of their name, "flying" squirrels (*Glaucomys volans* and *Glaucomys sabrinus*) glide, not fly, from tree to tree. The little marsupial known as a sugar glider (*Petaurus breviceps*) can also glide from tree to tree. Many other animals practice parachuting. The difference between parachuting and gliding is control. Parachuting is simply slowing the rate of descent with little or no attempt to control direction. Flying squirrels carefully steer themselves as they glide from the crown of one tree to the trunk of another.

Cynocephalus is a group of medium-sized gliding mammals closely related to bats. These mammals hang upside down in trees, leaping into the air to glide in search of fruit to eat. The group *Exocoetus* contains the "flying" fishes. Although a true glider, *Exocoetus* can extend the range of its glide by flapping its **pectoral** fins. Flying fishes glide when startled, as by a predator. They swim rapidly underwater, then launch themselves into the air, where they can glide over long distances. *Rhacophorus* is a tree-dwelling frog with expanded toe membranes that help it fall more slowly after it leaps off a tree. The frog is a true glider, as it can turn and maneuver while airborne.

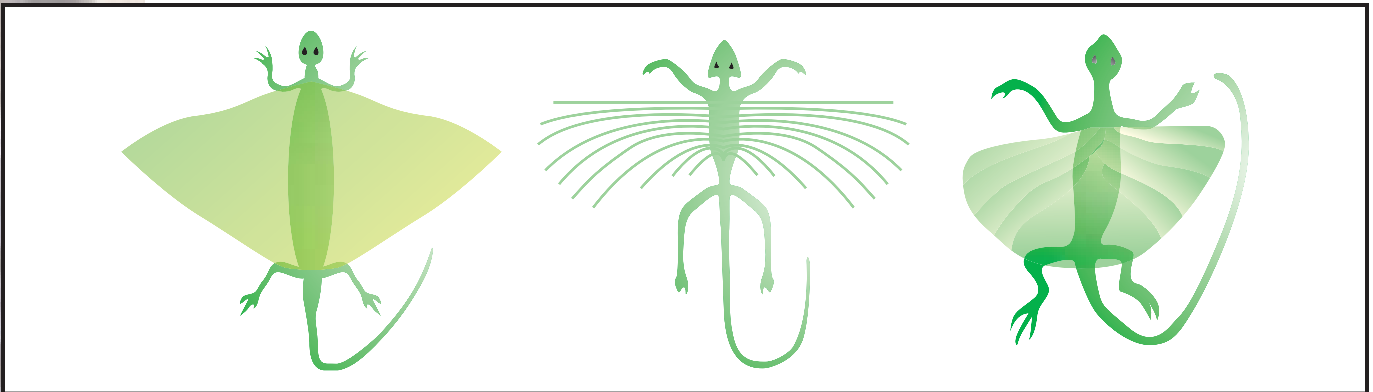
pectoral of, in, or on the chest

INDEPENDENT EVOLUTION

Many completely unrelated organisms seemed to have evolved similar structures at different times. For example, mollusks, arthropods, and vertebrates all evolved eyes. However they didn't "borrow" the idea from each other. Each class of animal evolved the structure separately from the others. Grasping appendages, eyes, wings, powerful legs for jumping, and many other features of our animal world are simply good ideas that have been discovered many times through the processes of evolution.

All gliders and parachuters can increase the relative width of their bodies, thus increasing the surface area exposed to wind resistance. A few gliding frogs flatten their bodies and spread their limbs outward. Gliding snakes not only flatten their bodies, but also draw in the scales on the lower side of the body to form a kind of trough. Some flying lizards, such as *Draco volans*, have evolved the ability to glide using specialized ribs that spread out like a fan.

Gliding mammals, such as flying squirrels, have a fold of skin on each side of their bodies that extend from the front leg or front wrist back along the side of the body to the hind leg or the ankle. To glide, the squirrel climbs to near the top of a tree and launches itself toward another tree, spreading the fold of skin by holding out its front and rear legs. The glide angle is quite steep, but accurate enough that the squirrel securely lands well



The flying lizards (from left to right) *Weigeltosaurus, Icarosaurus,* and *Draco* possess different structural features that allow them to glide.

up on the trunk of the target tree and can climb back to a safe height above ground.

Parachuting lacks the implied directional control of gliding. To parachute, the animal launches itself into the air and controls its fall by spreading toes, limbs, and membranes. Parachuters usually fall to the ground or to a lower branch of a tree. Most gliding and parachuting animals are fairly small. Their surface area is large relative to their weight, so air resistance effectively slows them down. If an animal is small enough, it needs no special adaptation for parachuting. For example, an insect can fall from the top of a tall tree all the way down to the ground without harm. The insect is its own parachute.

Gliding and parachuting are not generally evolutionary steps toward flying. They are independent adaptations acquired by animals that live primarily in forests. However, birds may have evolved the ability to fly as an extension of running along the ground with short, gliding hops that became longer and longer over time, evolving eventually into true flight. Roadrunners (*Geocòccyx californiànus*) regularly display this behavior. Although capable of flight over short distances, they prefer to run and occasionally glide. SEE ALSO FLIGHT.

Elliot Richmond

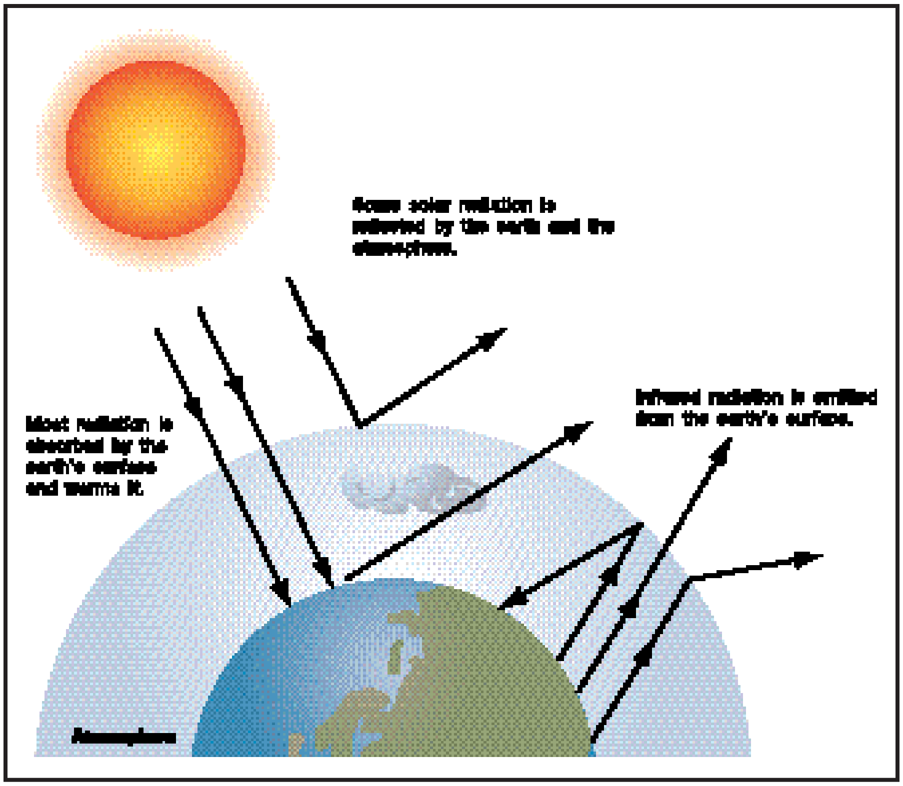
Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Hildebrand, Milton. *Analysis of Vertebrate Structure*, 4th ed. New York: John Wiley & Sons, Inc., 1995.

Global Warming

Global warming is an example of global climatic change. To understand the concept of global warming and make decisions about how to respond to the seemingly contradictory information received from various sources, it is important to distinguish between climate and weather. Weather applies to short-term changes in properties of the lower atmosphere such as temperature, relative humidity, precipitation, cloud cover, barometric pressure, and wind speed. Climate is the general pattern of weather conditions, seasonal



The "Greenhouse Effect" involves the effects of both solar and infrared radiation on Earth. Redrawn from Barnes-Svarney, 1995.

variation, and weather extremes over a long time—at least thirty years. A summer with record high temperatures is not a signal that global warming is occurring. A winter with record cold is not proof that global warming is not occurring. Climate change, especially global climate change, must be determined from global averages of weather conditions collected, averaged, and compared over decades.

Climate Change

Earth's climate has changed dramatically many times in the past and will almost certainly change many times in the future. Twenty thousand years ago, the places where Minneapolis, Milwaukee, Chicago, and Detroit now stand were covered with ice. Scientists do not know what caused the ice to spread or what caused it to retreat. Once the ice began to retreat, it did so very rapidly, completely disappearing in a few thousand years. Only a few remnants, such as the Greenland ice sheet, still exist. If the Greenland ice sheet were to melt, global sea levels would rise by 8 to 10 meters (26 to 33 feet), and many major seaports and coastlines would be flooded. If the Antarctic ice sheet melted, Earth's oceans would rise by 100 meters (330 feet).

Humans would survive climate changes of this magnitude, but social and political organizations probably would not. Scientists know this because past civilizations have not survived similar climate changes. Around 1000 C.E., a well-established Norse colony thrived in what is now southern Greenland. The colony had been established during a relatively warm period when the temperatures in the area were 2 to 4°C (4 to 7°F) above average. It vanished almost without trace as the climate returned to normal, an ice sheet moved

Meltwater filling deep crevasses in the surface of the Columbia Glacier in Alaska.

back over pastures, and the advancing sea ice cut off communications. That small temperature change made the difference between a thriving colony and disaster.

Earth's climate is still changing. Research strongly indicates that Earth is gradually warming up. According to the United States Environmental Protection Agency, the best estimates are that Earth's temperature has increased by 0.5°C (1.0°F) in the last century, precipitation has increased by 1 percent, and sea level has risen by 2 to 5 centimeters (1.0 to 2.0 inches). This is strong evidence for a small but significant increase in global average temperature. Almost all scientists agree with these facts. However, scientists cannot agree on what causes global warming. Many researchers are convinced the data show unequivocally that global warming is directly related to the increase in greenhouse gases such as carbon dioxide. Others feel the data simply indicate a short-term climatic phenomenon.

The "greenhouse" effect is somewhat misnamed. A greenhouse gets warm on a sunny winter day because the sunlight passes through the glass, warming the plants and other surfaces in the greenhouse. The plants warm the air, but the warm air cannot escape, so the temperature in the greenhouse rises. The planetary **greenhouse effect** operates a little differently. **Infrared** radiation from the sun passes through the atmosphere and warms the surface of Earth. As the surface warms, it also radiates infrared. However, since the temperature of Earth is much lower than the temperature of the surface of the sun, the infrared radiation emitted by the ground, building, rocks, and plants has a much longer wavelength. Radiation of this longer wavelength cannot pass through the atmosphere, and is absorbed by the air or reflected back to the ground.

greenhouse effect a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

infrared invisible part of the electromagnetic spectrum where the wavelengths are shorter than red, heat is carried on infrared waves

A little greenhouse effect is a good thing. If it were not for the greenhouse effect, Earth's average surface temperature would be well below the freezing point of water and life could not exist. The question is, can we have too much of a good thing? Is it possible that rising temperatures on Earth are due to increased levels of greenhouse gases in the atmosphere?

Greenhouse Gases

There are several greenhouse gases. Naturally occurring greenhouse gases include water vapor, carbon dioxide, methane (from plant decay and other sources), nitrous oxide (from volcanoes), and ozone. All these gases can also result from human activity. Carbon dioxide is released when fossil fuels are burned. Methane is emitted from livestock operations and the decomposition of organic waste. Nitrous oxide is emitted by internal combustion engines and by the burning of solid waste. Several synthetic materials are powerful greenhouse gases, including hydrofluorocarbons, perfluorocarbons, and sulfur hexafluoride.

Of all the greenhouse gases, carbon dioxide causes the most concern and is therefore closely monitored. Scientists know that carbon dioxide levels in the atmosphere have increased steadily since the beginning of the Industrial Revolution. Most scientists also agree that the average surface temperature of Earth has increased by about 0.5°C (1°F) over the last 100 years. In addition, most scientists now think there is a direct correlation between the increase of carbon dioxide in the atmosphere and the increase in the global average temperature. What remains uncertain is what will happen in the future and what should be done about it. Although the consensus among scientists is that Earth's temperature will continue to increase over the next 100 years, there is no consensus on the size of the increase. Estimates range from 1°C (2°F) to over 5°C (9°F). A 10°C rise will have little effect and is no cause for alarm. However, a 5°C rise could have disastrous consequences. Sea level could rise by 100 meters (330 feet), deserts could expand dramatically, and precipitation patterns would change in unpredictable ways.

Controversy Over Global Warming

Discussions about global warming have become intensely political, with "conservatives" and "liberals" taking contradictory positions. Two questions related to global warming should be discussed and debated. The first question is whether global warming is occurring and whether humans are causing it. The second question is this—if global warming is occurring and humans are causing it, what should be done about it? This second question is clearly a matter of public policy and political process. Public media, Congress, and other public forums are the appropriate arenas for the debate about this question.

Many national governments and international organizations continue to raise concerns about global warming and the possible link to carbon dioxide emissions. Most countries are firmly committed to strengthening international response to risks of adverse climate change. Since gases emitted into the atmosphere do not recognize political boundaries, this is a legitimate question of international concern. The United Nations Framework Convention on Climate Change currently provides a vehicle for discussion and continuing scientific research into this difficult problem. SEE ALSO Fossil Fuels.

Elliot Richmond

Bibliography

Barnes-Svarney, Patricia. *New York Public Library Desk Reference*. New York: Macmillan, 1995.

Berger, John J. *Beating the Heat: Why & How We Must Combat Global Warming*. Berkeley, CA: Berkeley Hills Books, 2000.

Gelbspan, Ross. *The Heat Is On: The Climate Crisis, the Cover-Up, the Prescription*. Cambridge, MA: Perseus Publishing Company, Inc., 1998.

Goodstein, Eban. *The Trade-Off Myth: Fact and Fiction About Jobs and the Environment.* Washington, D.C.: Island Press, 1999.

Goodall, Jane

British Zoologist
1934–

Jane Goodall, the world's leading expert on chimpanzees, was born in London, England. Almost nothing was known about chimpanzees until Goodall conducted her field studies in East Africa. Her study of these animals in the wild has revealed that chimpanzees have many striking similarities to humans. They are our closest relatives in the animal world, having 98 percent of the same genes.

Goodall grew up on the southern coast of England. From earliest childhood, she was obsessed with animals, her favorite reading being Dr. Doolittle and Tarzan books. Goodall's unusual dream of going to Africa to live with animals was encouraged by her mother. Goodall attended secretarial school, and then got a job. When a friend invited her on a trip to Kenya, she raised money by working as a waitress. At the age of twenty-three, Goodall began her adventure, traveling to Kenya by boat. There she sought out Dr. Louis Leakey, a famous scientist who studied paleontology (the study of ancient life) and anthropology (the study of humans). She became Leakey's assistant, and he soon decided Goodall was the person he had been looking for to lead a study of wild chimpanzees in East Africa. Because the British authorities thought it unsafe for a young woman to live alone among wild animals in Africa, Goodall's mother Vanne agreed to accompany her for the first three months. In 1960, Goodall arrived at Gombe National Park in Tanganyika (now Tanzania).

In the beginning, the chimpanzees were afraid of the young woman who silently and patiently watched them. It took nearly six months for the chim-

Jane Goodall's study of chimpanzees in the wild has made her the world's leading expert on human's closest relatives.

panzees to accept her presence, allowing Goodall to follow them on their daily travels through the forest. She named the chimpanzees and grew to love them. She made one important discovery after another. It was Goodall who first learned that chimpanzees make and use tools to obtain food and defend themselves. Previously, it was believed that only humans made tools. Goodall learned that chimpanzees hunt and are occasional meat eaters. She was also first to document their complex family relationships and emotional attachments.

Goodall left Africa to study **ethology** (the scientific study of animal behavior) at the University of Cambridge. When she received her Ph.D in 1965, she was one of very few candidates to receive a Ph.D. without first having an A.B. degree. She promptly returned to Tanzania to continue her field studies and establish the Gombe Stream Research Centre. Research at this facility is still being conducted to this day, mostly by Tanzanians.

ethology animal behavior

Despite her intense studies, Goodall found the time to marry twice and raise a son, Hugo. She wrote many famous books including *In the Shadow of Man* (1971) and *The Chimpanzees of Gombe: Patterns of Behavior* (1986). Goodall has received numerous awards, including the J. Paul Getty Wildlife Conservation Prize in 1984. In 1977, Goodall established the Jane Goodall Institute, located in Washington D.C., to educate people about chimpanzees and their preservation.

Denise Prendergast

Bibliography

Muir, Hazel, ed. *Larousse Dictionary of Scientists.* New York: Larousse, 1994.

Internet Resources

The Jane Goodall Institute. <http://www.janegoodall.org>.

Steven Jay Gould has straddled the scientific and literary communities as a successful author and researcher.

Gould, Stephen Jay

Evolutionary biologist, paleontologist, and science writer
1941–

Stephen Jay Gould (1941–) is an American evolutionary biologist, paleontologist, and science writer. Gould teaches at Harvard University and is known in the lay community for his essays in the *Natural History* journal. In the scientific community he is known for his ideas on evolutionary theory. He has been awarded many literary and academic honors, including the National Book Award and a MacArthur Prize.

Born on September 10, 1941, in New York City, Gould grew up in Queens, New York. His father was a court stenographer and an accomplished amateur naturalist. At five years of age, while taking a trip with his father to the American Museum of Natural History, Gould saw a reconstruction of the dinosaur *Tyrannosaurus rex.* From then on, he was intrigued by science.

During his high school years, Gould was disappointed in the way evolution was depicted in biology textbooks. As a consequence, he began to read the original works of Charles Darwin. Gould received a B.A. from Antioch College in 1963. He was awarded a Ph.D. in paleontology from Columbia University in 1967.

Gould then became assistant professor of geology at Harvard University. In addition, he was appointed curator of invertebrate paleontology at Harvard's Museum of Comparative Zoology. At around this time he expanded his study of land snails to the West Indies and other parts of the world.

In the early 1970s Gould introduced his most noted contribution to evolutionary theory, the concept of punctuated equilibrium. Along with Niles Eldridge, he proposed that new species are created by evolutionary changes that occur in rapid bursts over periods as short as a few thousand years, separated by periods of stability in which there is little further change. This contrasts with Darwin's classical theory in which species develop slowly over millions of years at fairly constant rates.

In 1981 Gould served as expert witness in a lawsuit in Little Rock, Arkansas, that challenged a state requirement that so-called creation science be taught. He challenged the literal interpretation of the Bible, stating that Noah's flood could not account for fossil remains around the world. Partly as a result of Gould's testimony, the State of Arkansas legally acknowledged that creationism was a religion and not a science and therefore could not take the place of a scientific curriculm taught in Arkansas public schools.

Gould is widely known for his many books on natural history, paleontology, and biological evolution, including *The Mismeasure of Man* (1981), *Hen's Teeth and Horse's Toes* (1983), *The Flamingo's Smile* (1985), *Wonderful Life* (1989), and *Eight Little Piggies* (1993).

Leslie Hutchinson

Bibliography

Holmes, Frederic L. *Dictionary of Scientific Biography*, vol. 3. Edited by Charles Coulston Gillispie. New York: Scribner, 1982.

Murray, Mary. "Paean to a Leader in Evolutionary Theory." *Science News* 128, no. 67 (1986):16–26.

Growth and Differentiation of the Nervous System

The nervous system is formed of specialized cells called neurons that use electrical and chemical signals to carry information to and away from the brain. Neurons contact each other, and other tissues, at a specialized region of the cell called a **synapse**. There, chemicals called **neurotransmitters** are released by one **neuron** and received by the other. Long, thin regions of the neuron that carry information from a distant location to the neuronal cell body are called **axons** and **dendrites**. Neurons connect to, or **innervate**, every type of tissue in the body, including bones, skin, organs, and muscles. The information they carry allows organisms to sense the world, think, react, and maintain body function. Normal growth and development of the nervous system is necessary for forming a normal organism.

Genetic Basis of Development

Many of the accepted underlying mechanisms for nervous system development were discovered through research on organisms such as the frog, the fruit fly, and the nematode worm. The results of this research are valid even for human development because of a type of gene called the **Hox genes**. These genes are remarkably similar in nearly all animals, as well as plants and yeast. This is because they are so important for development in all forms of life that they have not changed very much throughout the course of evolution. Hox genes encode proteins that are expressed in different combinations and locations of the embryo. The balance of Hox gene products is so fundamental for development that, by manipulating the amount and location of the Hox proteins, developmental biologists were able to observe improper development of body parts, and misplaced, multiple, or backward limbs in animals such as frogs, chickens, and fruit flies.

Hox genes are responsible for organizing development of the portion of neural tube located within the trunk and limbs of the embryo. Segmentation of internal tissues is an evolutionary remnant from distant ancestors that had clear segmentation, such as earthworms. Thus, in the human embryo, motor and sensory neurons, as well as muscle and bone, are organized into discrete sections called embryological **somites**. The size and location of somites are defined by the extent and location of Hox gene transcription. Somites become functional units in the adult, such that each region contains neurons from the same part of the spinal cord.

Differentiation of the Nervous System

The vertebrate nervous system arises from **ectodermal** tissue of the embryo, which also gives rise to the skin. All ectoderm cells have the ability to develop into neural tissue and skin, but only those cells that are adjacent to the **notochord** do so. The notochord is an elongated, tubelike structure that runs down the midline of the embryo, underneath what will become the **spinal cord**. At the stage when the embryo is still only a sack of cells (gastrula stage), the notochord forms and releases chemicals onto the overlying ectoderm, causing those cells to differentiate into neurons. **Differentiation** is the process by which an embryonic precursor cell develops into a specialized mature cell. The first step in the differentiation of the nervous system is the formation of

synapse the space between nerve cells across which impulses are chemically transmitted

neurotransmitters chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

neuron a nerve cell

axons cytoplasmic extension of a neuron that transmits impulses away from the cell body

dendrites branched extensions of a nerve cell that transmits impulses to the cell body

innervate supplied with nerves

Hox genes also known as selector genes because their expression leads embryonic cell through specific morphologic development

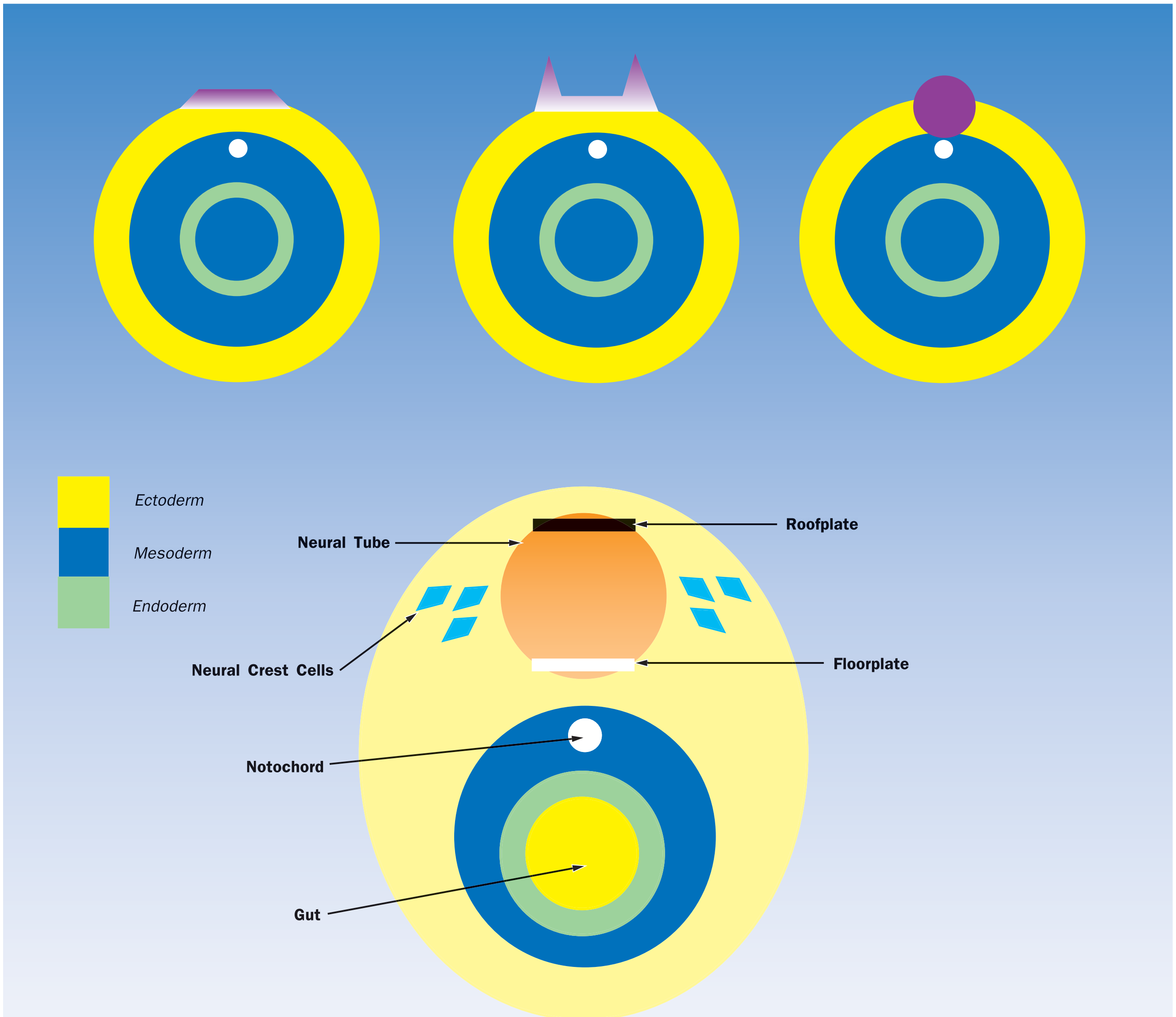
somites a block of mesoderm along each side of a chordate embryo

ectodermal relating to the outermost of the three germ layers in animal embryos

notochord a rod of cartilage that runs down the back of Chordates

spinal cord a thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

differentiation the differences in structure and function of cells in multicellular organisms as the cells become specialized



The neurula is the embryonic stage at which the neural tube forms and begins to differentiate. The neural plate is shown in the upper left figure, forming from the ectoderm. In the middle figure, the neural plate folds upwards, and in the right figure, it seals into the neural tube. In the bottom figure, ectoderm has grown over the neural tube. The floorplate has formed and begins releasing sonic hedgehog (white). The roofplate releases another differentiation factor (black). Neural crest cells (blue diamonds) migrate out of the neural tube to other regions of the body.

Cross section of the neurula.

notochord a rod of cartilage that runs down the back of chordates

a flat strip of cells called the neural plate. This structure is formed from rapidly dividing ectoderm cells. In the second step, the continued propagation of these cells forces the sides of the plate to curve upward into a neural fold, and then in the third step, the ends fuse into a neural tube. The neural tube lies above the **notochord**, and it will eventually give rise to all the nervous tissue in the body, including sensory neurons in toes and fingers, the spinal cord, optic neurons from the eye, and the brain. In the fourth step, ectodermal cells on either side of the neural tube grow over and shield the neural tube from the external environment, eventually becoming the skin that will overlie the spinal cord. In a rare congenital disease called spina bifida, this skin fails to fuse, and the baby will be born with its spinal cord exposed. When the neural tube is covered, also in the fourth step, a group of cells called neural crest cells migrates out of the neural tube and travels to different parts of the developing embryo. These cells will develop into facial bones, dentine-producing cells (for teeth), the tissue covering the brain, and glial cells, neuronal support cells, in the **peripheral nervous system**.

peripheral nervous system the sensory and motor nerves that connect to the central nervous system

The differentiation of the neural tube is most clearly illustrated by one of the best-known differentiation-inducing chemicals from the notochord, named sonic hedgehog after a Nintendo video game character. Sonic hedgehog is released from the dorsal (toward the back) notochord, and induces a specialized region of the neural tube called the floorplate. The roofplate then develops across from the floorplate at the ventral (toward the front) region, and begins to produce a different differentiating chemical called bone morphogenic protein (BMP). BMP is a completely different molecule than sonic hedgehog and it causes cells to differentiate into a different type of neuron. Large amounts of sonic hedgehog in the local environment of a cell cause it to develop into a motor (muscle-related) neuron, whereas a relatively high concentration of BMP causes differentiation into sensory (touch, temperature, and pain) neurons. This organization persists into adulthood, so that the ventral half of the spinal cord always contains sensory neurons and the dorsal half always contains motor neurons.

The portion of the neural tube located in the embryo's head uses some of the same chemical signals as the spinal cord, but differentiation occurs in a much different manner. Here, the neural tube will form into the brain. First, the tube forms into three distinct regions: the hindbrain, midbrain, and forebrain. Later, these regions specialize into the unique divisions of the mature brain. The hindbrain is very important in development because its sides swell into structures called rhombomeres, which exist only in the embryo. Rhombomeres are fundamental organizing centers because they release many chemicals that tell other parts of the neural tube how to differentiate. In the midbrain, specialized cells called isthmus cells release chemicals that establish an anterior-posterior axis. These chemicals tell cells that are located more anterior (nearer to the top of the head) to develop in a different way from those that are located more posterior (nearer to the spinal cord).

Development of the forebrain is very complex, but it is also mediated by the production of certain inducing chemical factors. Furthermore, development is shaped by the speed of cell division, meaning that regions that grow cells more quickly will be larger in the adult organism. Another means of controlling brain development is through cell migration. Many undifferentiated pre-neuronal cells are "born" near the ventricles, fluid-filled spaces located in the center of the brain, and then migrate to another region. The order of cell generations (i.e., born first, second, third, etc.) will determine what kind of neuron it will differentiate into and where it will eventually settle.

Growth of the Nervous System

As neurons mature, they grow dendrites and axons toward other cells. When dendrites and axons encounter the appropriate target cell, they will form synapses that may last for the life of the organism. Neuronal migration and growth are partly dependent on chemical guidance cues from the tissues through which they grow, and partly on specialized support cells that provide a framework along which migrating neurons can travel. One example of this migration is a sensory neuron in a seven-foot-tall person: the sensory neuron has its cell body in the spinal cord but must extend an axon to the big toe nearly three-and-a-half feet away. Chemicals in the back, thigh, leg, and foot tell the neuron in which direction to grow. Once a synapse is formed between two neurons, or between a motor neuron and a muscle fiber, the target cell releases a chemical trophic factor that sustains the synapse and the survival of the presynaptic neuron. Trophic factors keep the synapse alive and functional, but if the target cell stopped producing them the synapse would disintegrate.

Animals such as humans that are born helpless and underdeveloped do not achieve fully mature nervous systems until sexual maturity. During their first few years of life, human babies have very poor coordination, strength, perception, and cognitive abilities because their nervous system is still forming interconnections. Babies are therefore physically incapable of seeing, feeling, and understanding the world in the same manner as adults. This is one explanation for why memories from early childhood are cloudy and incomplete.

Brain growth after birth occurs by a great increase in the number of neurons and the number of synapses. However, many of these cells and many synapses die off before maturity. This is because the vertebrate method of development uses excess neurons for the embryo to accommodate environmental differences and the possibility of an accident. If the excess neurons are needed, they become active, and if active they will survive. If the neurons remain inactive, they will die. This process is inherent in the development of many organisms, even the human. Thus, if a baby is exposed to many bright colors, variable sounds, and interesting sensations, neurons in its brain will be very active and will survive. If the same baby is hidden from bright colors, hears few sounds, and is given no **tactile** stimulation, many of these neurons will die because they are not being used at an early age. Later in life, the baby in the first situation will be better able to interpret and understand the world than the baby in the second situation.

tactile related to the sense of touch

This example of neuron cell death illustrates critical periods in development. A critical period is a specific length of time in an organism's youth in which it is possible to save neurons from cell death. If the correct stimuli are not presented before the end of the critical period, that individual will never acquire normal abilities. The correct stimulus for a sensory neuron, for example, is touch, and the correct stimulus for a visual neuron is vision. One demonstration of this effect is manipulation of the visual system of the cat. If a kitten's eyes are covered between ten and twenty days after birth, the kitten will be blind for the rest of its life, even after the patches are removed. Human language, vision, hearing, and learning ability all have critical periods. These have been revealed through rare circumstances of neglect in which children are denied exposure to language and/or visual stimuli and tactile stimulation. Psychologists who studied these examples found that, after a certain age, children who have not had access to language or culture are not able to learn how to speak or interact with other humans in a normal manner. SEE ALSO NERVOUS SYSTEM.

Rebecca M. Steinberg

Bibliography

Hopkins, W. G., and M. C. Brown. *Development of Nerve Cells and Their Connections.* New York: Cambridge University Press, 1984.

Le Douarin, Nicole, and Chaya Kalcheim. *The Neural Crest.* Cambridge, U.K.: Cambridge University Press, 1999.

Rymer, Russ. *Genie: A Scientific Tragedy.* New York: Harper Perennial, 1994.

Spitzer, Nicholas C. *Neuronal Development.* New York: Plenum Press, 1982.

Stein, Donald G. *Development and Plasticity in the CNS: Organismic and Environmental Influences.* Worcester, MA: Clark University Press, 1988.

Habitat

A habitat is the environment in which an organism, species, or community lives. Habitats can be classified in a number of ways in order to compare them at different times, across different geographic areas, and in terms of different life history strategies.

Within nearly every type of habitat there exists a species that has adapted to that habitat, from the deep ocean floor to the polar ice caps. These specializations mean that the organism can survive in one type of habitat but not necessarily in another, a concept termed **habitat requirement**. Organisms that are free to move about can choose which habitat they will live in, and these choices are made based on the costs and benefits of each place.

habitat requirement the necessary conditions or resources needed by an organism in its habitat

In order to make comparisons between the many that exist, habitats need to be classified in some manner. First, it is important to understand that what is a good environment to one organism, such as the middle of the ocean for a shark, may not be good for another, such as a desert-dwelling lizard. Thus, classification of habitat types is usually done in reference to a certain species or group of species.

One method of classifying habitats is temporally. Over time a habitat may be constant, with little change from the viewpoint of a particular organism, or it may be seasonal, where there is a predictable pattern of favorable and unfavorable periods for that organism. An example of a constant environment is a cave. A cave's temperature stays at a constant temperature, within a few degrees of the mean annual temperature of the area; therefore, a bat can find refuge from the extreme high and low daily temperatures. The cave is also a consistent shelter for the bat because there is no rain in a cave.

Habitats can also be unpredictable, alternating between favorable and unfavorable periods for variable amounts of time, or ephemeral, meaning there are periods that are predictably short followed by unfavorable periods of variable, frequently extensive duration. To a water-loving amphibian, ephemeral habitats are intermittent streams that only run after heavy rainfalls and dry up to an uninhabitable state between rains.

If classifying habitats spatially, they can either be constant, with a fairly uniform distribution of resources like food and refuge, or they can be patchy, with resources occurring in small, dense locations that are scattered around an area that is otherwise without any resources. It is easy to see how these different habitats could select for different behaviors, including types of locomotion, searching, and communication among individuals to relay locations of food patches or defend territories.

Many species, such as the Canadian polar bear, have adapted to a variety of habitat changes.

Habitats can also be classified by their effects on the growth and life history of the species in question. On the one hand, in size-beneficial habitats large individuals have a greater chance to successfully compete and reproduce within their own species. For example, a large male deer that successfully defends a harem of females is more likely to mate. Also, the risk of predation may be greater for smaller adult deer, which are subject to attacks by wolves.

On the other hand, certain habitats are size-neutral or size-detrimental. In these habitats mortality may occur equally to all individuals, such as when a seasonal spring dries up. Or in such a habitat larger individuals may have a disadvantage; for example, an aerial predator may find it easier to see larger individuals or find it more worthwhile to chase them because of the greater food reward. Additionally, in a resource-rich environment there may be no within-species competition that would favor larger individuals.

The type of growth that is preferred in a given habitat will often correlate to the reproductive strategy of a species. In a size-beneficial habitat it is advantageous to reproduce less frequently and have fewer, larger offspring. This is also called a ***k*-selecting habitat**. A reproductive adult may have to delay reproduction for a long time in order to store the energy necessary to produce a large offspring. That offspring will then have a much better chance at survival. In a size-neutral or detrimental habitat, producing smaller, greater numbers of offspring is often a good strategy. This is also known as an ***r*-selecting habitat**.

***k*-selecting habitat** habitat where there is a high cost of reproduction and is sensitive to the size of the offspring

***r*-selecting habitat** the concept where a high reproductive rate is the chief determinant of life history

Habitats are as varied as the animals that live in them and each could be infinitely described, but another general way to think of them is according to their measurable characteristics, or parameters. Examples of habitat parameters, or characteristics, include temperature, moisture, substrate type, nutrient availability, altitude (or depth in water), and amount of light and wind (or current in water). Each of these parameters shapes the organisms that live there or imposes certain habitat requirements that limit the types of organisms that can move in.

Consider the cave example again. This habitat has a constant temperature, high moisture, low nutrient availability, and no light. Because of these characteristics, organisms that evolved to live in caves lose the ability to withstand temperature extremes and low moisture but in exchange gain the ability to withstand long periods with little food, partially by lowering their metabolism relative to their surface-dwelling relatives.

Other lost features of cave-dwelling organisms are sight, which takes considerable energy, and pigment, two things totally unnecessary in a habitat with constant darkness. These habitat parameters also restrict the kinds of animals that can successfully move into the cave environment. Raccoons, even though they are not cave adapted, can use the cave because they are nocturnal and accustomed to using their keen sense of smell to find their way through the dark and hunt for food.

These examples make it easier to understand the complexity of habitats and their specialized requirements. Because most organisms have adapted to their habitats and may not necessarily survive in another, it is extremely important to maintain habitats in their natural state in order to ensure the survival of the species that live there. SEE ALSO BIOMES; ECOSYSTEMS; ENVIRONMENT; HABITAT LOSS; HABITAT RESTORATION.

Jean K. Krejca

Bibliography

Begon, Michael, John L. Harper, and Colin R. Townsend. *Ecology*, 2nd ed. Cambridge, MA: Blackwell Scientific Publications, 1990.

Dunell, Lee. *State of the Ark: An Atlas of Conservation in Action*. London, U.K.: Gaia Books, 1986.

Shafer, Craig L. *Nature Preserves: Island Theory and Conservation Practice*. Washington, D.C.: Smithsonian Institution Press, 1990.

Smith, Robert L. *Elements of Ecology*, 2nd ed. New York:

Habitat Loss

Many biologists consider habitat loss, habitat degradation, and habitat fragmentation the primary threats to species survival. Habitat is the place or kind of place where an organism or a community of organisms lives and

This waste wood came from the mining of a tropical rain forest in Borneo.

thrives. Habitat loss occurs when habitat is converted to other uses, such as when a wetland is filled or a prairie is covered by housing developments. Habitat degradation occurs when the habitat is so diminished in quality that species are no longer able to survive. Urban development can degrade a habitat because plants and soil are replaced with asphalt and concrete. Water runs off instead of soaking in. Average temperature goes up because the asphalt and concrete absorbs more solar energy. Fragmentation occurs when terrestrial habitats are separated into small, isolated fragments. Even when the total acreage of habitat appears to be sufficient, the fragmentation prevents species from surviving.

Some species have a very limited habitat. For example, as its name implies, the habitat of the creosote bush grasshopper, *Bootettix argentatus*, is the creosote bush, *Larrea tridentata*. It is found nowhere else. Most animals avoid the creosote bush and find the leaves distasteful or even toxic, whereas this small grasshopper thrives on the leaves. If the creosote bush were to become extinct, so would the little grasshopper.

Fortunately for *Bootettix argentatus*, there are plenty of creosote bushes and neither the plant nor the grasshopper is in danger. This is not true for many other animals. The Texas horned lizard, *Phrynosoma cornatum*, has become so rare in much of its original range that it has been listed as a threatened species. Many people who grew up in Texas and Oklahoma in the 1940s and 1950s remember playing with this docile and easily caught lizard commonly called "horny toad" or "horned frog." The lizard's habitat is open dry country with loose soil (for burrows), supporting grass, mesquite, cactus, and plenty of the large ants they prefer to eat.

Several factors have caused the decline in population of Texas horned lizards (and the other horned lizard species as well). Many are taken for the pet trade. This is unfortunate, as they do not make good pets and most starve to death within a few months. Another factor contributing to the decline is the displacement of native ants by imported fire ants, *Solenopsis invicta*. Texas horned lizards feed almost exclusively on a few species of large red ants, such as harvester ants. Imported fire ants drive harvester ants and other ants out of their range, thus depriving the horned lizards of their primary food supply.

Many biologists believe that the major cause of the decline of the Texas horned lizard is the loss of habitat. The open areas with prickly pear, sparse grass, and mesquite are being converted into farmland and housing subdivisions. Of course, the first thing many homeowners do when moving into a new subdivision is to start eradicating the ants. People do require living space, clean water, food, and a safe environment, but there are many things that humans can do to reduce or prevent loss of habitat.

Causes

Many human activities can cause habitat loss, degradation, or fragmentation. In addition to urbanization, industrial agriculture, improper forest management, overgrazing, poorly managed mining, water development projects, pollution, the introduction of non-native species, and fire suppression all degrade habitat.

Urbanization. Industrial agriculture is the main cause of habitat loss while urbanization is the major hindrance to species recovery. Urbanization is a complex process that involves a progressive increase of the percentage of a population that lives in an urban area and a corresponding decrease in the percentage of people living in rural areas. Urbanization is often accompanied by urban sprawl as the city expands to accommodate an ever-increasing population. Managing urban sprawl is an enormously difficult and political process.

Many urban and suburban developments try to preserve "green belts" for aesthetic and other reasons, but habitat fragmentation still occurs. For example, by the early 1990s urban sprawl in California had reduced the indigenous coastal sage scrub ecosystem by more than 90 percent. Coastal sage is the habitat of the threatened California gnatcatcher. The remaining 10 percent of sage scrub is broken up into small fragments. Instead of four or five large patches containing thousands of hectares, there are now hundreds of widely separated tiny patches of a few hectares each. These patches are too small to support healthy populations of California gnatcatchers.

Industrial agriculture. Nearly half of the land area in the United States is devoted to agriculture. There are 472 million acres in cropland and 587 million acres in range or pasture. According to ecologist Curtis Flather and others, massive single crop industrial agriculture is the leading cause of habitat destruction in the United States, substantially affecting our forests, rangelands, and wetlands. Nearly 90 percent of recent wetland losses are due to agricultural practices.

Deforestation. In many parts of the world, logging, grazing, and mining are the major threats to endangered ecosystems and species. Deforestation occurs when trees are removed at a rate faster than they can be replanted. Habitat degradation occurs when the largest and oldest trees are removed, leaving behind scrubby stands of small and immature trees. Worldwide, deforestation is decimating tropical rain forests with enormous habitat loss.

RATES OF DESTRUCTION OF BRAZIL'S TROPICAL RAIN FORESTS

Brazil, a country that is 8,511,960 square kilometers (3,286,969 square miles), originally was home to 2,860,000 square kilometers of rainforest. In 2001, the coverage had been reduced to 1,800,000 square kilometers. The annual rate of deforestation, then, works out to be 2.3%, or 50,000 square kilometers. This is the equivalent of 1000 football fields every year in Brazil alone.

Worldwide, scientists estimate that nearly all the tropical rainforest ecosystems will be destroyed by the year 2030 if the current rate of deforestation continues.

Logging activities can have devastating impacts on habitats and the wildlife in those habitats. In the United States 260 threatened and endangered species live in our national forests. Poorly planned clear-cutting and building of logging roads degrade habitat by removing large stands of trees and fragmenting the remainder. Logging and the construction of timber roads also cause erosion that can clog streams with silt.

Grazing. Livestock grazing is the most widespread of the federally subsidized, private commercial practices operating on public lands. Commercial livestock grazing is allowed on 270 million acres of land managed by the federal government. Poorly managed livestock grazing (including overgrazing) can severely damage wildlife habitat by changing the species composition of native ecological communities. In addition to directly destroying habitat, overgrazing has a number of indirect impacts. For example, land users often try to kill predators or species that may compete with livestock for food.

riparian habitats in rivers and streams

Mining. Mining is the extraction of useful materials from the ground. Surface mining strips away overlying soil and rock, removing the useful material (usually coal) and then replacing the rock and soil. Properly done, surface mining can leave some habitats in good condition. Improperly managed mining significantly degrades ecosystems by degrading habitat and by polluting and degrading streams and waterways. Even well-managed mining increases road building. Poorly managed surface mining can destroy the surface ecosystem. In addition, mining requires a large amount of underground material to be brought to the surface. These materials, when exposed to rain, can create runoff that is highly acidic or has high concentrations of metal ore, both of which are highly toxic to aquatic species.

Mining for coal at this site in Pennsylvania is done using the "strip mining" method. This technique physically moves the soil back from the coal bed. Strip mining causes at least a temporary elimination of the native animals' habitat.

Water development projects. Water development projects include dams, dredging, stream channelization, flood control structures, and canals. These projects adversely affect species in a number of ways. The natural flow of rivers and streams may be disrupted. **Riparian** (stream bank) habitat may be destroyed, fragmented, or degraded. Because riparian habitat is often unique to a region, water development projects have the potential to destroy a habitat entirely. Water projects also alter water flow, which may change wetlands, marshes, and other downstream habitat. For example, in the portion of the Colorado River that flows through the Grand Canyon, the river habitat has been completely changed by the construction of Lake Powell and the Glen Canyon dam. The red, silt-laden Colorado River with its frequent floods has been replaced by a cold, clear river that never floods. Native species of fish cannot tolerate the cold water, although imported species such as rainbow trout do well. The riparian habitat has been completely changed as well. When the Colorado River flooded, it stripped vegetation from the banks and built large sandbars. Now the banks are covered with another imported species, tamarisk or salt cedar, and the sandbars are disappearing.

Introduction of non-native species. After outright habitat destruction, many biologists consider the introduction of exotic species to be the primary threat to rare and native species and even to complete ecosystems. Non-native species change the vegetation, compete with native species, and prey on native species. Hawaii, California, and Florida face particularly severe problems with exotic species. In Hawaii introduced species are now considered to be the single greatest cause of extinction of the state's native **fauna** and **flora**. For example, the introduction of cattle to the state has destroyed many plant communities. Many species in Hawaii, such as the hau hele 'ula (Hawaiian tree cotton), have been placed on the threatened or endangered species lists.

fauna animals

flora plants

Pollution. Pollution damages and degrades ecosystems in many ways. Airborne pollutants such as acid precipitation often affect natural communities miles away from the source. Acid rain and acid fog destroy northern forests, lakes, and streams hundreds or thousands of kilometers from the source of the pollutants. Acid precipitation can lower the pH of streams and lakes to the point that some fish are unable to reproduce and some die. Acid rain can cause chemical reactions in the soil that release metallic elements, such as aluminum. These elements can enter water supplies, damaging fish or other organisms. More than a billion pounds of toxic chemicals, including mercury and lead, were discharged directly into America's waters between 1990 and 1994, according to the Environmental Protection Agency. Thirty million pounds of these chemicals were known to cause cancer.

Fire suppression. For decades in the United States, we have assumed that suppression of fire was a good thing. Fire kills wildlife, destroys trees and grasslands, and damages property. Now we realize that many ecosystems depend on fire for their survival. Fire suppression allows other species to flourish, changing the species composition. For example, in Central Texas the hills are covered with Ashe juniper, a small native tree commonly called cedar. When Europeans first saw these hills, they were covered by thick, tall grass with only a few stands of cedar. Frequent wildfires swept over the hills, burning both grass and trees. However, the grass quickly recovered after the fire, whereas many trees were permanently removed. Thus the fire helped to maintain a balance between grass and trees. The suppression of fire and overgrazing disrupted that balance. Now the trees dominate and open grassy areas are rare. The distribution of animal species also changed.

Fire is an integral part of many ecosystems, maintaining the ecosystem's natural vegetation. There are many plant species that require fire to trigger the release of their seeds. Fire also clears out the underbrush in forests, and the prevention of all forest fires actually leads to fires that burn hotter and longer because of the accumulation of underbrush. Thus the suppression of all fires leads to habitat destruction and degradation. If handled judiciously to protect life and property, fires can restore an ecosystem's natural balance.

Recreation. Sometimes we love our natural areas to death. Recreation takes a great toll on wildlife and habitats, especially inappropriate recreational uses of open land. Probably the most destructive form of outdoor recreation is the improper use of off-road vehicles. These vehicles can provide access to remote areas otherwise unreachable. Improper operation of these vehicles can result in the harassment and inadvertent killing of wildlife. For example, vehicles can crush desert tortoises or the eggs of sea turtles and piping plover on beaches. These vehicles can also cause acceleration of soil compaction and erosion, pollution of water and air, and destruction of vegetation. Other forms of recreation, such as hiking and backpacking, are generally less harmful, but all recreational activities involve some harm to the environment.

Effects of Habitat Loss on Animal Species

Ecologists Curtis Flather, Linda Joyce, and Carol Bloomgarden studied the pattern of endangered species in the United States for the National Forest Service. In a report published in 1994, they concluded that habitat destruction was the leading cause of species endangerment, threatening 80 percent or more of federally listed species. They also found that habitat destruction and degradation was at least part of the reason why more than 95 percent of species listed as endangered or threatened were imperiled. In a different study of taxpayer-subsidized resource extraction, researchers found that logging affects approximately 14 to 17 percent of listed species, grazing affects 19 to 22 percent, water development affects 29 to 33 percent, recreation affects 23 to 26 percent, and mining affects 14 to 21 percent.

Habitat loss and degradation is a factor in the decline of every category of species. The decline of nearly 40 percent of migrant bird populations is directly linked to habitat destruction. For amphibians, declining populations are linked to habitat destruction, introduction of exotic species, water pollution, and ozone depletion.

Habitat Protection

The 1973 Endangered Species Act (ESA) has been a great success. Many species, such as the American alligator, have been brought back from the brink of extinction to healthy populations. However, many biologists question the species focus of the ESA. Rather, a focus on preserving extensive habitats is thought to be the best way to prevent the loss of wild species. Preservation can be achieved through a worldwide system of reserves, parks, and other protected areas. The plan put forward by biologists is ambitious, with a goal of setting aside 10 percent of Earth's land area. These preserves would conserve and manage entire ecosystems. This approach would be cheaper and more cost-effective than managing species one by one and would require less human intervention to prevent extinction. Activities in the preserves could include research and education as well as limited commercial activities such as **ecotourism**.

ecotourism tourism that involves travel to areas of ecological or natural interest usually with a naturalist guide

Elliot Richmond

Bibliography

Jasney, Michael. *Leap of Faith: Southern California's Experiment in Natural Community Conservation Planning.* New York: Natural Resources Defense Council, 1997.

LaRoe, Edward T. "Biodiversity: A New Challenge." In *Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems,* ed. by Edward T. LaRoe, Gaye S. Farris, Catherine E. Duckett, Peter D. Doran, and Michael J. Mae. Washington, D.C.: National Biological Service, U.S. Department of the Interior, 1995.

Losos, Elizabeth, Justin Hayes, Ali Phillips, David Wilcove, and Carolyne Alkire. "Taxpayer-Subsidized Resource Extraction Harms Species." *Bioscience* 45, no. 7, (1995): 446–455.

Miller, G. Tyler, Jr. *Living in the Environment,* 6th ed. Belmont, CA: Wadsworth, 1990.

Noss, Reed F., and Allen Y. Cooperrider. *Saving Nature's Legacy: Protecting and Restoring Biodiversity.* Washington, D.C.: Island Press, 1994.

———, Edward T. LaRoe, and J. Michael Scott. *Endangered Ecosystem of the United States: A Preliminary Assessment of Loss and Degradation.* Washington, D.C.: U.S. Geological Survey, 1995.

———, and Robert L. Peters. *Endangered Ecosystems: A Status Report on America's Vanishing Habitat and Wildlife.* Washington, D.C.: Defenders of Wildlife, 1995.

Snape William J., and Robert M. Ferris. *Saving America's Wildlife: Renewing the Endangered Species Act.* Washington, D.C.: Defenders of Wildlife, 1995.

Wilcove, David S., M. J. Bean, R. Bonnie, and M. McMillan. *Rebuilding the Ark: Toward a More Effective Endangered Species Act for Private Land.* Washington, D.C.: Environmental Defense Fund, 1996.

Wilson, E. O. *The Diversity of Life.* Cambridge, MA: Belknap Press of Harvard University Press, 1992.

Photo and Line Art Credits

The illustrations and tables featured in Animal Sciences were created by GGS Information Services. The photographs appearing in the text were reproduced by permission of the following sources:

Volume One

Acoustic Signals (**4**): Zig Leszczynski/Animals Animals; *Adaptation* (**7**): JLM Visuals, Ken Cole/Animals Animals; *African Cichlid Fish* (**9**): Gerard Lacz/Animals Animals; *Aggression* (**11**): Lynn Stone/Animals Animals; *Agnatha* (**14**): Omikron, National Audobon Society Collection/Photo Researchers, Inc.; *Allometry* (**16**): Redrawn from Scott Gilbert; *Allometry* (**15**): Redrawn from Scott Gilbert; *Altruism* (**18**): Robert J. Huffman/Field Mark Publications; *Amphibia* (**20**): Robert J. Huffman/Field Mark Publications; *Animal Rights* (**25**): AP/Wide World Photos; *Animal Testing* (**29**): Yann Arthus-Bertrand/Corbis; *Annelida* (**31**): E. R. Degginger/Animals Animals; *Antibody* (**34**): Redrawn from Hans and Cassady; *Antlers and Horns* (**35**): Kennan Ward/Corbis; *Apiculture* (**37**): Breck P. Kent/Animals Animals; *Aposematism* (**39**): R. Andrew Odum, Toledo Zoological Society; *Aquaculture* (**42**): David Samuel Robbins/Corbis; *Aristotle* (**45**): UPI/Bettmann Newsphotos/Corbis; *Arthropoda* (**47**): Dr. Dennis Kunkel/Phototake; *Arthropoda* (**50**): JLM Visuals; *Aves* (**53**): Joe McDonald/Animals Animals; *Bailey, Florence Augusta Merriam* (**57**): Courtesy of the Library of Congress; *Bates, Henry Walter* (**58**): Courtesy of the Library of Congress; *Behavior* (**60**): Ross, Edward S., Dr.; *Behavior* (**61**): Carl Purcell/Corbis; *Binomial (Linnaean System)* (**64**): Archive Photos, Inc.; *Biodiversity* (**68**): Joerg Sarback/AP/Wide World Photo; *Bioethics* (**71**): Jacques M. Chenet/Corbis; *Bioethics* (**70**): Robyn Beck/Corbis; *Biological Evolution* (**75**): Sally Morgan/Ecoscene/Corbis; *Biological Evolution* (**76**): P. Parks-OSF/Animals Animals; *Biological Pest Control* (**80**): Bill Beatty/Animals Animals; *Biomechanics* (**84**): Brad Nelson/Phototake; *Biomes* (**88**): W. Wayne Lockwood, M.D./Corbis; *Biomes* (**89**): Robert J. Huffman/Field Mark Publications; *Blood* (**98**): Richard T. Nowitz/Phototake; *Body Cavities* (**100**): Redrawn from Holt, Rinehart and Winston; *Body Cavities* (**101**): Nancy Sefton, National Audobon Society Collection/Photo Researchers, Inc.; *Body Plan* (**108**): JLM Visuals; *Bone* (**111**): CNRI/Phototake; *Burgess Shale and Ediacaran Faunas* (**113**): Lowell Laudon/JLM Visuals; *Cambrian Explosion* (**117**): Robert J. Huffman/Field Mark Publications; *Cambrian Period* (**119**): Mickey Gibson/Earth Scenes; *Camouflage* (**120**): Art Wolfe/The National Audubon Society Collection/Photo Researchers, Inc.; *Cancer* (**123**): Luis M. De La Maza/Phototake; *Carson, Rachel* (**128**): UPI/Bettmann Newsphotos/Corbis; *Cartilage* (**129**): Dr. Mary Notter/Phototake; *Cell Division* (**134**): Redrawn from Gale Research; *Cells* (**136**): Redrawn from New York Public Library Desk Reference; *Cephalization* (**139**): P. Parks-OSF/Animals Animals; *Cestoda* (**142**): Custom Medical Stock Photo, Inc.; *Chitin* (**143**): Chris McLaughlin/Animals Animals; *Chondricthyes* (**145**): Joyce and Frank Burek/Animals Animals; *Chordata* (**147**): Ralph White/Corbis; *Circadian Rhythm* (**150**): George McCarthy/Corbis; *Circulatory system* (**152**): GCA/CNRI/Phototake; *Cnidaria* (**155**): Nancy Rotenberg/Animals Animals; *Coevolution* (**161**): Robert J.

Huffman/Field Mark Publications; *Coevolution* (**159**): Michael and Patricia Fogden/Corbis; *Communication* (**165**): James E. Lloyd/Animals Animals; *Community Ecology* (**168**): Richard Baetson/U.S. Fish and Wildlife Service, Washington D.C.; *Competition* (**174**): Ross, Edward S., Dr.; *Conservation Biology* (**177**): Fred Whitehead/Animals Animals; *Constraints on Animal Development* (**179**): Robert Lubeck/ Animals Animals; *Convergence* (**185**): E. R. Degginger/Animals Animals; *Courtship* (**186**): Michael Fogden/Animals Animals.

Volume Two

Cretaceous (**2**): Richard P. Jacobs/JLM Visuals; *Cultures and Animals* (**6**): Duluth Convention and Visitor's Bureau; *Cultures And Animals* (**8**): Craig Lovell/Corbis; *Darwin, Charles* (**10**): Courtesy of the Library of Congress; *DDT* (**12**): AP/Wide World Photos; *Defense* (**14**): Mark N. Boulton/The National Audubon Society Collection/Photo Researchers, Inc.; *Diamond, Jared* (**18**): AP/Wide World Photos; *Digestive System* (**22**): Roger De La Harpe/ Animals Animals; *Dinosaurs* (**25**): Graves Museum of Archaeology and Natural History/ AP/Wide World Photos; *Domestic Animals* (**29**): Tim Thompson/Corbis; *Dominance Hierarchy* (**32**): Tim Wright/Corbis; *Drosophila* (**34**): UPI/Bettmann Newsphotos/Corbis; *Echinodermata* (**36**): Herb Segars/Animals Animals; *Ecology* (**42**): U.S. National Aeronautics and Space Administration (NASA); *Ecosystem* (**47**): James Watt/Animals Animals; *Elton, Charles Sutherland* (): Animals Animals/©; Scott Johnson; *Embryology* (**52**): Science Pictures Limited/Corbis; *Embryonic Development* (**54**): Redrawn from Scott Gilbert; *Embryonic Development* (**59**): Redrawn from Scott Gilbert; *Endangered Species* (**62**): Vince Streano/The Stock Market; *Entomology* (**72**): Doug Wechsler/Earth Scenes; *Environmental Degradation* (**74**): George H. H. Huey/Earth Scenes; *Environmental Impact* (**78**): David Barron/Earth Scenes; *Excretory and Reproductive Systems* (**88**): Joe McDonald/ Animals Animals; *Exotic Species* (**91**): C. C. Lockwood/Animals Animals; *Extinction* (**100**): Glen Smart/U.S. Fish and Wildlife Service/ Washington, D.C.; *Extremophile* (**103**): TC Nature/Animals Animals; *Farming* (**105**): Tim Page/Corbis; *Feeding* (**111**): Malcolm S. Kirk/Peter Arnold, Inc.; *Feeding Strategies* (**114**): Bruce Davidson/Animals Animals; *Fertilization* (**117**): Hank Morgan/National Audobon Society Collection/Photo Researchers, Inc.; *Flight* (**122**): Zefa Germany/ The Stock Market; *Foraging Strategies* (**130**): Suzanne Danegger/Photo Researchers, Inc.; *Fossey, Dian* (**131**): AP/Wide World Photos; *Fossil Fuels* (**133**): H. David Seawell/Corbis; *Functional Morphology* (**137**): Tim Davis/Photo Researchers; *Genes* (**140**): Biophoto Associates/ National Audobon Society Collection/Photo Researchers, Inc.; *Genetic Engineering* (**149**): Lowell Georgia/Corbis; *Genetic Variation In A Population* (**153**): Eastcott-Momatiuk/Animals Animals; *Genetically Engineered Foods* (**156**): Lowell Georgia/Corbis; *Geneticist* (**157**): Photo Researchers, Inc.; *Genetics* (**160**): AP/ Wide World Photos; *Gills* (**164**): Breck P. Kent/Animals Animals; *Global Warming* (**168**): Bernard Edmaier/Science Photo Library/ Photo Researchers, Inc.; *Goodall, Jane* (**171**): AP/Wide World Photos; *Gould, Steven Jay* (**172**): Wally McNamee/Corbis; *Habitat* (**178**): Johnny Johnson/Animals Animals; *Habitat Loss* (**180**): Ecoscene/Corbis; *Habitat Loss* (**182**): Francois Gohier/National Audubon Society Collection/Photo Researchers, Inc.

Volume Three

Habitat Restoration (**3**): Eastcott-Momatiuk/ Earth Scenes; *Haeckel's Law Of Recapitulation* (**5**): Courtesy of the Library of Congress; *Haldane, J. B. S.* (**6**): Courtesy of the Library of Congress; *Heterochrony* (**9**): Christian Testu/ BIOS; *Home Range* (**11**): Darren Bennet/ Animals Animals; *Hormones* (**17**): Barbra Leigh/Corbis; *Horse Trainer* (**19**): Jerry Cooke/Animals Animals; *Human Commensal and Mutual Organisms* (**31**): LSF OSF/Animals Animals; *Human Evolution* (**35**): John Reader/ Science Photo Library/Photo Researchers, Inc.; *Human Populations* (**41**): AP/Wide World Photos; *Human–Animal Conflicts* (**28**): John Nees/Animals Animals; *HunterGatherers* (**44**): Anthone Bannister/Earth Scenes; *Hunting* (**46**): Raymond Gehman/Corbis; *Imprinting* (**50**): Robert J. Huffman/Field Mark

Publications; *Instinct* (**52**): Anup Shah/Animals Animals; *Interspecies Interactions* (**55**): JLM Visuals; *Iteroparity And Semelparity* (**58**): Kennan Ward/The Stock Market; *Jurassic* (**60**): E. R. Degginger/Earth Scenes; *Keratin* (**63**): L. Lauber-OSF/Animals Animals; *Lamarck* (**69**): Courtesy of the Library of Congress; *Leakey, Louis And Mary* (**70**): UPI/Bettmann Newsphotos/Corbis; *Learning* (**72**): Erwin and Peggy Bauer/Animals Animals; *LeviMontalcini, Rita* (**74**): AP/Wide World Photos; *Linnaeus, Carolus* (**77**): U.S. National Library of Science; *Living Fossils* (**80**): Tom McHugh/Steinhart Aquarium/ Photo Researchers, Inc.; *Locomotion* (**88**): Jeffrey L. Rotman/Corbis, Richard Alan Wood/Animals Animals, Ross, Edward S., Dr., Robert Winslow/Animals Animals; *Lorenz, Konrad* (**91**): UPI/Bettmann Newsphotos/Corbis; *Malaria* (**95**): Redrawn from Hans and Cassady; *Malthus, Thomas Robert* (**98**): Archive Photos, Inc.; *Mammalia* (**103**): Leonard Lee Rue III/Animals Animals; *Mayr, Ernst* (**106**): AP/Wide World Photos; *Mendel, Gregor* (**108**): Archive Photos, Inc.; *Mesenchyme* (**110**): Lester V. Bergman/Corbis; *Migration* (**117**): AP/Wide World Photos; *Mimicry* (**122**): Breck P. Kent/Animals Animals; *Molecular Biologist* (**126**): Philippe Plailly/National Audubon Society Collection/ Photo Researchers, Inc.; *Molting* (**135**): Ross, Edward S., Dr.; *Morphological Evolution in Whales* (**137**): Bomford/T.Borrill-OSF/ Animals Animals; *Mouth, Pharynx, Teeth* (**141**): H. Pooley/OSF/Animals Animals; *Muscular System* (**143**): Custom Medical Stock Photo, Inc.; *Museum Curator* (**145**): Robert J. Huffman/Field Mark Publications; *Natural Resources* (**147**): Richard Hamilton Smith/Corbis; *Nematoda* (**151**): Eric V. Grave/ Photo Researchers, Inc.; *Nervous System* (**157**): Redrawn from Neil Campbell.; *Nervous System* (**155**): Secchi-Lecague/Roussel-UCLAF/ CNRI/Science Photo Library/National Audubon Society Collection/Photo Researchers, Inc.; *Osteichthyes* (**169**): A. Kuiter/OSF/ Animals Animals; *Parasitism* (**179**): Frank Lane Picture Agency/Corbis; *Pasteur, Louis* (**180**): Courtesy of the Library of Congress; *Peppered Moth* (**186**): Breck P. Kent/Animals Animals.

Volume 4

Permian (**2**): Richard P. Jacobs/JLM Visuals; *Pesticide* (**4**): Arthur Gloor/Earth Scenes; *Phylogenetic Relationships of Major Groups* (**6**): Redrawn from Caroline Ladhani.; *Plankton* (**12**): Douglas P. Wilson/Frank Lane Picture Agency/Corbis; *Pleistocene* (**16**): Breck P. Kent/Earth Scenes; *Pollution* (**21**): Wesley Bocxe/National Audubon Society Collection/ Photo Researchers, Inc.; *Population Dynamics* (**26**): Wolfgang Kaehler/Corbis; *Populations* (**32**): JLM Visuals; *Predation* (**37**): Johnny Johnson/Animals Animals; *Primates* (**40**): Barbara Vonn Hoffmann/Animals Animals; *Reproduction, Asexual and Sexual* (): Animals Animals/©; Zig Leszczynski; *Reptilia* (**52**): Animals Animals/©; Zig Leszczynski; *Respiration* (**55**): Ron Boardman, Frank Lane Picture Agency/Corbis; *Respiratory System* (**58**): Photo Researchers, Inc.; *Rotifera* (**60**): P. Parks/OSF/Animals Animals; *Scales, Feathers, and Hair* (**62**): Dr. Dennis Kunkel/Phototake; *Selective Breeding* (**65**): George Bernard/ Animals Animals; *Sense Organs* (**68**): Robert J. Huffman/Field Mark Publications; *Sexual Dimorphism* (**74**): Gregory G. Dimijian/Photo Researchers, Inc.; *Sexual Selection* (**77**): Animals Animals/©; Darren Bennett; *Shells* (**81**): Spreitzer, A.E., Mr.; *Simpson, George Gaylord* (**85**): Courtesy of the Library of Congress; *Skeletons* (**86**): E. R. Degginger/ Animals Animals; *Social Animals* (**91**): G. I. Bernard/OSF/Animals Animals; *Sociality* (**95**): JLM Visuals;*Stevens, Nettie Maria* (**99**): Science Photo Library/Photo Researchers, Inc.; *Sustainable Agriculture* (**101**): Michael Gadomski/Earth Scenes; *Territoriality* (**106**): Jack Wilburn/Animals Animals; *Threatened Species* (**113**): Kenneth W. Fink/Photo Researchers, Inc.; *Tool Use* (**115**): C. Bromhall/ OSF/Animals Animals; *Trematoda* (**123**): Photo Researchers, Inc.; *Triassic* (**125**): Robert J. Huffmann/Field Mark Publications; *Urochordata* (**130**): Joyce and Frank Burek/ Animals Animals; *Vertebrata* (**132**): Breck P. Kent/JLM Visuals; *Veterinarian* (**134**): Peter Weiman/Animals Animals; *Viruses* (**136**): Scott Camazinr/National Audubon Society Collection/Photo Researchers, Inc.; *Vision* (**139**): J. A. L. Cooke/OSF/Animals Animals;

Vocalization (**142**): Victoria McCormick/Animals Animals; *Von Baer's Law* (**143**): Courtesy of the Library of Congress; *Water Economy In Desert Organisms* (**147**): Langley, Cory, Mr., (**148**): Maslowski/Photo Researchers, Inc.; *Wild Game Manager* (**150**): Raymond Gehman/Corbis; *Wildlife Biologist* (**152**): Mark Stouffer/Animals Animals; *Wildlife Photographer* (**153**): Johnny Johnson/Animals Animals; *Wilson, E. O.* (**154**): AP/Wide World Photos; *Xenopus* (**156**): Zig Leszczynski/Animals Animals, Dr. Dennis Kunkel/Phototake; *Zoological Parks* (**159**): Alfred B. Thomas/Animals Animals; *Zoologist* (**162**): N. Rosing/OSF/Animals Animals; *Zooplankton* (**164**): M. I. Walker/Science Photo Library/National Audubon Society Collection/Photo Researchers, Inc.

Glossary

abiogenic: pertaining to a nonliving origin

abiotic: nonliving parts of the environment

abiotic factors: pertaining to nonliving environmental factors such as temperature, water, and nutrients

absorption: the movement of water and nutrients

acid rain: acidic precipitation in the form of rain

acidic: having the properties of an acid

acoelomate: an animal without a body cavity

acoelomates: animals without a body cavity

acoustics: a science that deals with the production, control, transmission, reception, and effects of sound

actin: a protein in muscle cells that works with myosin in muscle contractions

action potential: a rapid change in the electric charge of the cell membrane

active transport: a process requiring energy where materials are moved from an area of lower to an area of higher concentration

adaptive radiation: a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

adenosine triphoshate: an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

aestivate: a state of lowered metabolism and activity that permits survival during hot and dry conditions

agnostic behavior: a type of behavior involving a contest of some kind that determines which competitor gains access to some resource such as food or mates

alkaline: having the properties of a base

allele: one of two or more alternate forms of a gene

alleles: two or more alternate forms of a gene

allometry: relative growth of one part of an organism with reference to another part

allopatry: populations separated by a barrier

alluvial: sediments from flowing water such as silt, sand, mud, and gravel

alpha: the dominant member of a group

altruistic behavior: the aiding of another individual at one's own risk or expense

alveoli: thin-walled sacs in the lungs where blood in capillaries and air in the lungs exchange gases

ameloblasts: cells that form dental enamel

amiote: embryo of a vertebrate that is surrounded by a fluid-filled sac

ammonites: an extinct group of cephalopods with a curled shell

amnion: the membrane that forms a sac around an embryo

amniote: a vertebrate which has a fluid-filled sac that surrounds the embryo

amniotes: vertebrates which have a fluid-filled sac that surrounds the embryo

anadromous: moving from the ocean up a river to spawn

analogous: a similarity in structures between two species that are not closely related

anemia: a condition that results from a decreased number of red blood cells

angiosperms: a flowering plant that produces seeds within an ovary

annelids: segmented worms

anoxic: an environment that lacks oxygen

anterior: referring to the head end of an organism

anterior pituitary: the front part of the pituitary gland that produces hormones that stimulate the production of sperm and testosterone in the testes

antibodies: proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

antigen: foreign substances that stimulate the production of antibodies in the blood

anurans: the order of amphibians that contains frogs and toads

aphrodisiac: a substance or object that is thought to arouse sexual desire

aphrodisiacs: substances or objects that are thought to arouse sexual desire

aposematic: a feature or signal that serves to warn

aposematic coloration: a bright coloration in animals with physical or chemical defenses that act as a warning to predators

appendicular: having to do with arms and legs

appendicular skeleton: part of the skeleton with the arms and legs

aquatic: living in water

aragonite: a mineral form of calcium carbonate

arboreal: living in trees

Archae: an ancient lineage of prokaryotes that live in extreme environments

arthropod: a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

arthropods: members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

artificial pollination: manual pollination methods

asexual reproduction: a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

asymmetrical: lacking symmetry, having an irregular shape

aural: related to hearing

autonomic nervous system: division of the nervous system that carries nerve impulses to muscles and glands

autotroph: an organism that makes its own food

autotrophs: organisms that make their own food

axial skeleton: the skeleton that makes up the head and trunk

axon: cytoplasmic extension of a neuron that transmits impulses away from the cell body

axons: cytoplasmic extensions of a neuron that transmit impulses away from the cell body

B-lymphocytes: specialized cells produced from stem cells in the bone marrow that secrete antibodies that bind with antigens to form a pathogen fighting complex

bacterium: a member of a large group of single-celled prokaryotes

baleen: fringed filter plates that hang from the roof of a whale's mouth

Batesian mimicry: a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

behavioral: relating to actions or a series of actions as a response to stimuli

benthic: living at the bottom of a water environment

bilateral symmetry: characteristic of an animal that can be separated into two identical mirror image halves

bilaterally symmetrical: describes an animal that can be separated into two identical mirror image halves

bilateria: animals with bilateral symmetry

bilipid membrane: a cell membrane that is made up of two layers of lipid or fat molecules

bio-accumulation: the build up of toxic chemicals in an organism

bioactive protein: a protein that takes part in a biological process

bioactive proteins: proteins that take part in biological processes

biodiversity: the variety of organisms found in an ecosystem

biogeography: the study of the distribution of animals over an area

biological control: the introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

biological controls: introduction of natural enemies such as parasites, predators, or pathogens as a method of controlling pests instead of using chemicals

biomagnification: increasing levels of toxic chemicals through each trophic level of a food chain

biomass: the dry weight of organic matter comprising a group of organisms in a particular habitat

biome: a major type of ecological community

biometry: the biological application of statistics to biology

biotic: pertaining to living organisms in an environment

biotic factors: biological or living aspects of an environment

bipedal: walking on two legs

bipedalism: describes the ability to walk on two legs

birthrate: a ratio of the number of births in an area in a year to the total population of the area

birthrates: ratios of the numbers of births in an area in a year to the total population of the area

bivalve mollusk: a mollusk with two shells such as a clam

bivalve mollusks: mollusks with two shells such as clams

bivalves: mollusks that have two shells

body plan: the overall organization of an animal's body

bone tissue: dense, hardened cells that makes up bones

botany: the scientific study of plants

bovid: a member of the family bovidae which is hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

bovids: members of the family bovidae which are hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

brachiopods: a phylum of marine bivalve mollusks

brackish: a mix of salt water and fresh water

brood parasites: birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

buccal: mouth

budding: a type of asexual reproduction where the offspring grow off the parent

buoyancy: the tendency of a body to float when submerged in a liquid

Burgess Shale: a 550 million year old geological formation found in Canada that is known for well preserved fossils

calcified: made hard through the deposition of calcium salts

calcite: a mineral form of calcium carbonate

calcium: a soft, silvery white metal with a chemical symbol of Ca

capture-recapture method: a method of estimating populations by capturing a number of individuals, marking them, and then seeing what percentage of newly captured individuals are captured again

cardiac: relating to the heart

cardiac muscle: type of muscle found in the heart

cardiopulmonary: of or relating to the heart and lungs

carnivorous: describes animals that eat other animals

carrying capacity: the maximum population that can be supported by the resources

cartilage: a flexible connective tissue

cartilaginous: made of cartilage

catadromous: living in freshwater but moving to saltwater to spawn

character displacement: a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

chelicerae: the biting appendages of arachnids

chemoreceptors: a receptor that responds to a specific type of chemical molecule

chemosynthesis: obtaining energy and making food from inorganic molecules

chemosynthetic autotrophs: an organism that uses carbon dioxide as a carbon source but obtains energy by oxidizing inorganic substances

chemotrophs: animals that make energy and produce food by breaking down inorganic molecules

chitin: a complex carbohydrate found in the exoskeleton of some animals

chitinous: made of a complex carbohydrate called chitin

chloroquine: a drug commonly used to treat malaria

chromosomes: structures in the cell that carry genetic information

cilia: hair-like projections used for moving

circadian rhythm: daily, 24-hour cycle of behavior in response to internal biological cues

clades: a branching diagram that shows evolutionary relationships of organisms

Class Branchiopoda: a group of marine bivalve mollusks

Class Malacostraca: crustaceans such as lobsters, crabs, and shrimp

Class Maxillopoda: crustaceans such as barnacles, ostracods, and copepods

Class Merostomata: crustaceans such as horseshoe crabs and eurypterids

Class Pycnogonida: crustaceans such as sea spiders

cleavage: the process of cytokinesis in animal cells; as cells multiply, the plasma membrane pinches off to make two cells from one

climate: long-term weather patterns for a particular region

cnidaria: a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

cnidarians: aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

codominance: an equal expression of two alleles in a heterozygous organism

codon: the genetic code for an amino acid that is represented by three nitrogen bases

codons: the genetic code for an amino acid that is represented by three nitrogen bases

coelom: a body cavity

coevolution: a situation in which two or more species evolve in response to each other

coexist: live together

commensal: a symbiotic relationship wherein which one species benefits and the other is neither helped nor harmed

competitive exclusion principle: the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

compound eye: a multifaceted eye that is made up of thousands of simple eyes

compound eyes: multifaceted eyes that are made up of thousands of simple eyes

concentric: having the same center

conchiolin: a protein that is the organic basis of mollusk shells

coniferous, conifers: having pine trees and other conifers

connective tissue: cells that make up bones, blood, ligaments, and tendons

consumers: animals that do not make their own food but instead eat other organisms

continental drift: the movement of the continents over geologic time

contour feather: a feather that covers a bird's body and gives shape to the wings or tail

contour feathers: feathers that cover a bird's body and give shape to the wings or tail

controversy: a discussion marked by the expression of opposing views

convergence: animals that are not closely related but they evolve similar structures

copulation: the act of sexual reproduction

crinoids: an echinoderm with radial symmetry that resembles a flower

critical period: a limited time in which learning can occur

critical periods: a limited time in which learning can occur

crustaceans: arthropods with hard shells, jointed bodies, and appendages that mainly live in the water

ctenoid scale: a scale with projections on the edge like the teeth on a comb

cumbersome: awkward

cytoplasm: fluid in eukaryotes that surrounds the nucleus and organelles

cytosolic: the semifluid portions of the cytoplasm

death rate: a ratio of the number of deaths in an area in a year to the total population of the area

deciduous: having leaves that fall off at the end of the growing season

denaturing: break down into small parts

dendrites: branched extensions of a nerve cell that transmit impulses to the cell body

described: a detailed description of a species that scientists can refer to identify that species from other similar species

dessication: drying out

detritus: dead organic matter

deuterostome: animal in which the first opening does not form the mouth, but becomes the anus

deuterostomes: animals in which the first opening does not form the mouth, but becomes the anus

diadromous: animals that migrate between freshwater and saltwater

differentiation: differences in structure and function of cells in multicellular organisms as the cells become specialized

diffusion: the movement of molecules from a region of higher concentration to a region of lower concentration

dioecious: having members of the species that are either male or female

diploblastic: having two germ layers; ectoderm and endoderm

diploid cells: cells with two sets of chromosomes

direct fitness: fitness gained through personal reproduction

diurnal: active in the daytime

DNA replication: the process by which two strands of a double helix separate and form two identical DNA molecules

dominance hierarchies: the structure of the pecking order of a group of individuals of a group where the multiple levels of dominance and submission occur

dominant: an allele that is always an expressed trait

dorsal: the back surface of an animal with bilateral symmetry

dorsal root ganglia: nervous tissue located near the backbone

dorsoventrally: flattened from the top and bottom

dysentery: inflammation of the intestines that is characterized by pain, diarrhea, and the passage of mucous and blood

ecdysis: shedding the outer layer of skin or exoskeleton

ecdysone: hormone that triggers molting in arthropods

echinoderms: sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

ecological: relating to an organism's interaction with its environment

ecology: study of how organisms interact with their environment

ecosystem: a self-sustaining collection of organisms and their environment

ecosystems: self-sustaining collections of organisms and their environments

ecotourism: tourism that involves travel to areas of ecological or natural interest usually with a naturalist guide

ectodermal: relating to the outermost of the three germ layers in animal embryos

ectoparasite: an organism that lives on the surface of another organism and derives its nutrients directly from that organism

ectoparasites: organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

edentates: lacking teeth

El Niño: a periodic condition characterized by a warming of the central Pacific Ocean and the changes in global weather patterns that are brought about

emit: to send out or give off

endocrine system: the grouping of organs or glands that secrete hormones into the bloodstream

endoparasite: an organism that lives inside another organism and derives its nutrients directly from that organism

endoparasites: organisms that live inside other organisms and derive their nutrients directly from those organisms

endoskeleton: a skeleton that is surrounded by muscle tissue

endosymbionts: the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

endotrophic: deriving nourishment from within

enterocoelous: a cavity formed by the in-folding of the wall of the intestinal cavity in a gastrula

enzyme: a protein that acts as a catalyst to start a biochemical reaction

enzymes: proteins that act as catalysts to start biochemical reactions

epidermis: the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

epistasis: a phenomenon in which one gene alters the expression of another gene that is independently inherited

epithelial cells: cells that occur in tightly packed sheets that line organs and body cavities

epithelial lining: sheets of tightly packed cells that cover organs and body cavities

epitope: a localized region on an antigen that is recognized chemically by antibodies

equilibrium: a state of balance

erythrocytes: red blood cells, cells containing hemoglobin that carry oxygen throughout the body

estuaries: an area of brackish water where a river meets the ocean

ethology: animal behavior

eucoelomates: animals that have a true body cavity that is completely surrounded by mesoderm

eukaryota: a group of organisms containing a membrane bound-nucleus and membrane-bound organelles

eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles

eukaryotic cells: contains a membrane-bound nucleus and membrane-bound organelles

euryhaline: animals that can live in a wide range of salt concentrations

eusocial: animals that show a true social organization

evaporites: rocks formed from evaporation of salty and mineral-rich liquid

excrescence: an abnormal growth

excrescences: abnormal growths

exons: the coding region in a eukaryotic gene that is expressed

exoskeleton: a hard outer protective covering common in invertebrates such as insects

exoskeletons: hard outer protective coverings common in invertebrates such as insects

exponential growth: a population growing at the fastest possible rate under ideal conditions

extant: still living

facilitated diffusion: the spontaneous passing of molecules attached to a carrier protein across a membrane

facultative parasites: organisms that can survive either as a parasite or free-living

falconry: a sport where falcons are used for hunting

fascicle: a close cluster

fauna: animals

fertilization: the fusion of male and female gametes

fibroblasts: type of cells found in loose connective tissue that secretes the proteins for connective fibers

fight or flight response: an automatic, chemically controlled response to a stimulus that causes increased heart and breathing rates for increased activity

filter feeders: animals that strain small food particles out of water

fission: dividing into two parts

fixed action pattern: behaviors that are common to all members of a species

flagella (flagellum): cellular tail that allows the cell to move

flagellae: cellular tails that allow cells to move

flora: plants

fossil record: a collection of all known fossils

frequency-dependant selection: a decline in the reproductive success of a particular body type due to that body type becoming common in the population

frugivores: fruit-eating animals

functional morphology: studying form and function

fusion: coming together

gametes: reproductive cells that only have one set of chromosomes

gametocyte: cell that produces gametes through division

gametocytes: cells that produce gametes through division

ganoid scale: hard, bony, and enamel covered scales

gastropods: mollusks that are commonly known as snails

gastrovascular cavity: a single cavity where digestion occurs

gastrulation: the formation of a gastrula from a blastula

gene therapy: a process where normal genes are inserted into DNA to correct a genetic disorder

genes: segments of DNA located on chromosomes that direct protein production

genetic trait: trait related to biological inheritance

genetics: the branch of biology that studies heredity

genome: an organism's genetic material

genomes: the sum of all genes in a set of chromosomes

genotype: the genetic makeup of an organism

germ cell: an egg or sperm cell, a gamete

germ cells: egg or sperm cells, gametes

gill arches: arches of cartilage that support the gills of fishes and some amphibians

gill filaments: the site of gas exchange in aquatic animals such as fish and some amphibians

gills: site of gas exchange between the blood of aquatic animals such as fish and the water

gizzard: the muscular part of the stomach of some animals where food is ground

global warming: a slow and steady increase in the global temperature

glycoprotein: an organic molecule that contains a carbohydrate and a protein

gonad: the male and female sex organs that produce sex cells

gonads: the male and female sex organs that produce sex cells

granulocytes: a type of white blood cell where its cytoplasm contains granules

green house effect: a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

habitat: the physical location where organisms live in an ecosystem

habitat loss: the destruction of habitats through natural or artificial means

habitat requirement: necessary conditions or resources needed by an organism in its habitat

habitats: physical locations where organisms live in an ecosystem

Hamilton's Rule: individuals show less agression to closely related kin than to more distantly related kin

haplodiploidy: the sharing of half the chromosomes between a parent and an offspring

haploid cells: cells with only one set of chromosomes

hemocoel: a cavity between organs in arthropods and mollusks through which blood circulates

hemocyanin: respiratory pigment found in some crustaceans, mollusks, and arachnids

hemoglobin: an iron-containing protein found in red blood cells that binds with oxygen

hemolymph: the body fluid found in invertebrates with open circulatory systems

herbivore: an animal that eats plants only

herbivores: animals that eat only plants

herbivorous: animals that eat plants

heredity: the passing on of characteristics from parents to offspring

heritability: the ability to pass characteristics from a parent to the offspring

hermaphodite: an animals with both male and female sex organs

hermaphroditic: having both male and female sex organs

heterodont: teeth differentiated for various uses

heterotrophic eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles and do not make their own food

heterotrophs: organisms that do not make their own food

heteroxenous: a life cycle in which more than one host individual is parasitized

heterozygote: an organism whose chromosomes contain both genes of a contrasting pair

heterozygote advantage: a condition where a heterozygous individual has a reproductive advantage over a homozygous individual

Hippocrates: a central figure in medicine in ancient Greece, he is considered the father of modern medicine

home range: the area where an animal lives and eats

homeostasis: a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

homeothermic: describes animals able to maintain their body temperatures

hominid: belonging to the family of primates

hominids: belonging to the family of primates

homodont: teeth with a uniform size and shape

homologous: similar but not identical

homology: correspondence in the type of structure and its origin

homoplastic: similar but of different origins

homozygote: an animal with two identical alleles for one trait

hormone: a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

hormones: chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

Horseshoe crabs: "living fossils" in the class of arthropods

Hox genes: also known as selector genes because their expression leads embryonic cells through specific morphologic development

Human Genome Project: a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

hunting season: a period of time during which hunting is permited

hunting seasons: periods of time during which hunting is permited

hybrid: offspring resulting from the cross of two different species

hydrostatic skeleton: a pressurized, fluid-filled skeleton

hyperpolarizing potential: any change in membrane potential that makes the inside of the membrane more negatively charged

hypothalamus: part of the upper end of the brain stem that regulates activities in the nervous and endrocrine systems

IgA: imunoglobin A; a class of proteins that make up antibodies

IgD: imunoglobin D; a class of proteins that make up antibodies

IgE: imunoglobin E; a class of proteins that make up antibodies

IgG: imunoglobin G; a class of proteins that make up antibodies

IgM: imunoglobin M; a class of proteins that make up antibodies

inbreeding depression: loss of fitness due to breeding with close relatives

incomplete dominance: a type of inheritance where the offspring have an intermediate appearance of a trait from the parents

incus: one of three small bones in the inner ear

indirect fitness: fitness gained through aiding the survival of non-descendant kin

infrared: an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red; heat is carried on infrared waves

innate behavior: behavior that develops without influence from the environment

innervate: supplied with nerves

inoculation: introduction into surroundings that support growth

insectivore: an animal that eats insects

insectivores: animals that eat insects

instars: the particular stage of an insect's or arthropod growth cycle between moltings

integument: a natural outer covering

intercalation: placing or inserting between

intraspecific: involving members of the same species

introns: a non-coding sequence of base pairs in a chromosome

invagination: a stage in embryonic development where a cell layer buckles inward

invertebrates: animals without a backbone

involuntary muscles: muscles that are not controlled by will

isthmus: a narrow strip of land

iteroparous: animals with several or many reproductive events in their lives

***k*-selected species:** a species that natural selection has favored at the carrying capacity

***k*-selecting habitat:** habitat where there is a high cost of reproduction and is sensitive to the size of the offspring

key innovation: a modification that permits an individual to exploit a resource in a new way

keystone species: a species that controls the environment and thereby determines the other species that can survive in its presence

krill: an order of crustaceans that serves as a food source for many fish, whales, and birds

lancelet: a type of primitive vertebrate

lancelets: primitive vertebrates

lateral inhibition: phenomenon that amplifies the differences between light and dark

lateral line: a row of pressure sensitive sensory cells in a line on both sides of a fish

learned behavior: behavior that develops with influence from the environment

learning: modifications to behavior motivated by experience

leukocytes: a type of white blood cells that are part of the immune system

life history strategies: methods used to overcome pressures for foraging and breeding

life history strategy: methods used to overcome pressures for foraging and breeding

lipids: fats and oils; organic compounds that are insoluble in water

logistic growth: in a population showing exponential growth the individuals are not limited by food or disease

lungs: sac-like, spongy organs where gas exchange takes place

lymphocytes: white blood cell that completes development in bone marrow

macroparsite: a parasite that is large in size

macroparasites: parasites that are large in size

macrophages: white blood cell that attacks anything foreign such as microbes

malleus: the outermost of the inner ear bones

mantle: the tissue in mollusks that drapes over the internal organs and may secrete the shell

mantles: tissues in mollusks that drape over the internal organs and may secrete the shell

matrix: the nonliving component of connective tissue

megachiroptera: fruit bats and flying foxes

meiosis: a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

merozoite: a motile stage in some parastic protozoa

mesenchyme: the part of the mesoderm from which the connective tissues (bone, cartilage, and vascular system) arise

mesenteries: the membrane that suspends many internal organs in the fluid-filled body cavity of vertebrates

mesoderm: the middle layer of cells in embryonic tissue

messenger RNA: a type of RNA that carries protein synthesis information from the DNA in to the nucleus to the ribosomes

metamorphose: to change drastically from a larva to an adult

metamorphoses: changes drastically from its larval form to its adult form

metamorphosing: changing drastically from a larva to an adult

metamorphosis: a drastic change from a larva to an adult

metazoan: a subphylum of animals that have many cells, some of which are organized into tissues

metazoans: a subphylum of animals that have many cells, some of which are organized into tissues

microchiroptera: small bats that use echolocation

microparasite: very small parasite

microparasites: very small parasites

midoceanic ridge: a long chain of mountains found on the ocean floor where tectonic plates are pulling apart

mitochondria: organelles in eukaryotic cells that are the site of energy production for the cell

Mitochondrial DNA: DNA found within the mitochondria that control protein development in the mitochondria

mitosis: a type of cell division that results in two identical daughter cells from a single parent cell

modalities: to conform to a general pattern or belong to a particular group or category

modality: to conform to a general pattern or belong to a particular group or category

molecular clock: using the rate of mutation in DNA to determine when two genetic groups spilt off

molecular clocks: using the rate of mutation in DNA to determine when two genetic groups spilt off

mollusks: large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

molted: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

molting: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

monoculture: cultivation of a single crop over a large area

monocultures: cultivation of single crops over large areas

monocytes: the largest type of white blood cell

monophyletic: a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

monotremes: egg-laying mammals such as the platypus and echidna

monoxenous: a life cycle in which only a single host is used

morphogenesis: the development of body shape and organization during ontogeny

morphological: the structure and form of an organism at any stage in its life history

morphological adaptation: an adaptation in form and function for specific conditions

morphological adaptations: adaptations in form and function for specific conditions

morphologies: the forms and structures of an animal

mutation: an abrupt change in the genes of an organism

mutations: abrupt changes in the genes of an organism

mutualism: ecological relationship beneficial to all involved organisms

mutualisms: ecological relationships beneficial to all involved organisms

mutualistic relationship: symbiotic relationship where both organisms benefit

mutualistic relationships: symbiotic relationships where both organisms benefit

mutualists: a symbiotic relationship where both organisms benefit

myofibril: longitudinal bundles of muscle fibers

myofilament: any of the ultramicroscopic filaments, made up of actin and myosin, that are the structural units of a myofibril

myosin: the most common protein in muscle cells, responsible for the elastic and contractile properties of muscle; it combines with actin to form actomyosin

natural selection: the process by which organisms best suited to their environment are most likely to survive and reproduce

naturalist: a scientist who studies nature and the relationships among the organisms

naturalists: scientists who study nature and the relationships among the organisms

neuromuscular junction: the point where a nerve and muscle connect

neuron: a nerve cell

neurons: nerve cells

neurotransmitters: chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

niche: how an organism uses the biotic and abiotic resources of its environment

nocturnal: active at night

notochord: a rod of cartilage that runs down the back of Chordates

nucleotide: the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

nucleotide chain: a chain composed of five-carbon sugar groups that forms the basis for nucleic acid

nucleotides: building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

obligative mutualism: an animal that must exist as part of a mutually beneficial relationship

obligatory parasites: an animal that can only exist as a parasite

olfactory: relates to the sense of smell

omnivorous: eating both plants and animals

ontogeny: the embryonic development of an organism

oocyst: a cyst in sporozoans that contains developing sporozoites

operculum: a flap covering an opening

operculum chamber: space covered by a flap

organelles: membrane-bound structures found within a cell

ornithology: the study of birds

osmoregulatory functions: controlling the water balance within an animal

osmoregulatory system: system that regulates the water balance between an organism and its environment

osmosis: the diffusion of water across a membrane

ossification: deposition of calcium salts to form hardened tissue such as bone

osteoblasts: potential bone forming cells found in cartilage

oviparous: having offspring that hatch from eggs external to the body

ovoviparity: having offspring that hatch from eggs retained in the mother's uterus

ovoviviparous: having offspring that hatch from eggs retained in the mother's uterus

paleoanthropology: the study of ancient humans

parasitology: the study of parasites

parasympathetic division: part of the nervous system that generally enhances body activities that gain and conserve energy such as digestion and heart rate

parental imprinting: a process by which a gene's expression in a child depends on which parent donated it before development

passive diffusion: the passing of molecules across a membrane from an area of higher concentration to an area of lower concentration without any energy input

pathogens: disease-causing agents such as bacteria, fungi, and viruses

pecking order: the position of individuals of a group wherein multiple levels of dominance and submission occur

pectoral: of, in, or on the chest

pedipapls: one pair of short appendages near the mouth in some arthropods used for feeding and copulation

pericardial cavity: the space within the membrane that surrounds the heart

peripheral nervous system: the sensory and motor nerves that connect to the central nervous system

peritoneum: the thin membrane that lines the abdomen and covers the organs in it

pesticide: any substance that controls the spread of harmful or destructive organisms

pesticides: substances that control the spread of harmful or destructive organisms

pH: a measure of how acidic or basic a substance is by measuring the concentration of hydrogen ions

phalanges: bones of the fingers and toes

pharyngeal: having to do with the tube that connects the stomach and the esophagus

phenotype: physical and physiological traits of an animal

phenotypes: the physical and physiological traits of an animal

phenotypic: describes the physical and physiological traits of an animal

phenotypic trait: physical and physiological variations within a population

phenotypic variation: differences in physical and physiological traits within a population

pheromones: small, volatile chemicals that act as signals between animals that influence physiology or behavior

phlogenetic: relating to the evolutionary history

phospholipid: molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water

photoreceptors: specialized cells that detect the presence or absence of light

photosynthesis: the combination of chemical compounds in the presence of sunlight

photosynthesizing autotrophs: animals that produce their own food by converting sunlight to food

phyla: broad, principle divisions of a kingdom

phylogenetic: relating to the evolutionary history of species or group of related species

phylogeny: the evolutionary history of a species or group of related species

physiological: relating to the basic activities that occur in the cells and tissues of an animal

physiology: the study of the normal function of living things or their parts

placenta: the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placental: having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placoid scale: a scale composed of three layers and a pulp cavity

placoid scales: scales composed of three layers and a pulp cavity

plankton: microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

plate tectonics: the theory that Earth's surface is divided into plates that move

platelet: cell fragment in plasma that aids clotting

platelets: cell fragments in plasma that aid in clotting

pleural cavity: the space where the lungs are found

plumose: having feathers

pluripotent: a cell in bone marrow that gives rise to any other type of cell

poaching: hunting game outside of hunting season or by using illegal means

poikilothermic: an animal that cannot regulate its internal temperature; also called cold blooded

polymer: a compound made up of many identical smaller compounds linked together

polymerase: an enzyme that links together nucleotides to form nucleic acid

polymerases: enzymes that link together nucleotides to form nucleic acid

polymodal: having many different modes or ways

polymorphic: referring to a population with two or more distinct forms present

polymorphism: having two or more distinct forms in the same population

polymorphisms: having two or more distinct forms in the same population

polyploid: having three or more sets of chromosomes

polysaccharide: a class of carbohydrates that break down into two or more single sugars

polysaccharides: carbohydrates that break down into two or more single sugars

population: a group of individuals of one species that live in the same geographic area

population density: the number of individuals of one species that live in a given area

population dynamics: changes in a population brought about by changes in resources or other factors

population parameters: a quantity that is constant for a particular distribution of a population but varies for the other distrubutions

populations: groups of individuals of one species that live in the same geographic area

posterior: behind or the back

precursor: a substance that gives rise to a useful substance

prehensile: adapted for siezing, grasping, or holding on

primer: short preexisting polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase

producers: organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

progeny: offspring

prokaryota: a group of organisms that lack a membrane-bound nucleus and membrane-bound organelles

prokaryotes: single-celled organisms that lack a true cell nucleus

prokaryotic endosymbionts: single-celled organisms that lack a true cell nucleus that live inside of other cells

proprioceptors: sense organs that receive signals from within the body

protostome: animal in which the initial depression that starts during gastrulation becomes the mouth

protostomes: animals in which the initial depression that starts during gastrulation becomes the mouth

protozoa: a phylum of single-celled eukaryotes

protozoan: a member of the phylum of single-celled organisms

pseudocoelom: a body cavity that is not entirely surrounded by mesoderm

pseudocoelomates: animals with a body cavity that is not entirely surrounded by mesoderm

pterylae: feather tracks

quadrupedal: describes an animal with four legs

quadrupeds: animals with four legs

quinine: substance used to treat malaria

***r*-selected species:** a species that shows the following characteristics: short lifespan; early reproduction; low biomass; and the potential to produce large numbers of usually small offspring in a short period of time

***r*-selecting habitat:** the concept where a high reproductive rate is the chief determinant of life history

radially symmetric: wheel-like symmetry in which body parts radiate out from a central point

radially symmetrical: describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

recessive: a hidden trait that is masked by a dominant trait

recombinant DNA: DNA that is formed when a fragment of DNA is incorporated into the DNA of a plasmid or virus

regeneration: regrowing body parts that are lost due to injury

relative abundance: an estimate of population over an area

rennin: an enzyme used in coagulating cheese; is obtained from milk-fed calves

resorbed: absorption of materials already in the body

resorption: absorbing materials that are already in the body

respiratory pigments: any of the various proteins that carry oxygen

restriction enzymes: bacterial proteins that cut DNA at specific points in the nucleotide sequence

retina: a layer of rods and cones that line the inner surface of the eye

riparian: habitats in rivers and streams

ruminants: plant-eating animals with a multicompartment stomach such as cows and sheep

sagital plane: a plane that runs long-ways through the body

salamanders: four-legged amphibians with elongated bodies

sarcomere: one of the segments into which a fibril of striated muscle is divided by thin dark bands

scavengers: animals that feed on the remains of animals it did not kill

schizocoelous: the mesoderm originates from existing cell layers when the cells migrate

scleroblasts: cells that give rise to mineralized connective tissue

sedimentary rock: rock that forms when sediments are compacted and cemented together

semelparous: animals that only breed once and then die

serial homology: a rhythmic repetition

sessile: not mobile, attached

sexual reproduction: a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

sexual selection: selection based on secondary sex characteristics that leads to greater sexual dimorphorphism or differences between the sexes

sexual size dimorphism: a noticeable difference in size between the sexes

shoals: shallow waters

single-lens eyes: an eye that has a single lens for focusing the image

skeletal muscle: muscle attached to the bones and responsible for movement

smooth muscle: muscles of internal organs which is not under conscious control

somatic: having to do with the body

somatic nervous system: part of the nervous system that controls the voluntary movement of skeletal muscles

somatosensory information: sensory information from different parts of the body except for the eyesm tongue, ears, and other primary sense organs

somites: a block of mesoderm along each side of a chordate embryo

sonar: the bouncing of sound off distant objects as a method of navigation or finding food

spinal cord: thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

splicing: spliting

spongocoel: the central cavity in a sponge

sporozoa: a group of parasitic protozoa

sporozoans: parasitic protozoans

sporozoite: an infective stage in the life cycle of sporozoans

stapes: innermost of the three bones found in the inner ear

stimuli: anything that excites the body or part of the body to produce a specific response

stimulus: anything that excites the body or part of the body to produce a specific response

strata: layers of sedimentary rock consisting of approximately the same kinds of material

striated muscle: a type of muscle with fibers of cross bands usually contracted by voluntary action

striated muscles: muscles with fibers of cross bands usually contracted by voluntary actions

superposition: the order in which sedimentary layers are found with the youngest being on top

symbiosis: any prolonged association or living together of two or more organisms of different species

symbiotic relationship: close, long-term relationship where two species live together in direct contact

symbiotic relationships: close, long-term relationships where two species live together in direct contact

symmetrical: a balance in body proportions

synapse: the space between nerve cells across which impulses are chemically transmitted

systematic: study of the diversity of life

tactile: the sense of touch

tapetum: a reflective layer in the eye of nocturnal animals

taxa: named taxonomic units at any given level

taxon: named taxonomic unit at any given level

taxonomy: the science of classifying living organisms

terraria: a small enclosure or closed container in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrariums: small enclosures or closed containers in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrestrial: living on land

thoracic: the chest area

thromboplastin: a protein found in blood and tissues that promotes the conversion of prothrombin to thrombin

torpid: a hibernation strategy where the body temperature drops in relation to the external temperature

trachea: the tube in air-breathing vertebrates that extends from the larynx to the bronchi

transcription: process where enzymes are used to make an RNA copy of a strand of DNA

transgenic: an organism that contains genes from another species

transgenic organism: an organism that contains genes from another species

translation: process where the order of bases in messenger RNA codes for the order of amino acids in a protein

transverse plane: a plane perpendicular to the body

trilobites: an extinct class of arthropods

triploblasts: having three germ layers; ectoderm, mesoderm, and endoderm

trophic level: the division of species in an ecosystem by their main source of nutrition

trophic levels: divisions of species in an ecosystem by their main source of nutrition

ungulates: animals with hooves

urea: soluble form of nitrogenous waste excreted by many different types of animals

urethra: a tube that releases urine from the body

uric acid: insoluble form of nitrogenous waste excreted by many different types of animals

ventral: the belly surface of an animal with bilateral symmetry

vertebrates: animals with a backbone

viviparity: having young born alive after being nourished by a placenta between the mother and offspring

viviparous: having young born alive after being nourished by a placenta between the mother and offspring

vocalization: the sounds used for communications

voluntary muscles: a type of muscle with fibers of cross bands usually contracted by voluntary action

wavelength: distance between the peaks or crests of waves

zooplankton: small animals who float or weakly move through the water

zygote: a fertilized egg

zygotes: fertilized eggs

zymogens: inactive building-block of an enzyme

Topic Outline

ADAPTATIONS

Adaptation
Antlers and Horns
Aposematism
Biological Evolution
Biomechanics
Blood
Camouflage
Catadromous—Diadromous and Anadromous Fishes
Colonization
Communication
Community Ecology
Comparative Biology
Defense
Echolocation
Egg
Extremophile
Locomotion
Mimicry
Peppered Moth
Tool Use
Water Economy in Desert Organisms

AGRICULTURE

Apiculture
Aquaculture
Classification Systems
Dinosaurs
Domestic Animals
Farmer
Farming
Selective Breeding
Sustainable Agriculture

ANIMAL DIVERSITY

Animal
Biodiversity
Biogeography
Biological Evolution
Cambrian Explosion
Camouflage
Cephalization
Coevolution
Colonization
Community Ecology
Constraints on Animal Development
Diversity of Major Groups
Extremophile
Functional Morphology
Kingdoms of Life
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Prokaryota
Sexual Dimorphism
Taxonomy

ANIMAL GROUPS

Agnatha
Amphibia
Annelida
Arthropoda
Aves
Cephalochordata
Cestoda
Chondricthyes
Chordata
Cnidaria
Dinosaurs
Echinodermata

Eukaryota
Mammalia
Metazoan
Molluska
Nematoda
Osteicthyes
Platyhelmithes
Porifera
Primates
Prokaryota
Reptilia
Rotifera
Trematoda
Turbellaria
Urochordata
Vertebrata

ANIMAL HISTORY

African Cichlid Fishes
Animal
Burgess Shale and Ediacaran Faunas
Cambrian Explosion
Coevolution
Colonization
Constraints on Animal Development
Domestic Animals
Eukaryota
Extinction
Fossil Record
Horses
Kingdoms of Life
Living Fossils
Paleontologist
Paleontology
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Tetropods—From Water to Land
Xenopus

ANATOMY

Acoustic Signals
Biomechanics
Body Cavities
Body Plan
Bone
Cartilage
Cells
Cephalization
Comparative Biology
Echolocation
Embryology
Embryonic Development
Feeding
Functional Morphology
Gills
Growth And Differentiation of the Nervous System
Homology
Keratin
Locomotion
Mouth, Pharynx, and Teeth
Muscular System
Neuron
Scales, Feathers, and Hair
Sense Organs
Skeletons
Vision

BEHAVIOR

Acoustic Signals
Aggression
Altruism
Behavior
Behavioral Ecology
Circadian Rhythm
Courtship
Crepuscular
Diurnal
Dominance Hierarchy
Ethology
Homeostasis
Imprinting
Instinct
Learning
Migration
Nocturnal
Social Animals
Sociality
Sociobiology
Territoriality

BIOCHEMISTRY AND PHYSIOLOGY

Absorption
Allometry
Antibody

Blood
Cancer
Cell Division
Cells
Digestion
Egg
Homeostasis
Hormones
Keratin
Molecular Biologist
Molecular Biology
Molecular Systematics
Physiologist
Physiology
Respiration
Transport

BIODIVERSITY

Biodiversity
Biogeography
Biomass
Biomes
Colonization
Community Ecology
Diversity of Major Groups
Eukaryota
Habitat
Habitat Loss
Habitat Restoration
Zooplankton

CAREERS IN ANIMAL SCIENCE

Ecologist
Environmental Lawyer
Farmer
Functional Morphologist
Geneticist
Horse Trainer
Human Evolution
Livestock Manager
Marine Biologist
Medical Doctor
Molecular Biologist
Museum Curator
Paleontologist
Physiologist
Scientific Illustrator
Service Animal Trainer
Systematist
Taxonomist
Veterinarian
Wild Game Manager
Wildlife Biologist
Wildlife Photographer
Zoologist

CELL BIOLOGY

Absorption
Blood
Cell Division
Cells
Viruses

ECOLOGY

African Cichlid Fishes
Behavioral Ecology
Biotic Factors
Camouflage
Community Ecology
Competition
Competitive Exclusion
Conservation Biology
DDT
Ecologist
Ecology
Ecosystem
Evolutionary Stable Strategy
Exotic Species
Expenditure per Progeny
Feeding Strategies
Fitness
Food Web
Foraging Strategies
Growth And Differentiation of the Nervous System
Habitat
Habitat Loss
Habitat Restoration
Home Range
Human Commensals and Mutual Organisms
Interspecies Interactions
Iteroparity and Semelparity
Keystone Species
Life History Strategies

Malthus, Thomas Robert
Parasitism
Plankton
Population Dynamics
Populations
Predation
Territoriality
Trophic Level
Zooplankton

ENVIRONMENT

Biological Pest Control
Biomass
Biomes
Biotic Factors
Carson, Rachel
DDT
Ecosystem
Endangered Species
Environment
Environmental Degradation
Environmental Impact
Environmental Lawyer
Fossil Fuels
Global Warming
Human Populations
Natural Resources
Pesticide
Pollution
Silent Spring
Threatened Species

ETHICS

Animal Rights
Animal Testing
Bioethics

EVOLUTION

Adaptation
African Cichlid Fishes
Aposematism
Biological Evolution
Camouflage
Coevolution
Constraints on Animal Development
Continental Drift
Convergence
Darwin, Charles
Genetic Variation in a Population
Heterochrony
Homology
Human Evolution
Lamarck
Leakey, Louis and Mary
Modern Synthesis
Morphological Evolution in Whales
Morphology
Natural Selection
Peppered Moth
Sexual Dimorphism
Sexual Selection
Spontaneous Generation

FORM AND FUNCTION

Acoustic Signals
Adaptation
African Cichlid Fishes
Antlers and Horns
Aposematism
Biomechanics
Blood
Body Cavities
Body Plan
Bone
Burgess Shale and Ediacaran Faunas
Camouflage
Cell Division
Cells
Cephalization
Chitin
Circulatory System
Communication
Defense
Digestion
Digestive System
Echolocation
Endocrine System
Excretory and Reproductive Systems
Feeding
Flight
Gills
Gliding and Parachuting
Locomotion
Mimicry

Nervous System
Respiratory System
Sexual Selection
Shells
Vision
Vocalization

GENETICS

Drosophila
Genes
Genetic Engineering
Genetic Variation in a Population
Genetically Engineered Foods
Geneticist
Genetics
Mendel, Gregor
Modern Synthesis
PCR
Viruses

GEOLOGIC HISTORY

Cambrian Period
Carboniferous
Continental Drift
Cretaceous
Devonian
Geological Time Scale
Jurassic
K/T Boundary
Oligocene
Ordovician
Permian
Pleistocene
Quaternary
Silurian
Tertiary
Triassic

GROWTH AND DEVELOPMENT

Allometry
Antlers and Horns
Body Cavities
Body Plan
Bone
Cartilage
Cell Division
Cells
Comparative Biology
Constraints on Animal Development
Egg
Embryology
Embryonic Development
Haeckel's Law of Recapitulation
Heterochrony
Mesenchyme
Metamorphosis
Molting
Ontogeny
Serial Homology
Von Baer's Law

HISTORICAL FIGURES IN SCIENCE

Aristotle
Bailey, Florence Augusta Merriam
Bates, Henry Walter
Carson, Rachel
Darwin, Charles
Diamond, Jared
Elton, Charles Sutherland
Fausto–Sterling, Anne
Fossey, Dian
Goodall, Jane
Gould, Steven Jay
Haldane, J. B. S.
Lamarck, Jean-Baptiste
Leakey, Louis and Mary
Linnaeus, Carolus
Lorenz, Konrad
Malthus, Thomas Robert
Mayr, Ernst
McArthur, Robert
Mendel, Gregor
Montalcini, Rita Levi
Pasteur, Louis
Simpson, George Gaylord
Stevens, Nettie Maria
Wallace, Alfred Russel
Wilson, E. O.

HUMANS AND THE ANIMAL WORLD

Cultures and Animals
Human Commensals and Mutual Organisms
Human Populations
Human–Animal Conflicts

Hunter-Gatherers
Hunting
Malaria

LIFE CYCLES

Catadromous—Diadromous and Anadromous Fishes
Cell Division
Colonization
Courtship
Endosymbiosis
Iteroparity and Semelparity
Malaria
Metamorphosis
Parasitism

REPRODUCTION

Antlers and Horns
Asexual And Sexual Reproduction
Cell Division
Excretory and Reproductive Systems
Fertilization

SCIENTIFIC FIELDS OF STUDY

Behavioral Ecology
Community Ecology
Comparative Biology
Conservation Biology
Ecology
Embryology
Entomology
Functional Morphology
Herpetology
Icthyology
Molecular Biology
Morphology
Mouth, Pharynx, and Teeth
Paleontology
Physiology
Sociobiology
Taxonomy

animal sciences

animal sciences

VOLUME 3
Hab–Pep

Allan B. Cobb, Editor in Chief

MACMILLAN
REFERENCE
USA™

THOMSON
GALE™

New York • Detroit • San Diego • San Francisco • Cleveland • New Haven, Conn. • Waterville, Maine • London • Munich

Macmillan Reference USA
1633 Broadway
New York, NY 10019

The Gale Group
27500 Drake Rd.
Farmington Hills, 48331-3535

Printed in the United States of America
1 2 3 4 5 6 7 8 9 10

Library of Congress Cataloging-in-Publication Data
Animal Sciences / Allan B. Cobb, editor in chief.
p. cm.
Includes bibliographical references and index.
ISBN: 0-02-865556-7 (set) - ISBN 0-02-865557-5 (vol. 1) - ISBN 0-02-865558-3 (vol. 2) - ISBN 0-02-865559-1 (vol. 3) - ISBN 0-02-865560-5 (vol. 4)
1. Animal Culture. 2. Livestock. I. Title.
SF61.C585 2001
590.3-dc21 2001026627
Rev

Preface

Six hundred million years of animal evolution and adaptation have produced a stunning range and variety of life on Earth. From the oldest, single-celled creatures to the most complex mammalian forms, animal diversity defies easy categorization or explanation. The Macmillan *Animal Sciences* encyclopedia provides a clear and comprehensive resource for better understanding this vast domain. By the nature of its interdisciplinary scope, the subject of animal sciences demands an approach that is both specific and general, detailed and thematic. *Animal Sciences* achieves this end in the course of nearly three hundred well-researched, clearly presented entries that explore the wide ranging diversity that exists within the animal kingdom.

Students will learn how animals develop throughout their lives, how they adapt to their changing environments, and how they develop specialized structures over time. Entries in this category explain how animals develop from fertilized eggs to adults. While some forms of development are straightforward—like a puppy maturing to become a dog—other changes are more dramatic—like a caterpillar changing its body forms over the course of its metamorphosis into a butterfly. Other entries study the various forms of animals and how body parts function.

The encyclopedia gives significant attention to animal ecology and behavior. Entries show how animals are part of the world environment while exhibiting unique behaviors within their own particular environments. Animal ecology addresses how animals are a part of ecosystems and how they interact with plants and other animals, both within and beyond their individual species. Given the close relationship of animal behavior and ecology, a number of entries discuss how animals select mates, whether they live alone or as members of groups, or how they share resources within an ecosystem, to give just a few examples.

Finally, *Animal Sciences* surveys the connection between animals and humans. Humans are unique in the animal kingdom because of their ability to alter environments significantly. Agriculture, which includes the domestication of animals and farming, serves as the chief example of such human-inspired environmental change and its impact on animal life worldwide. In addition, humans are the most social of animals and have developed complex social interactions. As human populations grow, habitat once occupied

by other animals is converted to human use. One consequence of such socialization is the pollution generated from an expanding human population and its deleterious effect on animal environments.

Animal Sciences also presents biographies of selected scientists who have made significant contributions to the many related fields, and introduces readers to the myriad career opportunities in the discipline.

The authors who contributed entries to *Animal Sciences* represent diverse backgrounds, and include members of academic and research institutions, as well as practicing scientists. The editorial board sought informative, up-to-date, and engaging articles, most of which include cross references, photographs or illustrations that prove helpful in understanding challenging concepts. A generous collection of sidebars accent related subjects. Every attempt has been made to avoid overly technical terms or scientific jargon, and whenever necessary such terms are highlighted and defined in the margin. Selected bibliographies guide readers to additional up-to-date resources, including those found on the Internet. Each of the four volumes also includes a geologic time scale, with particular emphasis on animals, as well as a phylogenetic tree and an alternative table of contents that groups articles under more general topic headings.

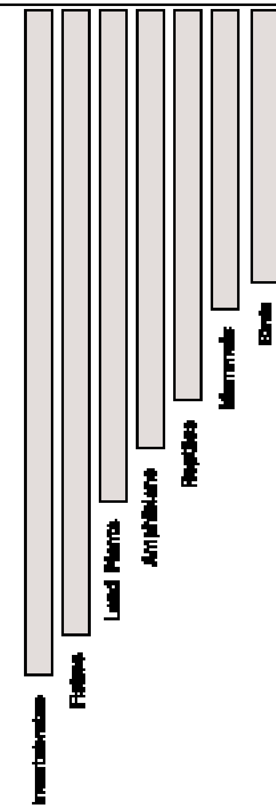
I wish to thank the staff at Macmillan Reference USA and the Gale Group for their hard work and attention to detail. In particular, I would like to thank Hélène Potter, Elly Dickason, Linda Hubbard, and Christa Brelin. I want to offer special thanks to Kate Millson for all her efforts and long hours in helping guide this project to fruition. I wish to thank the editorial board members—Amy Bryan, Andrew Gluesenkamp, and Marvin Elliot Richmond—for their vast knowledge and hard work. Finally, it is my hope that *Animal Sciences* can spark the interest of the next generation of committed scholars, researchers, and laypersons.

Allan B. Cobb
Editor in Chief

Geological Time Scale

Eon	Era	Period	Epoch	Significant Events	Million Years Before Present
Phanerozoic	Cenozoic	Quaternary	Holocene	recorded human history, rise and fall of civilizations, global warming, habitat destruction, pollution mass extinction	0.01
			Pleistocene	Homo sapiens, ice ages	1.6
		Tertiary	Pliocene	global cooling, savannahs, grazing mammals	5.3
			Miocene	global warming, grasslands, Chalicotherium	24
			Oligocene		37
			Eocene	modern mammals flourish, ungulates	58
			Paleocene		66
	Mesozoic	Cretaceous		last of age of dinosaurs, modern mammals appear, flowering plants, insects	144
		Jurassic		large plant-eating dinosaurs, carnivorous dinosaurs, first birds, breakup of Pangea	208
		Triassic		lycophytes, glossopterids, and dicynodonts, and the dinosaurs	245
	Paleozoic	Permian		Permian ends with largest mass extinction in history of Earth, most marine invertebrates extinct	286
		Pennsylvanian		vast coal swamps, evolution of amniote egg allowing exploitation of land	320
		Mississippian		shallow seas cover most of Earth	360
		Devonian		vascular plants, the first tetrapods, wingless insects, arachnids, brachiopods, corals, and ammonites were also common, many new kinds of fish appeared	408
		Silurian		Coral reefs, rapid spread of jawless fish, first freshwater fish, first fish with jaws, first good evidence of life on land, including relatives of spiders and centipedes	438
		Ordovician		most dry land collected into Gondwana, many marine invertebrates, including graptolites, trilobites, brachiopods, and the conodonts (early vertebrates), red and green algae, primitive fish, cephalopods, corals, crinoids, and gastropods, possibly first land plants	505
		Cambrian		most major groups of animals first appear, Cambrian explosion	570
Precambrian	Proterozoic			stable continents first appear, first abundant fossils of living organisms, mostly bacteria and archaebacteria, first eukaryotes, first evidence of oxygen build-up	2500
	Archean			atmosphere of methane, ammonia, rocks and continental plates began to form, oldest fossils consist of bacteria microfossils stromatolites, colonies of photosynthetic bacteria	3800
	Hadean			pre-geologic time, Earth in formation	4600

Time Range of Several Groups of Plants & Animals



COMPARISON OF THE FIVE-KINGDOM AND SIX-KINGDOM CLASSIFICATION OF ORGANISMS

Five Kingdom

- Kingdom: Monera
  - Phylum: Bacteria
  - Phylum: Blue-green algae (cyanobacteria)

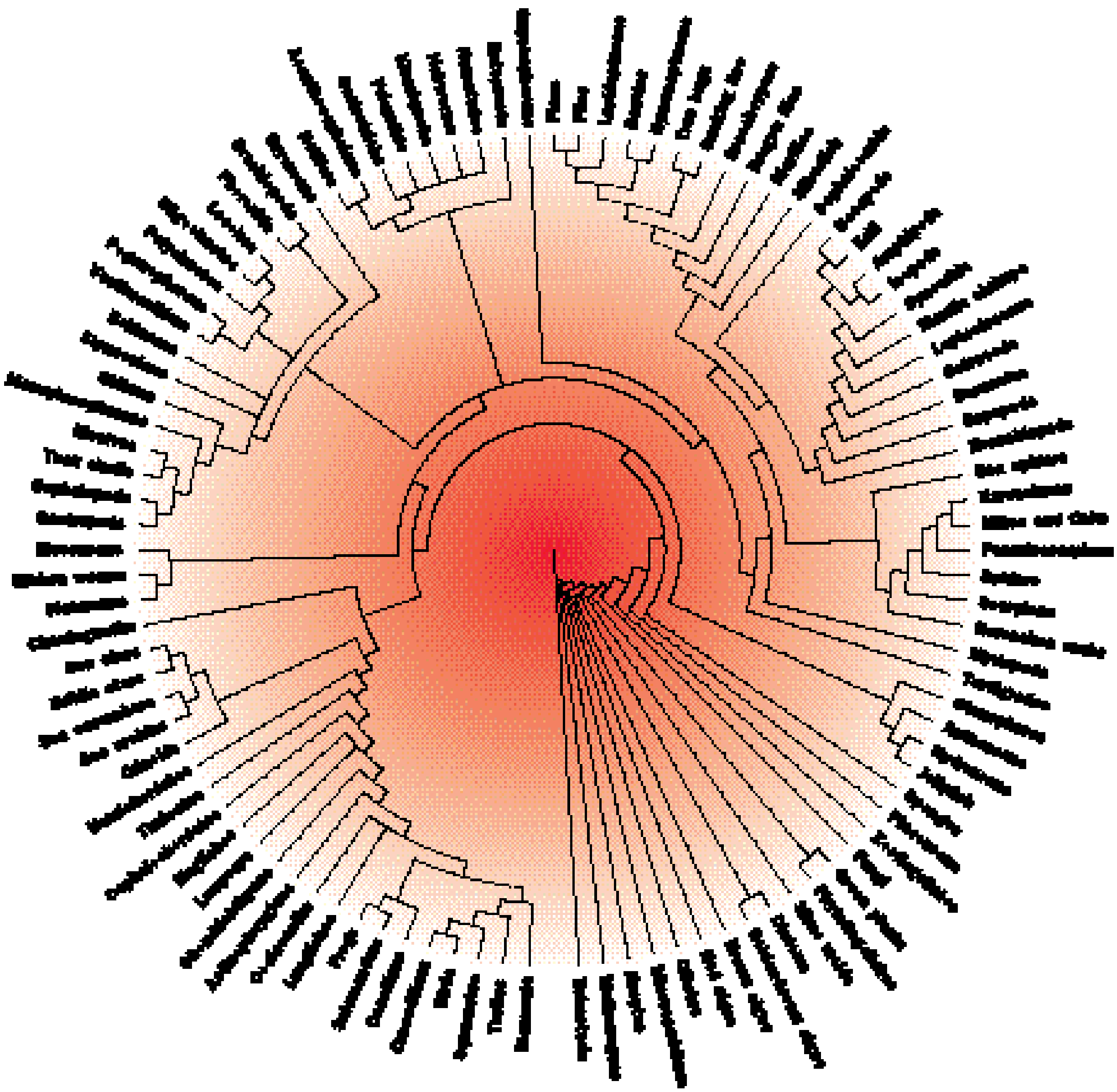
Six Kingdom

- Kingdom: Archaebacteria
- Kingdom: Eubacteria

- Kingdom: Protista
  - Phylum: Protozoans
    - Class: Ciliophora
    - Class: Mastigophora
    - Class: Sarcodina
    - Class: Sporozoa
  - Phylum: Euglenas
  - Phylum: Golden algae and diatoms
  - Phylum: Fire or golden brown algae
  - Phylum: Green algae
  - Phylum: Brown algae
  - Phylum: Red algae
  - Phylum: Slime molds
- Kingdom: Fungi
  - Phylum: Zygomycetes
  - Phylum: Ascomycetes
  - Phylum: Basidiomycetes
- Kingdom: Plants
  - Phylum: Mosses and liverworms
  - Phylum: Club mosses
  - Phylum: Horsetails
  - Phylum: Ferns
  - Phylum: Conifers
  - Phylum: Cone-bearing desert plants
  - Phylum: Cycads
  - Phylum: Ginko
  - Phylum: Flowering plants
    - Subphylum: Dicots (two seed leaves)
    - Subphylum: Monocots (single seed leaves)
- Kingdom: Animals
  - Phylum: Porifera
  - Phylum: Cnidaria
  - Phylum: Platyhelminthes
  - Phylum: Nematodes
  - Phylum: Rotifers
  - Phylum: Bryozoa
  - Phylum: Brachiopods
  - Phylum: Phoronida
  - Phylum: Annelids
  - Phylum: Mollusks
    - Class: Chitons
    - Class: Bivalves
    - Class: Scaphopoda
    - Class: Gastropods
    - Class: Cephalopods
  - Phylum: Arthropods
    - Class: Horseshoe crabs
    - Class: Crustaceans
    - Class: Arachnids
    - Class: Insects
    - Class: Millipedes and centipedes
  - Phylum: Echinoderms
  - Phylum: Hemichordata
  - Phylum: Cordates
    - Subphylum: Tunicates
    - Subphylum: Lancelets
    - Subphylum: Vertebrates
      - Class: Agnatha (lampreys)
      - Class: Sharks and rays
      - Class: Bony fishes
      - Class: Amphibians
      - Class: Reptiles
      - Class: Birds
      - Class: Mammals
        - Order: Monotremes
        - Order: Marsupials
        - Subclass: Placentals
          - Order: Insectivores
          - Order: Flying lemurs
          - Order: Bats
          - Order: Primates (including humans)
          - Order: Edentates
          - Order: Pangolins
          - Order: Lagomorphs
          - Order: Rodents
          - Order: Cetaceans
          - Order: Carnivores
          - Order: Seals and walruses
          - Order: Aardvark
          - Order: Elephants
          - Order: Hyraxes
          - Order: Sirenians
          - Order: Odd-toed ungulates
          - Order: Even-toed ungulates

PHYLOGENETIC TREE OF LIFE

This diagram represents the phylogenetic relationship of living organisms, and is sometimes called a "tree of life." Often, these diagrams are drawn as a traditional "tree" with "branches" that represent significant changes in the development of a line of organisms. This phylogenetic tree, however, is arranged in a circle to conserve space. The center of the circle represents the earliest form of life. The fewer the branches between the organism's name and the center of the diagram indicate that it is a "lower" or "simpler" organism. Likewise, an organism with more branches between its name and the center of the diagram indicates a "higher" or "more complex" organism. All of the organism names are written on the outside of the circle to reinforce the idea that all organisms are highly evolved forms of life.



SI BASE AND SUPPLEMENTARY UNIT NAMES AND SYMBOLS

Physical Quality	Name	Symbol
Length	meter	m
Mass	kilogram	kg
Time	second	s
Electric current	ampere	A
Thermodynamic temperature	kelvin	K
Amount of substance	mole	mol
Luminous intensity	candela	cd
Plane angle	radian	rad
Solid angle	steradian	sr

Temperature

Scientists commonly use the Celsius system. Although not recommended for scientific and technical use, earth scientists also use the familiar Fahrenheit temperature scale (°F). 1°F = 1.8°C or K. The triple point of H_2O, where gas, liquid, and solid water coexist, is 32°F.

- To change from Fahrenheit (F) to Celsius (C): °C = (°F-32)/(1.8)
- To change from Celsius (C) to Fahrenheit (F): °F = (°C x 1.8) + 32
- To change from Celsius (C) to Kelvin (K): K = °C + 273.15
- To change from Fahrenheit (F) to Kelvin (K): K = (°F-32)/(1.8) + 273.15

UNITS DERIVED FROM SI, WITH SPECIAL NAMES AND SYMBOLS

Derived Quantity	Name of SI Unit	Symbol for SI Unit	Expression in Terms of SI Base Units
Frequency	hertz	Hz	s-1
Force	newton	N	m kg s-2
Pressure, stress	Pascal	Pa	N m-2 =m-1 kg s-2
Energy, work, heat	Joule	J	N m =m2 kg s-2
Power, radiant flux	watt	W	J s-1 =m2 kg s-3
Electric charge	coulomb	C	A s
Electric potential, electromotive force	volt	V	J C-1 =m-2 kg s-3 A-1
Electric resistance	ohm	_	V A-1 =m2 kg s-3 A-2
Celsius temperature	degree Celsius	C	K
Luminous flux	lumen	lm	cd sr
Illuminance	lux	lx	cd sr m-2

UNITS USED WITH SI, WITH NAME, SYMBOL, AND VALUES IN SI UNITS

The following units, not part of the SI, will continue to be used in appropriate contexts (e.g., angtsrom):

Physical Quantity	Name of Unit	Symbol for Unit	Value in SI Units
Time	minute	min	60 s
	hour	h	3,600 s
	day	d	86,400 s
Plane angle	degree	°	(π/180) rad
	minute	'	(π/10,800) rad
	second	"	(π/648,000) rad
Length	angstrom	Å	10^{-10} m
Volume	liter	l, L	1 dm^3 = 10^{-3} m^3
Mass	ton	t	1 mg = 10^3 kg
	unified atomic mass unit	u (=m_a(^{12}C)/12)	≈1.66054 x 10^{-27} kg
Pressure	bar	bar	10^5 Pa = 10^5 N m^{-2}
Energy	electronvolt	eV (= e X V)	≈1.60218 x 10^{-19} J

CONVERSIONS FOR STANDARD, DERIVED, AND CUSTOMARY MEASUREMENTS

Length

1 angstrom (Å)	0.1 nanometer (exactly) 0.000000004 inch
1 centimeter (cm)	0.3937 inches
1 foot (ft)	0.3048 meter (exactly)
1 inch (in)	2.54 centimeters (exactly)
1 kilometer (km)	0.621 mile
1 meter (m)	39.37 inches 1.094 yards
1 mile (mi)	5,280 feet (exactly) 1.609 kilometers
1 astronomical unit (AU)	1.495979 x 10^{13} cm
1 parsec (pc)	206,264.806 AU 3.085678 x 10^{18} cm 3.261633 light-years
1 light-year	9.460530 x 10^{17} cm

Area

1 acre	43,560 square feet (exactly) 0.405 hectare
1 hectare	2.471 acres
1 square centimeter (cm^2)	0.155 square inch
1 square foot (ft^2)	929.030 square centimeters
1 square inch (in^2)	6.4516 square centimeters (exactly)
1 square kilometer (km^2)	247.104 acres 0.386 square mile
1 square meter (m^2)	1.196 square yards 10.764 square feet
1 square mile (mi^2)	258.999 hectares

MEASUREMENTS AND ABBREVIATIONS

Volume

1 barrel (bbl)*, liquid	31 to 42 gallons
1 cubic centimeter (cm^3)	0.061 cubic inch
1 cubic foot (ft^3)	7.481 gallons 28.316 cubic decimeters
1 cubic inch (in^3)	0.554 fluid ounce
1 dram, fluid (or liquid)	⅛ fluid ounce (exactly) 0.226 cubic inch 3.697 milliliters
1 gallon (gal) (U.S.)	231 cubic inches (exactly) 3.785 liters 128 U.S. fluid ounces (exactly)
1 gallon (gal) (British imperial)	277.42 cubic inches 1.201 U.S. gallons 4.546 liters
1 liter	1 cubic decimeter (exactly) 1.057 liquid quarts 0.908 dry quart 61.025 cubic inches
1 ounce, fluid (or liquid)	1.805 cubic inches 29.573 milliliters
1 ounce, fluid (fl oz) (British)	0.961 U.S. fluid ounce 1.734 cubic inches 28.412 milliliters
1 quart (qt), dry (U.S.)	67.201 cubic inches 1.101 liters
1 quart (qt), liquid (U.S.)	57.75 cubic inches (exactly) 0.946 liter

* There are a variety of "barrels" established by law or usage. For example, U.S. federal taxes on fermented liquors are based on a barrel of 31 gallons (141 liters); many state laws fix the "barrel for liquids" as 31½ gallons (119.2 liters); one state fixes a 36-gallon (160.5 liters) barrel for cistern measurement; federal law recognizes a 40-gallon (178 liters) barrel for "proof spirits"; by custom, 42 gallons (159 liters) comprise a barrel of crude oil or petroleum products for statistical purposes, and this equivalent is recognized "for liquids" by four states.

Units of mass

1 carat (ct)	200 milligrams (exactly) 3.086 grains
1 grain	64.79891 milligrams (exactly)
1 gram (g)	15.432 grains 0.035 ounce
1 kilogram (kg)	2.205 pounds
1 microgram (μg)	0.000001 gram (exactly)
1 milligram (mg)	0.015 grain
1 ounce (oz)	437.5 grains (exactly) 28.350 grams
1 pound (lb)	7,000 grains (exactly) 453.59237 grams (exactly)
1 ton, gross or long	2,240 pounds (exactly) 1.12 net tons (exactly) 1.016 metric tons
1 ton, metric (t)	2,204.623 pounds 0.984 gross ton 1.102 net tons
1 ton, net or short	2,000 pounds (exactly) 0.893 gross ton 0.907 metric ton

Pressure

1 kilogram/square centimeter (kg/cm^2)	0.96784 atmosphere (atm) 14.22334 pounds/square inch (lb/in^2) 0.98067 bar
1 bar	0.98692 atmosphere (atm) 1.02 kilograms/square centimeter (kg/cm^2)

Contributors

Allan B. Cobb
Austin, Texas
Jes Marie Creech
University of Texas, Austin
Emily H. DuVal
University of California, Berkeley
Andrew G. Gluesenkamp
University of Texas, Austin
Ann Guidry
Austin, Texas
Brook Ellen Hall
California State University, Sacramento
Laura A. Higgins
University of Texas, Austin
Ryan I. Hill
University of Texas, Austin

Alisha K. Holloway
University of Texas, Austin
Leslie Hutchinson
Flagstaff, Arizona
Jean Krejca
University of Texas, Austin
Stephanie A. Lanoue
Panama City Beach, Florida
Denise Prendergast
Austin, Texas
Ian Quigley
University of Texas, Austin
Elliot Richmond
Austin Community College
Karen Rogowski
University of Texas, Austin

Gil G. Rosenthal
University of California, San Diego
Todd A. Schlenke
University of Texas, Austin
Danielle Schnur
Austin, Texas
Judy P. Sheen
University of California, Berkeley
Kathrin F. Stanger-Hall
University of Texas, Austin
Rebecca M. Steinberg
University of Texas, Austin
Nancy Weaver
Driftwood, Texas
Brian R. West
University of Texas, Austin
Jennifer Yeh
University of Texas, Austin

Table of Contents

VOLUME 1:

VOLUME TWO:

D

E

F

G

Habitat Restoration

The human race is in a precarious situation as a result of its exploitation of natural **ecosystems**. Humans must balance their current resource needs with the future land-use needs of wildlife and people. As such, it makes sense to care for **habitats** by reducing damage to them and restoring those that have been damaged. With careful planning, healthy habitats can be maintained for people as well as wildlife. The goal of habitat restoration is to identify disturbed habitats and restore the native **flora** and **fauna** that occur there to ensure the continued use of the land by both wildlife and humans.

ecosystems self-sustaining collections of organisms and their environments

habitats physical locations where an organism lives in an ecosystem

flora plants

fauna animals

Historical Background

Habitat restoration is a recent concept in human history. It began in the early 1900s with the recognition that protective measures must be given to wildlife to ensure its survival. A historical landmark is the Pittman-Robertson Act of 1937, which funds wildlife research and habitat restoration. This act was financed by a tax on sporting arms and ammunition. Hunting and fishing continue to provide revenue for wildlife research today. The Endangered Species Act, which was enacted in 1973, provides protection for wildlife, and organizations such as the National Audubon Society and the Nature Conservancy play important roles in habitat acquisition, restoration, and protection.

The Importance of Habitat Restoration

Habitat restoration seeks to repair areas that have been subjected to habitat destruction. Habitat destruction is one of the primary factors involved in causing species of plants and animals to be threatened with extinction. Activities important to maintaining civilization such as agriculture, development, mining, oil drilling, logging, and road building alter natural ecosystems. Habitat destruction can be obvious, such as clearing old-growth forests for timber and draining wetland areas to use the land for raising crops, but it can also be more insidious. Habitat destruction alters the normal abundance and distribution of species in the habitat. All of these types of disturbances require restoration if the land is to be viable in the future.

Habitat restoration is important for reasons varying from aesthetic and recreational to economic and pragmatic. Wild lands and wilderness have aesthetic properties that help to maintain mental health for millions of people every year. Restoring habitats can facilitate the return of wildlife to disturbed areas for its own sake or for the sake of recreational activities such as hiking, hunting, fishing, and bird-watching. Returning disturbed land to health can add to existing habitats, making them larger and thereby helping to protect species against the dangers of small **population** sizes. Restoring areas that have been damaged through human use can allow an area to be used again for another purpose. For example, areas that have been mined are often **acidic** and have high heavy-metal concentrations, making it difficult for native plants to be reestablished in the area. Restoring these areas can help to make the habitat healthy again. In the future, the same land could be available for timber harvesting or recreational parkland, or as a wildlife refuge. Healthy forests and **riparian** zones help control erosion and maintain good water quality in streams and lakes. Reforestation and restoring damaged riparian zones helps ensure clean drinking water, control floods, and maintain healthy fish and amphibian populations.

population a group of individuals of one species that live in the same geographic area

acidic having the properties of an acid

riparian habitats in rivers and streams

Restoration Methods

Habitat restoration is accomplished through management, protection, and reestablishment of plants by returning **abiotic factors** (e.g., soil chemistry, water content, disturbance) and **biotic factors** (e.g., species composition, interactions among species) to historical levels. Properly restored ecosystems demonstrate the historical species diversity of the area instead of one species in monoculture. Reestablishing plants provides a food source for animals and thus helps restore animal populations.

abiotic factors pertaining to nonliving environmental factors such as temperature, water, and nutrients

biotic factors biological or living aspects of an environment

In reestablishing plants, soil conditions are very important, because they will determine what will grow and where. Soil moisture and mineral content, aeration, and presence of microorganisms are important factors that must be considered. Most plants are associated with fungi called mycorrhizal fungi (also called mycorrhizae), an association that is integral to a plant's system for absorbing nutrients and water. These fungi associate with the roots of the plants and help in gathering and transporting nutrients and minerals to the plant. These **symbiotic relationships** are often species specific, and this makes them essential in reestablishing native plants. Without their symbiotic fungi, many native plants are weak competitors with nonnative species. Therefore, it is often necessary to introduce the correct mycorrhizal fungus into the plants through inoculation. In addition, members of the soil community such as bacteria and earthworms, which create healthy soil food chains and aid in soil aeration, respectively, may also be added to disturbed habitat. Knowledge of the appropriate fungus, bacteria, and worm species for each habitat is necessary. The organisms must also be available for inoculation. In severely disturbed or unique habitats, knowledge of the proper organisms may not exist, or the organisms themselves may unavailable, resulting in an inability to restore the habitat properly.

symbiotic relationships close, long-term relationships where two species live together in direct contact

Situations where the native flora is intact but is not functioning normally because of human activities require management and protection

This forest in Hawkes Bay, New Zealand, had once been cleared for farming purposes, but has been restored to its original composition.

to accomplish restoration. In some cases removal of dense underbrush and thinning young trees is necessary to restore a habitat to health. Another method to restore habitats is controlled fire. In habitats historically subjected to fire, some species require occasional fires to set seed and to thin out young trees that are otherwise stunted as a result of competing for limited resources. Without periodic fire the densely growing trees will be stressed and subject to pest outbreaks that do more damage than the fire.

Drainage patterns and soil water content can be altered to facilitate natural reestablishment of native vegetation. Large earthmoving machines can alter drainage patterns while smaller tools can help shape water movement in the soil. Wetlands can be restored by flooding drained areas. Once the water is in place, revegetation can proceed with species appropriate for the area. Waterfowl and wetland bird species may assist in seed dispersal from nearby wetlands.

Stream habitats may also be restored through appropriate management. For example, flooding can be problematic for inhabitants of small streams, particularly the eggs and young of salmonid fishes in the northwestern United States. Large-scale timber harvesting can add silt to streams, and with fewer trees, heavy rains reach streams more rapidly and with more force. This can lead to the covering of fish eggs by silt, which suffocates them, and the removal of young fish and eggs from protected areas into the main stream channel, which results in increased rates of predation. Restoration projects aimed at redirecting the streambed to slow floods and the placement of in-stream obstructions such as large rocks and logs can prevent these problems while creating spawning habitat at the same time.

Maintenance of adequate riparian zones can eliminate the need for such restoration measures by reducing the impact of floods.

Restoration Difficulties

Habitat restoration is difficult and problems are often encountered. Exotic and invasive species, problematic soils, and variation in populations can make habitat restoration a challenge. Exotic or invasive species may outcompete natives for nutrients in the early stages of restoration. Inoculation with mycorrhizal fungi can alleviate this by helping the natives absorb nutrients, but often the problem persists. This is because habitat destruction releases nutrients into the soil that may be used by the exotic species. Sometimes, fertilizers are added with the intent of helping the native species grow, but the excess nutrients encourage exotic species to grow instead. One solution to this problem is to limit the nutrients available to the exotic species by removing excess nutrients. Removing excess nutrients, not adding them, allows the native species to persist with assistance from their mycorrhizal associates, while not giving the invasive species the nutrients they require to compete with the natives. Subtle differences in moisture, altitude, slope aspect, and other variables over species' ranges may make some restoration projects difficult. Individuals of a species from one area may be difficult to establish in another area because they may be adapted to local conditions.

A caveat of habitat restoration is that to do it properly one must have a thorough understanding of the ecological requirements, both **abiotic** and **biotic**, for the species involved. Also necessary for proper restoration is an understanding of historical land-use patterns coupled with the knowledge of what locally similar, pristine habitat looks like. This knowledge can be difficult to collect and can require substantial investment of money, time, and energy. The result, however, is a better understanding of ecosystems, and with this, one can make educated decisions about how to restore habitats. Habitat restoration is important for the health of the planet and the human race, and continued research on ecosystems and restoration techniques is vital.

abiotic nonliving parts of the environment

biotic pertaining to living organisms in an environment

Restoration need not only take place in rural settings. Suburban gardens of native plants encourage beneficial native insects and bird species that can act as biocontrol for pests. Gardening with native species also conserves water, increases awareness and appreciation of regional diversity, and can create small islands of habitat for local species to use as gateways to larger habitat areas. This type of habitat restoration can be done individually on a local level and can turn the tide from wildlife in a sea of people to people in a sea of wildlife. SEE ALSO Ecosystem; Environment; Habitat; Habitat Loss.

Ryan I. Hill

> Aldo Leopold (1886–1946), American forester, director of the Audubon Society (1935) and one of the founders of the Wilderness Society (1935), stated in *A Sand County Almanac* (1949) that land is a community in which all individuals depend on one another. For Leopold, "individuals" include soil, water, plants, and animals. This idea of mutually dependent individuals within a community has been the moral center of the modern ecosystem-centered environmental movement.

Bibliography

Berger, John J., ed. *Environmental Restoration: Science and Strategies for Restoring the Earth*. Washington, D.C.: Island Press, 1990.

Decamps, H. "River Margins and Environmental Change." *Ecological Applications* 3 (1993):441–445.

Ferris-Kaan, Richard, ed. *The Ecology of Woodland Creation.* London: Wiley, 1995.

Peterjohn, W. T., and D. L. Correll. "Nutrient Dynamics in an Agricultural Watershed: Observations on the Role of a Riparian Forest." *Ecology* 65 (1984): 1,466–1,475.

Prasse, Rüdiger, and Reinhard Bornkamm. "Effect of Microbiotic Soil Surface Crusts on Emergence of Vascular Plants." *Plant Ecology* 150 (2000):65–75.

Smith, Robert Leo, and Thomas M. Smith. *Elements of Ecology*, 4th ed. San Francisco: Benjamin/Cummings, 1998.

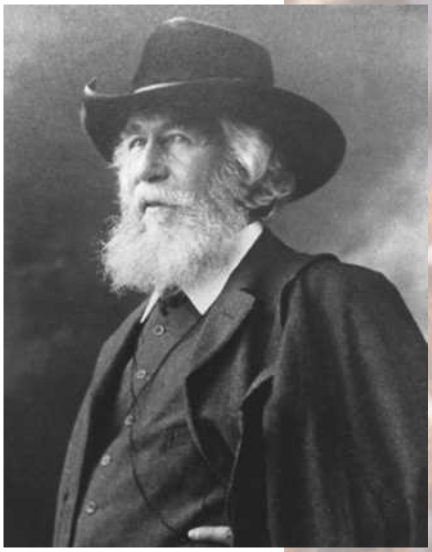
Urbanska, Krystyna M., Nigel R. Webb, and Peter J. Edwards, eds. *Restoration Ecology and Sustainable Development.* Cambridge, U.K.: Cambridge University Press, 1997.

Whisenant, Steven G. *Repairing Damaged Wildlands: A Process-Oriented, Landscape-Scale Approach.* Cambridge, U.K.: Cambridge University Press, 1999.

Yaalon, Dan H., and Richard W. Arnold. "Attitudes Toward Soils and Their Societal Relevance: Then and Now." *Soil Science* 165, no. 1 (2000):5–12.

Haeckel's Law of Recapitulation

German zoologist Ernst Haeckel famously—and inaccurately—uttered, "Ontogeny recapitulates **phylogeny**." While investigating the developing embryos of a variety of **vertebrates**, Haeckel thought they all closely resembled one another. This observation led to his conclusion that embryonic development echoed **morphological** evolution. Specifically, gill depressions in human embryos led Haeckel to conclude that humans were derived from fishes. He therefore felt that the study of embryonic development, or **ontogeny**, retold the story of evolution, or phylogeny. As he wrote in 1866, "During its rapid evolution, an individual repeats the most important changes in form evolved by its ancestors during their long and slow paleontological development." (Haeckel)



Ernst Haeckel incorrectly stated, "Ontogeny recapitulates phylogeny."

phylogeny the evolutionary history of a species or group of related species

vertebrates animals with a backbone

morphological the structure and form of an organism at any stage in its life history

ontogeny the embryonic development of an organism

There are a number of flaws with Haeckel's theory. For example, Haeckel confused a fish embryo with a young human one. Haeckel's drawings strongly suggest that a variety of vertebrates share a common developmental phase, but he does not account for the entire process of development, nor does he compensate for size differences. His drawings were grossly oversimplified and ignored or obfuscated many salient differences. This did not stop Haeckel's law from being widely accepted for the majority of the twentieth century. Many otherwise up-to-date textbooks, such as *Molecular Biology of the Cell*, written in 1994 by Nobel laureate James Watson and National Academy of Sciences President Bruce Alberts, continue to cite Haeckel.

In 1997 a group headed by Michael Richardson of St. George's Hospital Medical School in London published a serious investigation of Haeckel's claims. Photographs of a variety of vertebrate embryos showed conclusively that, despite some similarities, there is no stage in vertebrate development when all embryos are identical. That said, there are definitely some common features among developing vertebrates. In the nineteenth century, embryologist K. E. von Baer wrote, "The embryo of the mammal, bird, lizard, and snake and probably also the turtle, are in their early stages so uncommonly similar to one another that one can distinguish them only according to their size" (Richards 1992). Common structures do not imply that vertebrate development retells the story of evolution.

Haeckel was a strong supporter of evolution, particularly after reading Charles Darwin's *The Origin of Species*. However, Darwin argued that **natural selection** was the mechanism that advanced evolution. Haeckel's view was that developing embryos strove to meet the needs of their environment by adding more and more complex structures. Examining Haeckel's law, one could conclude that it is possible to reach backwards through development and find the alleged evolutionary forerunner of all vertebrates. In normal development, a ball of cells known as a gastrula develops soon after **fertilization** and eventually becomes the gut. As each embryonic stage was supposed to represent another species, Haeckel postulated the existence of a "gastraea"—an organism that resembled the gastrula and was, by extension, the ancestor of all the vertebrates.

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

fertilization the fusion of male and female gametes

Despite mainstream acceptance of Haeckel's ideas, gastraea do not exist. Nor does evolution advance by adding traits to developing embryos. While there are definite similarities among developing vertebrates, Haeckel's famous utterance can be safely dismissed. Despite the acceptance he found elsewhere, scientists in Haeckel's native Germany considered his findings suspect. He was accused of academic fraud and pled guilty, claiming that many of his drawings were reproduced from memory. When comparing photographs of actual embryos to the drawings, however, one could conclude that Haeckel remembered only one embryo and claimed that all vertebrates looked just like it. As Michael Richardson said, "These are fakes. In the paper, we call them 'misleading and inaccurate,' but that is just polite scientific language" (*Times* London, August 11, 1997). SEE ALSO ONTOGENY; PHYLOGENETICS SYSTEMATICS.

Ian Quigley

Bibliography

Gould, S. J. *Ontogeny and Phylogeny*. Cambridge, MA: Harvard University Press, Belknap Press, 1977.

Haeckel, Ernst. *The Evolution of Man: A Popular Exposition of the Principal Points of Human Ontogeny and Phylogeny* (1866; New York, 1896).

Richards, R. J. *The Meaning of Evolution.* Chicago: University of Chicago Press, 1992.

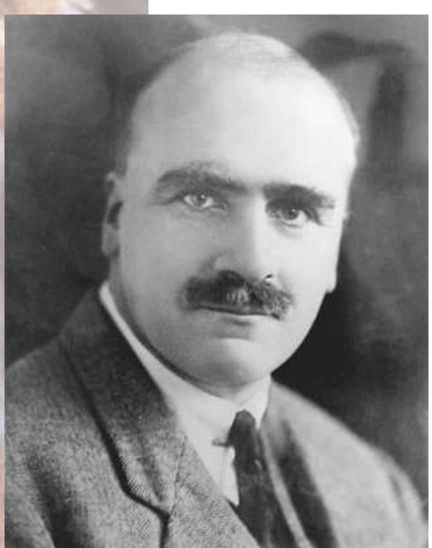
Richardson, M. K., J. Hanken, L. Selwood, G. M. Wright, R. J. Richards, C. Pieau, and A. Raynaud. "Haeckel, Embryos, and Evolution." Science 280 (1997):983–984.

Times (London), August 11, 1997.

Haldane, J. B. S.

Geneticist

1892–1964



John Burdon Sanderson Haldane made several important discoveries about human physiology and respiration.

John Burdon Sanderson Haldane was born on November 5, 1892. His father, John Scott Haldane, was a physiologist at Oxford University who worked on respiration and contributed to the safety of miners. The elder Haldane encouraged his son to assist him, and he was soon bringing the child down mine shafts during his experiments to prove that the air in them was breathable.

Haldane attended New College at Oxford on a mathematical scholarship and worked with the rediscovered laws of Mendelian **genetics**. It was while experimenting on his sister Naomi's guinea pig colony that he discovered genetic linkage. About the same time, in 1912, Haldane published his first of some 400 scientific articles, on **hemoglobin** binding of carbon monoxide.

Many of Haldane's gas absorption experiments were designed to help the British Navy and its divers. Haldane lost two teeth, which exploded due to the rapid decompression in his sinuses, during one experiment.

One of Haldane's specialties was the **physiology** of gas **absorption** and binding in humans. He frequently experimented on himself and his second wife, Dr. Helen Spurway. To assess carbon dioxide regulation of blood pH, for example, he ingested large quantities of sodium bicarbonate to make his blood basic or ammonium chloride to make it more **acidic**. He inhaled the highly toxic carbon monoxide and described its effects.

genetics the branch of biology that studies heredity

hemoglobin an iron containing protein found in red blood cells that binds with oxygen

physiology the study of the normal function of living things or their parts

absorption the movement of water and nutrients

abiotic nonliving parts of the environment

enzyme a protein that acts as a catalyst to start a biochemical reaction

acidic having the properties of an acid

biometry the biological application of statistics to biology

Aside from his work in human physiology and respiration, Haldane created the discipline of population genetics nearly single-handedly, starting with the publication of *The Causes of Evolution*, in 1932. He laid down the foundations for **enzyme** kinetics in 1930 with *Enzymes*. He also studied biochemical genetics and human genetics, discovering what effects ionizing radiation had on humans.

Haldane postulated that the early Earth might be able to produce life-supporting molecules such as nucleic acids from **abiotic** processes. The theory was later shown to be true. At New College, he was a fellow in physiology. And he occupied the chair of **biometry** at University College, London, for twenty years (1937–1957). Haldane also served as an editor for the influential *Journal of Genetics* for seventeen years (1947–1964). Before his death, in 1964, he studied tropical biology in India. Despite his monumental contributions to physiology, genetics, enzyme kinetics, and biochemistry, Haldane never held a science degree or any scientific certification from Oxford.

Ian Quigley

Bibliography

Dronamraju, Krishna R. *Haldane: The Life and Work of J. B. S. Haldane with Special Reference to India.* Aberdeen, Scotland: Aberdeen University Press, 1985.

Herpetology

Herpetology is the study of amphibians and reptiles. The scientists who study these animals are called herpetologists. They research the structure, physiology, and behavior of these animals, as well as how they live and are related to one another. Medical researchers have been able to gain valuable knowledge from the study of these animals because they are able to survive well in captivity and they can survive operations that would kill many birds and mammals. Herpetological research also includes the extraction and biochemical study of venoms—a growing subspecialty. Because of their unique biochemistry, some venoms hold great promise as therapies for incurable or chronic diseases.

The field of herpetology appears to stem from the ancient tendency to group all creeping animals together. The Greek word *herpeton* means "crawling thing." Modern herpetology, as a popular and important science, tends to focus more narrowly on issues specific to orders or suborders of animals (e.g., the global decline of frog populations). Most technical research in herpetology is carried out in the field or at universities.

Herpetologists may work in zoos or for wildlife agencies, do environmental assessments, care for museum collections, or teach the public in a museum setting. Some herpetologists work as writers, photographers, or animal breeders. The majority of herpetologists work as professors or researchers in colleges and universities. While most herpetologists do have a doctorate, there have been some cases where novices were so renowned for their expertise, that they were invited to teach at the college and university level. Smaller colleges may hire teachers with a master's degree. Herpetologists with an entrepreneurial spirit may go into business for themselves, breeding and selling amphibians and reptiles, or marketing related herpetological merchandise and publications. SEE ALSO Amphibia, Reptilia.

Stephanie A. Lanoue

Bibliography

Porter, Kenneth. *Herpetology.* Philadelphia: W.B. Saunders Company, 1972.

Heterochrony

Heterochrony—literally, "different timing"—describes the occurrence of a change in the timing of the development of different body parts between an ancestor and its descendants. The concept of heterochrony is intimately associated with **allometry**, which describes the relationship between the size of different structures or organs of an organism throughout its life; both concepts involve the study of growth patterns.

allometry relative growth of one part of an organism with reference to another part

Describing Heterochrony

Heterochronic phenomena may be described with respect to **somatic** (body) and gonadal (reproductive) maturation and may be global (effecting the entire individual) or local (affecting only one structure, organ, or system). Further, the growth of a structure or organ may be isometric with respect to other structures (shape does not change with growth) or it may follow either a positive or negative allometric path (shape changes with growth). Finally, different kinds of heterochronies can occur in different parts of the body, producing ontogenies (courses of development in an organism) that are "dissociated" or "mosaic." That is, some aspects of development are accelerated while others are retarded. Any change in a body part's growth rate relative to that of other structures is described as either acceleration or retardation (also called neoteny).

somatic having to do with the body

Classes of Heterochronic Development

Developmental heterochronic phenomena result in either paedomorphosis or peramorphosis. Paedomorphosis describes the retention of juvenile traits in a structure (the trait in the descendant resembles that of juveniles in the ancestor). Peramorphosis describes cases where a trait in the descendant has a more extreme morphology than in its ancestor.

The axolotl, a type of salamander, has feathery appendages that have evolved from its ancestors by heterochrony.

Heterochrony can be further classified in terms of changes in the length of the duration, rate, or timing of events in **ontogeny**. Change in the duration of growth without any change in rate or timing is described as hypermorphosis (increased period of somatic growth with respect to gonadal development) or progenesis (decreased period of somatic growth with respect to gonadal development). Change in the timing at which growth of a structure occurs is described as predisplacement (onset of growth occurs earlier in ontogeny) or postdisplacement (onset of growth occurs later in ontogeny).

ontogeny the embryonic development of an organism

Effects of Heterochronic Changes

Heterochronic changes are often driven by selection on life history traits. For example, some species may be under selection to reproduce at an earlier age than others and correlate with paedomorphic or hypermorphic results. Paedomorphosis by means of progenesis (structures stop developing at an earlier stage than in the ancestral ontogeny) may occur when there is selection for rapid maturation. Paedomorphosis is frequently associated with small adult size in many groups of animals (some tiny **salamanders** have simplified skeletons that are reminiscent of earlier developmental stages in their ancestors). Paedomorphosis via neoteny often results from selection operating under particular stable larval environments.

salamanders four-legged amphibians with elongated bodies

Peramorphosis via hypermorphosis can result from selection for increased body size or **sexual selection** and may result in exaggerated features. The relatively more elaborate antlers of some large deer species compared to those of smaller, ancestral species are hypermorphic. Peramorphosis by acceleration can result from selection for acceleration of prenatal growth. An example of peramorphosis via acceleration is the rapid larval development of many desert-adapted frogs (including the spadefoot toads of the American Southwest), which breed in temporary pools of water. Some species can transform from egg to froglet in less than three weeks compared to the three months required in many species whose tadpoles live in more stable environments.

sexual selection selection based on secondary sex characteristics that leads to greater sexual dimorphism or differences between the sexes

Predisplacement (initiation of development of a structure occurs earlier in development in the descendant than in the ancestor) may occur in response to selection in unstable larval environments. In some frog species, adult skull structures may begin to form during the larval stage depending on the availability of food. The presence of these structures allows the tadpoles to eat larger food items, including other tadpoles. This development expands the range of food the tadpole is capable of consuming, therefore increasing its chances of survival.

aquatic living in water

metamorphose to change drastically from a larva to an adult

metamorphosis to change drastically from a larva to an adult

gills site of gas exchange between the blood of aquatic animals such as fish an the water

lungs sac-like, spongy organs where gas exchange takes place

terrestrial living on land

genetics the branch of biology that studies heredity

Perhaps the best known example of heterochrony in nature is the axolotl, an **aquatic** salamander from Mexico. Axolotls were not thought to be salamanders until 1863, when some individuals on display at the Natural History Museum in Paris began to **metamorphose** (probably because of some environmental stress associated with their conditions in captivity). Ordinarily, amphibians undergo **metamorphosis** from egg to larva, and finally, to the adult form. The axolotl, along with a number of other amphibians, remains in its larval form, meaning that it retains its **gills** and fins and doesn't develop protruding eyes, eyelids, and characteristics of other adult salamanders. It reaches sexual maturity in the larval stage. The axolotl is completely aquatic, and although it possesses rudimentary **lungs**, it breathes primarily through its gills and to a lesser extent, the skin. This species descended from a **terrestrial** ancestor with an aquatic larval stage (probably the tiger salamander, *Ambystoma tigrinum*). These salamanders were historically found in lakes with relatively constant temperatures, abundant food sources, and no competition from or predation by fish. Unfortunately, introduced predatory fish and heavy pollution threaten most wild populations. The unusual life history and large eggs of this species make it an excellent organism for studies of **genetics** and development, and large colonies are maintained in universities and research institutions throughout the world.

Conclusion

mutations abrupt changes in the genes of an organism

Identification of heterochronic phenomena requires a hypothesis of relationships among the life-forms being considered and information on the development patterns of the ancestor and descendant. Detailed information on the duration, timing, and rate of developmental phenomena in both the ancestral and descendant ontogeny may be required to discriminate between various types of paedomorphosis and peramorphosis. **Mutations** causing heterochronic changes play an important role in evolution and developmental constraints and can result in powerful relationships between the processes of embryonic development and the resulting evolutionary history. SEE ALSO ALLOMETRY; EMBRYONIC DEVELOPMENT; ONTOGENY; PHYLOGENETICS SYSTEMATICS.

Andrew G. Gluesenkamp

Bibliography

Duellman, W. E., and L. Trueb. *Biology of Amphibians.* New York: McGraw-Hill, 1986.

Futuyma, D. J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, Inc., 1986.

Gould, S. J. *Ontogeny and Phylogeny.* Cambridge, MA: Harvard University Press, Belknap Press, 1977.

Jeffery, W. R., and R. A. Raff, eds. *Time, Space, and Pattern in Embryonic Development.* New York: Alan R. Liss, 1983.

Raff, R. A. *The Shape of Life.* Chicago: University of Chicago Press, 1996.

Home Range

In the course of its daily activities, an animal travels through familiar places to obtain food, seek shelter, or find mates. The actual physical area covered in the course of these regular movements is the animal's home range. An animal's familiarity with the features of its home range allows it to forage efficiently and escape predators when necessary. For example, a house cat in its home range may begin to stalk as it approaches a familiar birdfeeder even if it cannot tell whether there are birds on the feeder. The cat has learned that the birdfeeder is a reliable source of prey and behaves accordingly. An individual animal, a mated pair, a family, or a group of families may occupy a given home range, and home ranges of several individuals or groups may overlap. Animals do not defend the boundaries of their home ranges against intruders of their own species. An area that is defended is called a territory, and is usually a smaller area within an animal's home range. Some species may carry out all their daily activities within a defended territory, especially during the breeding season. In this case, territory is equivalent to home range.

A grizzly bear debarks a tree in the La-Sal Mountains in Utah. Animals move about in their home range, a comfortable environment in which to forage and evade predators efficiently.

An animal's need for resources and the distribution of resources in the environment determine the size of its home range. This general ecological trend is known as the resource dispersion hypothesis. When resources are sparsely distributed, an individual must travel farther to obtain the same amount of food as an individual of the same species living in a **habitat** where food resources are concentrated. Variation in the sizes of home ranges within species reflects the quality of the habitat; home ranges will be smaller in resource-rich habitats and larger in those that are resource-poor.

habitat physical location where an organism lives in an ecosystem

The size of an animal's home range is directly affected by its body size. Large animals generally require large amounts of food and therefore have larger home ranges than individuals or species that are smaller but eat the same types of food. The type of resources an animal requires also greatly influences the size of its home range. For example, **herbivores** have smaller home ranges than omnivores of the same size: The leaves and grass that herbivores eat tend to be easier to find than the fruits and seeds more common in an **omnivorous** diet. Similarly, omnivores have smaller home ranges than carnivores of the same body size. The prey of carnivores are distributed even more sparsely than the food of omnivores, so carnivores must cover greater distances to meet their resource needs.

herbivores animals who eat plants only

omnivorous eating both plants and animals

Social systems can also influence the size of a home range. In some species, such as voles (*Microtis* sp.), males do not care for offspring but instead travel among the home ranges of multiple females seeking mates. In a classic experiment testing the factors that determine home ranges, researchers placed female voles in movable enclosures mimicking a home range and then monitored the movements of uncaged males. When the females were close together, males had small home ranges. When females were farther apart, males increased the size of their home range. Another experiment showed that free-ranging females do not change the size of their home ranges when caged males are close together or far apart. The home range size of female voles is determined by the dispersion of resources, but the home range size of males is determined by the dispersion of females.

In general, scientists measure a home range by plotting the movements of an individual onto a map over an extended period of time, often several months or years. This plotting can be done by watching the movements of an animal, capturing and recapturing marked individuals in a grid of traps, or by monitoring individuals with radiotelemetry. Radiotelemetry is a tracking technique in which a scientist attaches a signal-emitting transmitter to an animal which is then released. Using an antenna and receiver, the scientist can then locate the unique signal frequency emitted by an individual's transmitter and follow that animal's movements in the wild. The resulting map of points shows the major activity areas of the study animal, but is not completely precise. An animal will not necessarily visit all areas of its home range during the observation period, and not all areas of the home range will be equally important. For example, a bobcat might spend very little time at a pond in its home range, indicating that fresh water is not very important, yet the availability of fresh water is a key **habitat requirement** of the species. Many mathematical approaches can be used to analyze home range data, but all approaches have the underlying goal of estimating the probability that an animal will be found in a particular place. Studies of home range are an important part of the science of **ecology** and can provide insight into the social organization, foraging behavior, limiting resources (those resources that limit the number of individuals that can live in a particular area), and habitat requirements of animals. SEE ALSO Foraging Strategies; Habitat.

habitat requirement the necessary conditions or resources needed by an organism in its habitat

ecology the study of how organisms interact with their environment

Emily H. DuVal

Bibliography

Harestad, A. S., and E. L. Bunnell. "Home Range and Body Weight—A Reevaluation." *Ecology* 60 (1979):389–402.

Ims, R. A. "Spatial Clumping of Sexually Receptive Females Induces Space Sharing Among Male Voles." *Nature* 335, no. 6190 (1988):541–543.

McNab, B. K. "Bioenergetics and the Determination of Home Range Size." *American Naturalist* 97 (1963):133–140.

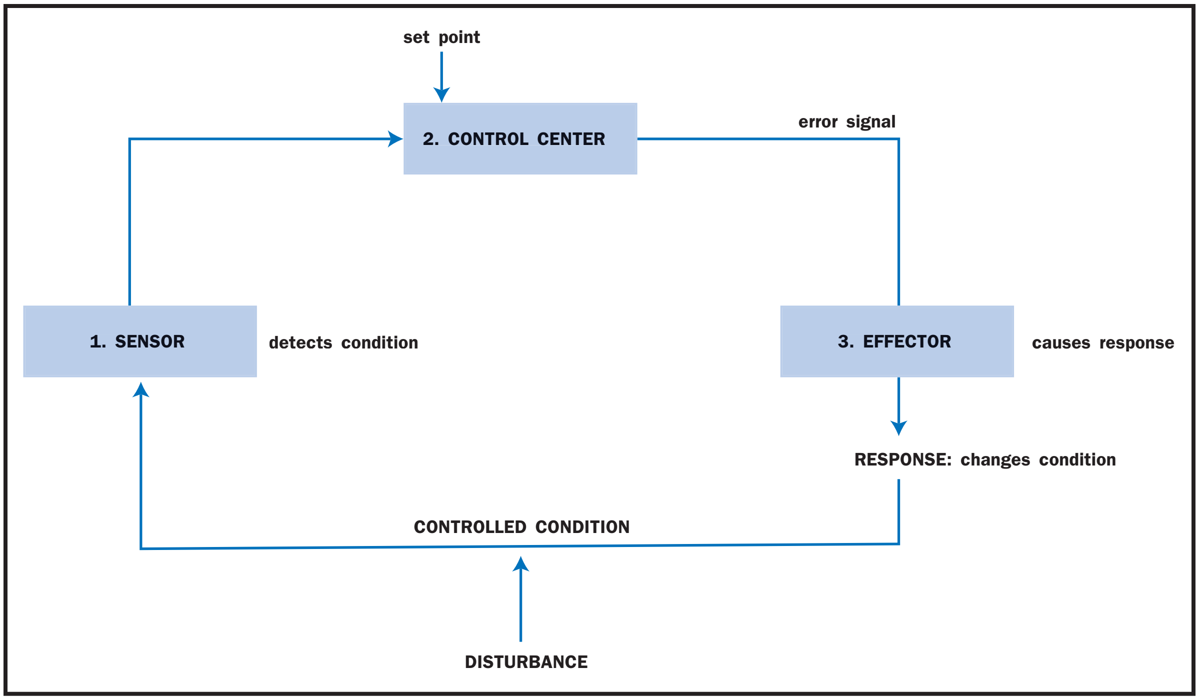
Powell, Roger A. "Animal Home Ranges and Territories and Home Range Estimators." *Research Techniques in Animal Ecology, ed.* Luigi Boitani and Todd K. Fuller, New York: Columbia University Press, 2000.

Smith, Robert Leo. *Ecology and Field Biology*, 5th ed. New York: Harper Collins College Publishers, 1996.

Homeostasis

In 1865 French physiologist Claude Bernard pointed out that in order for an organism to survive, a constant, or stable, internal environment was required. Based on this insight, and more than half a century later, in 1929, a physiologist from Harvard University, Walter B. Cannon, coined the term "homeostasis." Homeostasis means a stable state of the internal environment that is maintained by regulatory processes despite changes that may occur in the external environment.

Like the first animals to evolve, simple animals such as sponges and jellyfish have a body wall that is only a few cell layers thick, and each cell has direct access to the external environment. As a result, cells can take up nutrients and dispose of wastes by direct exchange with the external environment, but they are also directly exposed to fluctuations in that external environment. Such fluctuations (e.g., in ion concentrations or temperature),



Homeostatic feedback diagram.

will affect the ability of the cells to perform the chemical processes necessary for survival, and therefore restrict the occurrence of these simple animals to more favorable environments.

When animals evolved that had a bulkier shape (like earthworms, fish, or humans today), only some of their cells were still in contact with the external environment. This required specializations such as a digestive system to bring food inside the body for digestion, and a circulatory system to disperse the nutrients to all the cells. The big advantage was that these internal cells were no longer directly exposed to the external environment but were surrounded by extracellular fluid creating an internal environment. Living cells can thrive in certain kinds of conditions and not in others. Various homeostatic control mechanisms regulating the internal environment can now cooperate to maintain the optimal conditions, independent from the external environment. This allows these animals to thrive in areas with less favorable external conditions. Homeostatic regulation of the extracellular fluid can include ion composition, pH levels, oxygen and carbon dioxide levels, nutrient and waste product levels, as well as temperature.

When studying the physiology (structure and function) of animals, scientists are often concerned with the question of how the animals maintain homeostasis. Homeostatic control relies on negative feedback. This means that any deviation from the desired state of the internal environment will be reduced (hence negative) as a result of homeostatic control and bring the internal environment back to the desired state (e.g., regulation of body temperature).

This is in contrast to positive feedback that would enhance (hence positive) the difference leading to an escalation (e.g., child birth). Positive feedback is not useful for the homeostatic control of the internal environment.

There are three main structures that are part of all homeostatic control systems (see homeostatic feedback diagram): (1) sensors that sense the

actual state of the condition that is being controlled. This information is passed on to the (2) control center, which compares the information from the sensors with the stored information, or set point, about what the condition should be. When the information from the sensors differs from the stored set point, the control center will send an error signal to (3) effectors to trigger an adequate response that will lead to a change in the controlled condition and bring it closer to the set point. When a difference between the controlled condition and the set point is no longer registered by the control center, the error signal ceases, and homeostasis is maintained until another disturbance causes a change in the controlled condition.

endocrine system the grouping of organs or glands that secrete hormones into the bloodstream

enzymes proteins that act as catalysts to start biochemical reactions

The nervous system and the **endocrine system** play a major role in homeostatic control by relaying the signals from the sensors to the control center and from the control center to the effectors.

An important example of homeostatic control is temperature regulation. Cellular processes are temperature dependent. For example, protein **enzymes** that catalyze the chemical reactions in cells have a preferred temperature range at which they perform optimally. Lower temperatures will slow them down, higher temperature may destroy them. Mammals and birds are two animal groups that have evolved the ability to maintain a stable body temperature independent of the environmental conditions (endothermy). This allows them to be active in environments over a wide temperature range. Humans normally regulate their body core temperature in a relatively narrow range (between 36 and 39°C [96.8° and 102.2°F]). To maintain this temperature, heat production has to balance heat loss. Homeostatic control of body temperature ensures that heat production and heat loss are approximately equal.

neurons nerve cells

hypothalamus part of the upper end of the brain stem that regulates activities in the nervous and endrocrine systems

action potentials rapid changes in the electric charge of the cell membrane

For example, when humans exercise, the muscle activity generates a lot of heat as a byproduct of muscle contraction. This additional heat (disturbance) will increase the body core temperature (controlled condition). The temperature is monitored by temperature sensors, and this information is passed on by **neurons** to a specific brain region, the **hypothalamus** (the temperature control center). If the core temperature exceeds the desired temperature (set point), an error signal is generated by the control center. This error signal in the form of **action potentials** (electric signals that travel along neurons) triggers sweat glands (effectors) to secrete sweat over the body surface (response). The evaporation of sweat leads to cooling off of the body surface. When heat loss through evaporation balances heat gain through exercise, a stable core temperature (and temperature homeostasis) will be maintained.

skeletal muscles muscles attached to the bones; are responsible for movement

When humans experience severe heat loss (disturbance), the body temperature (controlled condition) monitored by the sensors drops below the desired temperature (set point). As a result, the hypothalamus (control center) sends action potentials (error signal) to **skeletal muscles** (effectors) to trigger muscle contractions and cause shivering (response). As a byproduct of this muscle activity heat is produced. When heat gain through shivering balances heat loss a stable core temperate (and temperature homeostasis) will be maintained. SEE ALSO Allometry; Cells; Functional Morphology.

Katrin F. Stanger-Hall

Bibliography

Campbell, Neil A. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman Inc., 1999.

Homology

The term "homology" was defined in 1843 by Richard Owen, a noted British paleontologist, as the "same organ under every variety of form and function." Thus **homologous** structures can be defined in an evolutionary context as elements whose similarity in various **taxa** derives from their common origin in a shared ancestor. Homology may be based on:

homologous similar but not identical

taxa named taxonomic units at any given level

1. similarities in structure, or how an organ is shaped;
2. topography, or the location of an organ;
3. associations with other structures, an example of which would be bone–muscle relationships;
4. development, including shared expression patterns of homologous **genes**.

genes segments of DNA located on chromosomes that direct protein production

The concept of homology is fundamental to comparative biology and **phylogenetics** systematics. Homology has historically been defined in terms of inheritance of a structure, with more or less modification, from a common ancestor. In this sense, attributes of two organisms are homologous when they are derived from an equivalent characteristic of the common ancestor. For example, whale flippers, bat wings, and human hands are homologous with respect to one another despite obvious differences in size, structure, and function. Whales, bats, and humans are descendants of a common mammalian ancestor, and their specialized appendages are simply modifications of the ancestral forelimb.

phylogenetic relating to the evolutionary history of species or group of related species

If two or more species have a similar trait that was not inherited from their common ancestor, the traits are said to be **homoplastic**. For example, insect wings, bird wings, and bat wings are considered to be homoplastic with respect to one another despite that they are all specialized appendages used for flight. The common ancestor of insects and **amniotes** (terrestrial vertebrates, including mammals and birds) did not have wings. Specialized appendages used in flight have evolved several times independently in the history of **metazoans** (multicellular animals). The developmental origins and underlying structural patterns are very different in these two groups of organisms. Insects and amniotes acquire wings in different ways during development and, despite similarities in the early development of bats and birds, the common ancestor of birds and bats did not have wings but rather some other type of forelimb. In addition, insect wings are foils made up primarily of **chitin**, a type of tissue, while bird and bat wings are highly complex with various tissue types organized into different structures such as feathers, skin, bone, blood, muscle, and nerves.

homoplastic similar but of different origins

amniotes vertebrates that have a fluid-filled sac that surrounds the embryo

metazoans a subphylum of animals that have many cells and some are organized into tissues

chitin a complex carbohydrate found in the exoskeleton of some animals

The question of whether an identical trait shared by two or more taxa is the result of homology or homoplasy usually cannot be decided based on a single character alone. In the above examples, one might be misled by grouping organisms based solely on the presence or absence of "wings." Rather, multiple characters are needed to provide an accurate hypothesis of relationships. Whales, bats, and humans have many more traits in common than are shared by bats, birds, and insects despite the fact that the latter three have wings. Therefore, mammals are considered to be a natural group and the forelimbs of mammals are considered homologous, whereas the wings of birds, bats, and insects (an unnatural group whose members do not

share a common, winged ancestor) are considered homoplastic. It is the pattern of relationships among taxa with the trait in question that determines the nature of the similarity. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS; PHYLOGENETICS SYSTEMATICS.

Andrew G. Gluesenkamp

Bibliography

Futuyma, Douglas J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, Inc., 1986.

Gould, Stephen J. *Ontogeny and Phylogeny.* Cambridge, MA: Harvard University Press, Belknap Press, 1977.

McKinney, Michael L. *Evolution of Life.* Englewood Cliffs, NJ: Prentice Hall, 1993.

Raff, Rudolf A. *The Shape of Life.* Chicago: University of Chicago Press, 1996.

Hormones

A hormone is a chemical that is produced in one tissue and transported via the circulatory system to a different target tissue. There, it causes a physiological change in the target.

endocrine system the grouping of organs or glands that secrete hormones into the bloodstream

Hormones are the chemical messengers of the **endocrine system**. The endocrine system also includes the ductless glands that synthesize and secrete hormones, and incorporates the responding target cells as well. Hormones are secreted by endocrine glands directly into the circulatory system, from which they contact nearly all cells of the body. Some endocrine glands, such as the adrenal glands, form organs of their own, while others are just parts of organs. The brain, for example, performs certain critical endocrine functions.

The endocrine system is one of two physiological systems responsible for the control of all biological processes. The other is the nervous system. While the nervous system controls specific, rapid biological responses, often to external stimuli, endocrine control generally involves comparatively broad, long-term, gradual physiological processes.

equilibrium a state of balance

The endocrine system is essential to diverse aspects of an organism's biology, including its development, growth, reproduction, metabolism, water and ionic balance, and maintenance of homeostasis (internal **equilibrium**). In general, animal species that are characterized by well-developed nervous and circulatory systems also possess endocrine control systems.

Because hormones are transported through the circulatory system, they come into contact with all cells and are able to affect numerous tissues simultaneously. Some hormones affect a wide variety of tissues. The sex hormone testosterone, for example, affects multiple parts of the body, whereas others have a considerably more limited effect.

Only cells that possess receptors specific to a hormone will respond to its presence. In addition, depending on the hormone receptor and the pathway coupled to it, different tissues can respond to the same hormone in different ways. Thus, despite their relatively low concentrations in the bloodstream, hormones can have dramatic effects on an organism's physiology.

A male giraffe sniffs a urinating female giraffe to test the hormone level of the female in the wilderness of Kenya.

The Two Major Hormone Groups

Hormones have been divided into two major groups that differ in their biochemical attributes, as well as in the mechanisms by which they affect the activity of target cells. These are steroid hormones and peptide hormones.

Steroid hormones are synthesized by endocrine glands in the gonads (ovaries and testes) and adrenal cortex. They are not stored but, rather, secreted into the circulatory system as soon as they are synthesized.

Steroid hormones are derived from cholesterol and are lipid soluble. Lipid solubility enables steroid hormones to cross cell membranes and enter directly into the **cytoplasm**. Once there, hormone molecules bind to cytoplasmic receptors, cross the nuclear membrane, and interact directly with DNA to affect cellular activity. Some well-known steroids are estrogen and testosterone.

cytoplasm a fluid in eukaryotes that surround the nucleus and organelles

Peptide hormones, on the other hand, are proteins and composed of amino acids. Peptide hormones are water soluble and range greatly in size. They are synthesized in endocrine cells and then stored in vesicles within the cell for secretion later.

Peptides are the more diverse group of hormones by far. Unlike steroids, peptide hormones are not lipid soluble and do not penetrate their target cells directly. Instead, they function via what is referred to as a second messenger pathway. The hormone binds to a receptor protein on the target cell membrane, which then signals a second messenger within the cellular cytoplasm. This second messenger initiates an **enzyme** cascade, which affects

enzyme a protein that acts as a catalyst to start a biochemical reaction

the activity of the cell. Examples of second messengers involved in peptide hormone function include cyclic AMP and inositol triphosphate.

Endocrine Control

The maintenance of appropriate hormone concentrations in the bloodstream is absolutely critical. Numerous diseases result from hormone levels that are too high or too low. Diabetes is one well-known example.

Feedback systems are often used to regulate hormone synthesis and secretion. Some of these cycles can be extremely complex, involving numerous hormones and endocrine glands.

anterior pituitary the front part of the pituitary gland that produces hormones that stimulate the production of sperm and testosterone in the testes

A particularly well-studied example is the control of thyroid hormone levels. The hypothalamus, an endocrine organ in the brain, secretes a hormone called the thyroid-releasing hormone (TRH). TRH targets the **anterior pituitary**, which responds by secreting thyroid-stimulating hormone (TSH).

TSH targets the thyroid, inducing it to secrete the thyroid hormones known as T3 and T4. However, when T3 and T4 reach a certain concentration in the bloodstream, they act on the hypothalamus, inhibiting it from secreting more TRH. As a result, TSH is no longer secreted, and T3 and T4 secretion is also terminated. This type of negative feedback is common in endocrine regulation. When the levels of thyroid hormones fall below a certain concentration in the bloodstream, the inhibitory, or restraining, effect on the hypothalamus is removed.

The hypothalamus and the anterior pituitary (which is often referred to as the master gland) are critical to endocrine control because many of the hormones they produce affect the activity of other endocrine glands. The hypothalamus is located at the base of the middle portion of the brain, and the pituitary lies immediately below it. The two are directly connected by blood vessels, an unusual organization of the circulatory system referred to as a portal system. The portal system allows for the direct and efficient transport of hormones from the hypothalamus to targets within the pituitary.

circadian rhythms daily, 24-hour cycles of behavior in response to internal biological cues

Other hormones are under cyclical control. Cycles can be short, lasting hours, or much longer, spanning several months. Melatonin is a hormone produced by the pineal gland whose level follows a daily cycle. It establishes **circadian rhythms**. Hormone cycling over longer periods is responsible for the control of activities such as menstruation, hibernation, and seasonal mating behavior.

Important Endocrine Glands and Hormones

posterior behind or the back

One major endocrine gland is the anterior pituitary. It secretes growth hormone as well as gonadotropins, which stimulate sex hormone production in the gonads, and prolactin, which is associated with lactation. Another important endocrine gland is the **posterior** pituitary. It secretes antidiuretic hormone, one of the key players involved in water balance, and oxytocin, which induces uterine contractions during childbirth.

Other significant endocrine glands can be cited. The thyroid is responsible for the thyroid hormones T3 and T4, which regulate growth, development, and metabolism. Of the adrenal glands, the adrenal medulla produces epinephrine and norepinephrine, while the adrenal cortex produces steroid hormones including the mineralocorticoids and glucocorticoids. The pancreas secretes insulin and glucagon, two antagonistic hormones that together regulate blood glucose levels. Finally, there are the thymus, the pineal gland, and the ovaries and testes, which produce sex hormones. SEE ALSO BEHAVIOR; DOMINANCE HIERARCHY.

Jennifer Yeh

Bibilography

Curtis, Helena. *Biology*. New York: Worth Publishers, 1989.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Hickman, Cleveland P., Larry S. Roberts, and Allan Larson. *Animal Diversity*. Dubuque, IA: William C. Brown, 1994.

Hildebrand, Milton, and Viola Hildebrand. *Analysis of Vertebrate Structure*. New York: John Wiley, 1994.

Withers, Philip C. *Comparative Animal Physiology*. Fort Worth, TX: Saunders College Publishing, 1992.

Horse Trainer

The ancient Irish believed that certain people had the ability to whisper in the ears of horses and magically influence their behavior. Mary Twelveponies, John Lyons, Monty Roberts, and Buck Brannaman are all professional horse trainers who are sometimes described as horse whisperers. These trainers take wild, dangerous, or simply young horses into a round pen and in a matter of hours—without using force or fear—make friends with the horse, acquaint it with a saddle, and place a rider on its back. As Brannaman says, this is a phenomenal act of trust on the horse's part, as their historic enemies leaped on their backs to kill them.

This horse trainer leads her student through an exercise in an outdoor show ring.

The trainers describe what they do with phrases such as: seeing the world from the horse's point of view; turning frightened horses into friends using respect and trust rather than mastery or manhandling; thinking in harmony with the horses; trusting the horse; and treating it with love and understanding.

Though a horse trainer might work with wild mustangs or Olympic competitors, dressage horses or draft horses, cutting horses or jumpers, the basic approach remains the same. Respecting and working with the horse's nature is the most important step. Conveying calmness and deliberation with their movements, trainers allow the natural curiosity, cooperation, and playfulness of the horse to express itself. They teach one thing at a time, reinforcing learned behavior through constant repetition and approval, and remembering that, like any learner, the horse can grow tired and confused and need a break.

To begin a career in horse training, the novice can read books, watch videos, and get first-hand experience in an apprenticeship program or training clinic with a good teacher. It is also helpful to spend as much time as possible immersed in horses—observing them and enjoying their generous, affectionate personalities.

Nancy Weaver

Bibliography

Browning, Sinclair, and John Lyons. *Lyons on Horses*. New York: Doubleday, 1991.

Morris, Desmond. *Horsewatching*. New York: Crown, 1988.

Twelveponies, Mary. *Starting the Colt*. New York: Penguin Group, 1990.

Horses

One common misconception about evolution is that it occurs in a straight line, from an ancestor to a descendant. Although it is possible to trace the lineage, or history, of a certain species, the wider view shows that evolution is actually a very broad process. It may be helpful to visualize evolution as a tree from which many branches sprout, with each branch representative of a line of organisms evolving from the center of the tree. Many of these branches, or lineages, may die out. Other branches continue to grow and branch out further, resulting in the great diversity of life on Earth today. The history of the horse is an excellent example of this evolutionary "tree." Horses did not evolve in a straight line from a common ancestor, through species after species, until the modern wild horse appeared. In fact, the evolution of the horse is a story of great divergence and extinctions that continued through time, until only one species remained.

Paleontologists have discovered a very good record of horse fossils in North America, where the horse first appeared, and have learned much about its early history. Other continents have been subsequently searched for fossils, and the migration and distribution of the horse is now well-known. From the remains of a few small **populations** of true wild horses in Europe and possibly central Asia, thriving communities of horses now exist in most regions on Earth.

populations groups of individuals of one species that live in the same geographic area

The Beginning

The ancestors of the horse were browsers who fed on the bushy and leafy types of vegetation found in forests. They ate leaves of trees and shrubs and occasionally fed on tender grasses. Scientists deduced what they ate from studying the fossil teeth of animals that had a similar bone structure to the modern horse, but that had bumpy teeth, instead of the flat, grinding teeth horses have today. These early ancestors were small animals, about the size of a fox or a medium-sized dog.

Evolutionary scientists recognize that environment often drives **natural selection**, and that natural selection leads to evolution. One force causing the transformation in horses was the constant alteration of **climate** that began about 60 million years ago and continues through the present. As the climate became hotter and drier, two important events occurred. First, the forests shrank and became patchy throughout North America. This reduced the **habitat** of the forest-dwelling members of the horse group. Second, different forms of grasses, called "C4 grasses," evolved. These grasses were tougher than the fragile forest grasses and better able to withstand harsh conditions. They spread throughout the more arid regions and formed vast plains. These plains created a less nutritious but more stable food source for the animals. The formation of the grasslands provided a new habitat in which many forms of animals, like the camels and horses, thrived. C4 grasses contained a high concentration of a glassy mineral called silica. The horse species that survived this new diet developed stronger, flatter, and more complex teeth than their forest relatives. Most of the evolution of horses was identified and traced by studying these changes in tooth shape and structure.

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

climate long-term weather patterns for a particular region

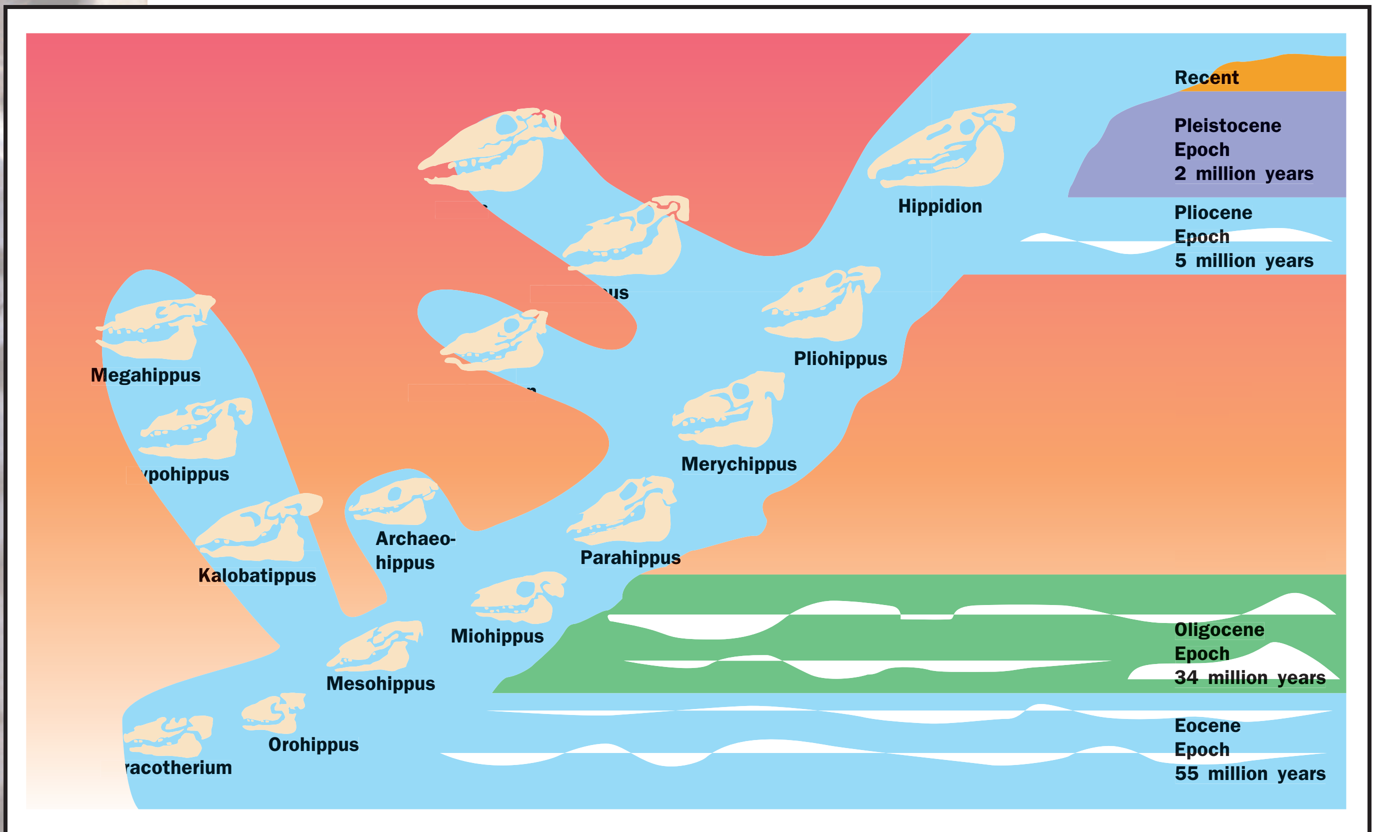
habitat physical location where an organism lives in an ecosystem

The second major factor that affected the evolution of the horse was the emergence of more effective competitors, such as the artiodactyls (**herbivores** like camels, deer, and bison), and swifter predators, especially the cats with their saberlike canine teeth. These swift and efficient predators found the smaller, forest-dwelling horses to be easy prey, resulting in the swift extinction of the horses. This kind of selection pressure favored the swifter and more wary equids of the open grasslands. So as one horse lineage died out, another evolved quickly. This pattern continued until the end of the Pleistocene epoch about 11,000 years ago. Only one species of horse, *Equus equus*, remains from this once diverse group of animals.

herbivores animals who eat plants only

The Story of the Bones

All information scientists know about ancient horses has been gathered from the fossil remains of their skeletons. The skull, and the teeth it contains, can be read almost like a book, revealing how and when physical changes occurred and in what order. While no real "trends" are apparent in the overall picture of horse evolution because so many different species are involved, there were some general changes. As horses evolved, their toes were continually reduced in number until the condition of standing on one toe, like the modern horse, was achieved. The teeth became larger, with a more complex surface. The face became longer. In addition, the overall body size increased, growing from the tiny size of the forest dwellers to the significantly larger modern horse size.



Evolution of the horse charted by geologic time period. Redrawn from the Florida Museum of Natural History.

An animal called *Eohippus* is often cited as the first identifiable horse ancestor. *Eohippus* lived about 60 million years ago and is nicknamed the "dawn horse." It was a small, dog-sized animal with five toes on its front feet and three toes on its hind feet. The animal stood high on its toes, the tips of which were covered with strong little hooves. The teeth were the browsing type that had small bumps like those on human molars, but which more closely resembled those of a pig. Scientists estimate that this little horse was about 35 centimeters (14 inches) high and weighed a little over 5 kilograms (12 pounds).

fossil record a collection of all known fossils

The next candidate for selection in the **fossil record** is *Hyracotherium*, an animal that lived about 55 million years ago. *Hyracotherium* was more horselike than *Eohippus*, with its skeleton showing the characteristics that became unique to horses. The skull was longer and larger, and had a shallow basin at the end of shortened nasal bones where the nose is. The lower jaw was bigger and stronger than its relatives. The top and bottom incisors, or front teeth, met squarely and formed a "nipping-type" set of teeth. The back of the head no longer sloped backward but was now straight up and down. The neck bones were shaped so that the neck not only was longer, but could be rotated upward. Eventually, this feature helped the descendants of *Hyracotherium* to reach downward for grasses. Scientists believe that *Hyracotherium* (and many other species of horses at this time) had a short, **prehensile** proboscis, or snout, that could pick tasty leaves from high up in trees and bushes.

prehensile adapted for siezing, grasping, or holding on

The legs of *Hyracotherium* were longer than those of *Eohippus* and other horses. The front legs of its ancestors had been about 40 percent longer than the hind legs, but the two sets of legs of *Hyracotherium* were more evenly lengthened. The feet began to change shape as their function for running became greater. The carpals and tarsals (wrist and ankle bones) became smaller and more square. The metacarpals and metatarsals (equivalent to the bones of a human palm) were longer and more slender. The wrist and ankle became more stabilized to prevent side-to-side motion and aid in more efficient running. One of the ankle bones, the astragalus, formed a unique notch where it met the lower leg bone, the tibia. This permitted greater force to be exerted on the foot when pushed against for running. In the wrist, the carpals interlocked with the lower row, providing a stronger pull stroke when running.

These trends continued in species named *Orohippus* and *Mesohippus*. The fossil record reveals a divergence of evolution around the time of *Mesohippus*, about 34 million years ago. One line contained the species *Kalobatippus* and *Hypohippus*, and died out with *Megahippus*. The other line, which leads to *Equus*, contained *Miohippus* and a tiny *Archaeohippus* and continued the skull and leg transformation. *Archaeohippus* was not highly successful, and its lineage died out relatively quickly. The ankle and wrist of *Miohippus* and its ancestors continued to strengthen, and the legs finally lengthened so that the animal stood higher in front than in the back. *Mesohippus* was the first ancestor of the horse to have one fewer front toe, although all the remaining horses eventually had three toes on each foot.

By the Oligocene (the end of the Tertiary epoch), major changes in the horses began to take place. The forest dwellers were no longer dominant, and horses who ate the newly rising C4 grasses began to spread into the great grasslands. These horses were larger, with increasingly long legs, and were able to explore new territory. The wrist and ankle bones continued to become more square and flat so that the force of running would not destabilize the foot. The side-to-side motion of the wrist and ankle was reduced to prevent wobbling, with the back-and-forth motion becoming stronger.

The trend toward an enlarged skull continued for the rest of horse history. The teeth, which were so important for grazing on tougher grasses, lost their roots and became hypsodont, or very high-crowned. One of the most identifiable characteristics of the horse is complex enamel, the tough outer coating of the tooth. Enamel resists the grinding actions of chewing. During the evolution of the horse, the enamel on the molars infolded from the sides, increasing the number of bumpy grinding surfaces. This trend continued for millions of years as horses ate more and more fibrous food. Many scientists believe that horses have the most complex and resistant teeth of almost all the large mammals. Some rodents have complex teeth, but like horses, they eat tough, fibrous foods, like seeds and silica-containing grasses.

The skeleton of the horse continued to grow from about 24 million years ago to the present. While the legs got longer and longer, the scapular (shoulder bone) and pelvis (hip bones) stayed relatively the same size. The neck and back elongated. This change resulted in two advantages for the horse. First, it allowed the horse's head to flex down to the ground to get the grasses. Second, the longer back gave greater flexure for a fast running pace. When an animal like a horse or cheetah runs, one of the important parts of the running pace is the springlike flexure of the back. Some species of horses that showed these changes were *Parahippus*, *Merychippus*,

Neohipparion, *Pliohippus* (the first single-toed horse), *Dinohippus*, *Hippidion*, and *Equus*.

Hippidion and *Equus* lived at the same time, but *Hippidion* became extinct sometime in the Pleistocene. By this time, horses were gone from North America and it is believed that only a few populations continued in remote places. One population—a small, stocky, pony-type horse resistant to cold and wet—was discovered in northwest Europe. Another population—horses that were larger and resistant to heat—was found in central Asia. These central Asian horses were the ancestors of the desert horses of today.

The horse was reintroduced to North America by the Spanish during their explorations in the early sixteenth century. Many escaped or were let go and are the ancestors of the wild mustang. Horses now thrive all over the world. They are considered animals of beauty and grace and many cultures, such as the Native Americans of the North American plains and nomadic peoples in Mongolia, depend on the horse. SEE ALSO Biological Evolution; Physiology.

Brook Ellen Hall

Bibliography

MacFadden, Bruce. *Fossile Horses: Systematics, Paleobiology, and Evolution of the Family Equidae.* Cambridge, U.K.: Cambridge University Press, 1994.

Simpson, George Gaylord. *Horses: The Story of the Horse Family in the Modern World and Through Sixty Million Years of History.* New York: Oxford University Press, 1951.

Internet Resources

The International Museum of the Horse. Lexington, Kentucky. <http://www.imh.org/imh/kyhpl1a.html#xtocid224361>.

The Equine Studies Institute. Ed. Deb Bennett. Smithsonian Institution. <http://www.equinestudies.org/historical.htm>.

Horses. PBS/Nature. <http://www.pbs.org/wnet/nature/horses/>.

The Florida Museum of Natural History. <http://www.flmnh.ufl.edu>.

Human–Animal Conflicts

Conflicts and controversies involving interactions between human beings, their communities, and the environment have become defining issues of our time. There is a growing awareness of both the physical effects of people on the environment and the ways in which beliefs, cultural norms, and economic conditions shape the human response to these issues. Human beings are increasing in number worldwide. Many of our lifestyle choices now appear to have a measurable and harmful impact on biological and environmental systems in the United States as well as around the world. Continued growth in **population** and the resulting sprawl of people into previously unsettled land forces individuals, governments, and society as a whole to examine current and future priorities in regard to lifestyle and the natural world.

population a group of individuals of one species that live in the same geographic area

biodiversity the variety of organisms found in an ecosystem

One of the serious environmental problems facing humankind today is the loss of biological diversity. **Biodiversity** is the vast and varied combi-

nation of **habitats**, plants, and animals that thrive together to support life on Earth. Scientists feel that these losses are the direct result of the transformation of natural landscapes and **ecosystems** for farming, grazing, recreational, and residential uses.

habitats physical locations where an organism lives in an ecosystem

ecosystems self-sustaining collections of organisms and their environments

Biodiversity is lost when farmers clear land to increase crop yield, when loggers clear forests to provide lumber for houses and furniture, and when city dwellers need more land for homes, schools, and industry. Cutting old-growth forests has encouraged erosion on slopes and mountains. Wetlands have been drained and rivers dammed and diverted to provide water for irrigation and drinking water. Overgrazing of grasslands and the use of fertilizers and **pesticides** have polluted lakes, rivers, and streams, creating fragmented habitats where native species have difficulty surviving.

pesticides substances that control the spread of harmful or destructive organisms

Demographic shifts and population growth have encouraged people to live in areas once populated by wild animals. These habitats are increasingly affected by human-imposed changes including roads, new uses for private and public lands, and the environmental demands associated with agricultural and urban life. Species such as wolves, mountain lions, polar bears, and the northern spotted owl do not recognize these artificial restrictions on their habitats and have thus come into direct conflict with human beings and their way of life.

While government officials, environmentalists, developers, and industry representatives fashion regulations designed to protect, preserve, and safeguard both ecosystems and human beings, wild animals and people continue to come into conflict with one another. How these issues are resolved will depend on the ways in which conflicting priorities and questions are addressed. What are the ecological, sociological, aesthetic, and scientific benefits of preservation? What are the rights of animals? Do people have an obligation to preserve species? Can society balance economic interests and human needs with efforts to preserve and protect the natural world?

Spotted Owls vs. Loggers

For hundreds of years, the northern spotted owl has made its home in the lush old-growth forests of the Pacific Northwest. The owl feeds on the rich plant and invertebrate life created by decaying timber and nests in the cavities of old trunks. But the towering cedars, firs, hemlocks, and spruces have become a primary source of timber for a multibillion dollar logging industry. As a result of heavy logging since the mid-nineteenth century, only 10 percent of these ancient forests still exist, mostly on federally managed lands. As the forests have dwindled so have the number of spotted owls. Biologists estimated that fewer than 2,000 pairs were in existence in the early 1990s.

In 1986 the U.S. Fish and Wildlife Service was petitioned to list the spotted owl as an endangered species, a move that would bar the timber industry from cutting on these lands. In June 1990, after years of heated **controversy** among timber industry representatives, environmentalists, and government agencies, the northern spotted owl was declared a threatened species. Because of this, timber companies are required to leave 40 percent of the remaining old growth intact within a 2.1 kilometer (1.3-mile) radius of any spotted owl nest or site. This policy is opposed by the timber industry. Industry representatives claim that this requirement will leave thousands

controversy a discussion marked by the expression of opposing views

of loggers and mill workers jobless. They believe that this policy and others like it do not take into account the economic consequences of preservation. Environmentalists, on the other hand, argue that society has a fundamental obligation to preserve this rare species and the wilderness in which it lives.

The controversy over the spotted owl mirrors similar debates over dolphins, whales, and desert tortoises. In each situation, conflicting opinions exist concerning society's obligation to protect animals threatened by extinction. The question raised repeatedly is, "To what extent, if any, should preservation of endangered species and their habitats take precedence over economic considerations?"

Restoring Wolves in Yellowstone National Park

Wolves once ranged over most of the United States but were eliminated from the northern Rockies by the 1930s. From 1918 to 1935, government bounty hunters shot and killed predators including coyotes, wolves, and mountain lions. By 1926, the last wolf was eliminated from Yellowstone National Park. This was the result of an aggressive government-sponsored predator control program and public policy that was based on the assumption that wolves had no value.

This perception and policy continued until the 1970s, when many environmental protection provisions were implemented. In 1972 the U.S. Department of the Interior began an initiative to return native biodiversity to the national parks. As part of this effort, the Endangered Species Act required that the Fish and Wildlife Service have a recovery plan for threatened and endangered species.

In 1987 a Rocky Mountain Wolf Recovery plan was proposed to reintroduce grey wolves into the northern Rockies, including Yellowstone National Park. Local opposition was strong and vocal. Nearby residents worried that wolves would kill their domestic animals and perhaps cause injury to humans. Ranchers and hunters expressed concern that a top predator such as the wolf would reduce cattle, sheep, deer, and bison populations and travel outside the boundaries of the park.

Environmentalists countered that, as large predators, wolves were an essential part of the natural ecosystem that would help control the swelling populations of elk, deer, and bison and increase the numbers of eagles, pronghorn, foxes, and wolverines. An organization called the Defenders of Wildlife agreed to establish a $100,000 fund to reimburse any rancher who lost livestock because of wolves.

In May 1994, the Interior Department and the Fish and Wildlife Service finally approved the plan for reintroducing wolves into Yellowstone National Park and central Idaho. This led to the successful reintroduction of sixty-six wolves in 1995 and 1996.

Monitoring suggests that the wolves are indeed having a positive effect by controlling the populations of elk, bison, and deer. Coyote numbers have dropped, allowing smaller predators such as foxes to regain strength. The reduction of elk, deer, and bison has allowed willow and aspen trees to regenerate and restore overgrazed areas.

In addition, the grey wolves have begun to recover. They are to be taken off the endangered species list when there are ten breeding pairs in Yel-

> In the spring of 2001, the *Great Falls Tribune* (Great Falls, Montana) ran a front page story about the Interagency Annual Wolf Report. According to the report, the wolf population is reaching recovery level (30 breeding pairs). Removal of the wolf from the endangered species list, the report concluded, is probably only three years away.

lowstone, Idaho, and Montana. Ranchers are allowed to kill wolves that attack livestock. Some have also accepted reimbursement for livestock losses from the Compensation Trust set up by the Defenders of Wildlife.

Mountain Lions and Public Safety

Since the mid-1980s, encounters with mountain lions have become more frequent throughout the United States. Hikers, joggers, mountain bike riders, and suburban residents have unexpectedly found themselves in the company of these lions. Some encounters have led to the deaths of human beings.

Although unusual, these incidents have rekindled public debate about mountain lion management. Issues include the shrinking habitat of mountain lions, increased competition for space, the legalities of hunting the lions, and ways to increase public awareness and safety in areas where human beings are encroaching on the traditional habitat of mountain lions.

California has been at the forefront of this debate since the mid-1980s. The rising population of both humans and mountain lions in the state led to an intensive study of the problem by the Department of Game and Fish. Prior to 1986 there was very little concern for public safety from lions. Between 1986 and 1995, however, ten attacks were verified by state officials; a number of them resulted in deaths.

The study's findings concluded that an increase in the mountain lion population and its geographic range, combined with an increase in California's human population, had indeed resulted in increased encounters between animals and people. Research also revealed that the lions were expanding their range into new areas as competition for habitat increased. Since animals compete for food and space, some lions were being forced out of their ranges and ending up in residential or recreational areas where problems were more likely to occur. Wildlife officials recommended controversial safety precautions as well as habitat protection for the lions.

California voters approved a mountain lion initiative in 1990 that prohibited the hunting of lions. In 1996 the National Rifle Association filed a suit that resulted in the repeal of the 1990 initiative and once again allowed hunting and the use of steel-jawed traps, leghold traps, and poison, and decreased the amount of money to be used for habitat protection. Concern for public safety was given as the main reason for not giving any protection to the mountain lion.

> In 1993, professor Paul Beier, a wildlife ecology professor at Northern Arizona University, launched a five-year study of mountain lions in the Santa Ana Mountains of California. He fitted 32 animal with electronic collars. In 1998, there were only 25 survivors. A third of the animals that died were hit by cars. Other causes of death ranged from fights with other animals to being trapped for the protection of livestock.

Adventure Travel and Climate Change: Polar Bears in Canada

Churchill, Manitoba, is called the polar bear capital of the world. Nearly 15,000 tourists visit this northwestern Canadian town each winter to observe, film, and photograph the bears as they congregate near the mouth of the Churchill River, waiting for the Hudson Bay to freeze so that they can head out on the ice to hunt ringed seals, which are their primary food source.

During the tourist season, more than 500 people per day are allowed to go out on adventure expeditions to observe the polar bears. The sole means of observing the bears is from the "tundra buggy," which is best described as a large, roomy bus mounted on 1.8-meter (six-foot) high, all-terrain rubber tires. The vehicle is designed to transport tourists across the tundra look-

These polar bears rifling through a garbage dump in Manitoba, Canada, illustrate concerns of human-animal conflict. Polar bears, naturally, do not adhere to human-devised artificial boundaries.

ing for bears. Many wildlife managers are concerned about the effect of this human encroachment on the fragile tundra. They are also concerned that the polar bears, who are at their weakest after months with limited food resources, are suffering from a lack of undisturbed time in their natural habitat at a critical point in their life cycle.

There is another concern about the human impact on the habitat of the polar bears in the Hudson Bay area, however. Researchers have been studying a group of 1,200 bears in the Churchill area for nearly thirty years. These bears are giving scientists glimpses of long-term changes in the climate that may be caused by **global warming**. The ice is melting earlier and earlier each year, causing the bears to come ashore sooner than they used to. These shorter feeding seasons have led to near starvation among the bears.

global warming a slow and steady increase in the global temperature

The combination of climate changes and increased tourism is putting stress on the population of polar bears and increasing the possibility that polar bears desperate for food will encounter people on a more regular basis, endangering human safety. Wildlife officials say that the bear population is declining. The adventure travel companies report that they are seeing fewer bears, and thinner bears. They are also reporting more encounters between humans and polar bears on the tundra.

In all of these conflicts involving human enterprise and wildlife habitats, there are few easy choices to be made. Environmentalists and animal rights activists raise reasonable questions about the preservation of wildlife for future generations and the right of wild animals to live peacefully in their native forests, deserts, tundras, or wetlands. Communities that are economically dependent on tourism, the harvesting of forests, the raising of livestock, or the expansion of their boundaries express reasonable concern about how to balance human needs with environmental protection measures. Meanwhile, both human beings and native wildlife continue to adapt to each other's presence in environments they now share. SEE ALSO HABITAT LOSS; HABITAT RESTORATION.

Leslie Hutchinson

Bibliography

Andre, Claire. "Ethics and the Spotted Owl Controversy." *Issues in Ethics*, 4, no. 1 (1993).

Bolgiano, Chris. *Mountain Lion: An Unnatural History of Pumas and People.* Mechanicsburg, PA: Stackpole Books, 1995.

Center for Philosophy and Public Policy. "The Preservation of Species: Why Should We Care." Report from the Center for Philosophy and Public Policy, Vol. 5, no. 4, fall 1985.

Eldridge, Niles. *Life in the Balance: Humanity and the Biodiversity Crisis.* Princeton, NJ: Princeton University Press, 1998.

Grumbine, Edward R. *Ghost Bears: Exploring the Biodiversity Crisis.* Washington, D.C.: Island Press, 1992.

Phillips, Michael K., and Douglas Smith. *The Wolves of Yellowstone.* Stillwater, MN: Voyageur Press, 1996.

Torres, Steve. *Mountain Lion Alert: Safety Tips for Yourself, Your Children, Your Pets, and Your Livestock in Lion Country.* Helena, MT: Falcon Press, 1997.

Human Commensal and Mutual Organisms

From the moment of birth and throughout our entire lives, humans share their bodies with a surprising variety of microscopic organisms. Dust mites remove dead skin, amoeba live on their teeth and scavenge food particles, and eyebrow mites live on their eyebrows.

Scientists estimate that the human body has around 7.5×10^{13} cells. Many of these cells are not of human origin, but represent microscopic **commensal** and mutual organisms. In commensal interactions, one species of organism benefits and the other is unaffected. In mutual interactions, both organisms benefit.

commensal symbiotic relationship in which one species benefits and the other is neither helped nor harmed

The term "commensal" is derived from a Latin word *mensa*, meaning "table." Commensal organisms share their food from a common table. In the case of human commensals, the human host is the table. It is often difficult to identify a relationship between organisms as purely commensal, mutual, or parasitic, as the way in which one organism benefits or harms its host may not be obvious. A commensal or mutual organism may depend on its host for food, shelter, support, transport, or a combination of these factors. The host may receive a variety of benefits, including protection from infection, improved digestion, or cleaner skin.

While in the womb, humans live in a sterile environment, protected by the **placenta** and the amniotic sac. After birth, humans are introduced and subjected to an array of new organisms. If these organisms find themselves in a suitable ecological **niche**, whether on the internal or external parts of the human body, they will multiply and form complex communities, or colonies, with their host. The first step in this colonization process requires the microscopic organisms to adhere to their host. If the organisms find a suitable location, they will form long-term, stable, interdependent relation-

placenta structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

niche how an organism uses the biotic and abiotic resources of its environment ships with other organisms in the same location and the human that harbors them. Since the benefit to one or the other species may be subtle and hard to identify, it is often difficult to distinguish between true commensalism and **mutualism**. Humans certainly derive considerable benefit from many resident organisms.

mutualism an ecological relationship beneficial to all involved organisms

A wide variety of microorganisms interact with humans, taking advantage of several microenvironments. Certain parts of the body, such as the solid organs, blood, cerebrospinal fluid, and urine, are normally sterile. However, established microbial **populations** may be found on the skin and in the lower respiratory tract, mouth, and lower gut. Throughout life, these resident organisms vary in type and number, and individuals can have significant differences in their resident populations. If for any reason the commensals gain access to inappropriate body sites, infections may occur.

populations groups of individuals of one species that live in the same geographic area

Skin and Eyes

The skin is a highly complex organ that provides a variety of ecological niches for colonies of microscopic organisms. It is also the first line of defense against infection. The skin on the head, armpits, groin, hands, and feet has more microscopic organisms than on other places on the body. Bacteria, fungi, and mites form the commensal **flora** and **fauna** on the skin. The fungi *Malassezia furfur* and *Candida albicans* are found on the skin of some individuals. All humans can act as hosts to skin mites such as *Demodex folliculorum* and *Demonex brevis.* It is thought that a large majority of the human population acts as hosts to these mites. These microscopic animals survive on a diet of dead epithelial (skin) cells and sebum, an oil excreted by hair follicles and other skin glands.

flora plants

fauna animals

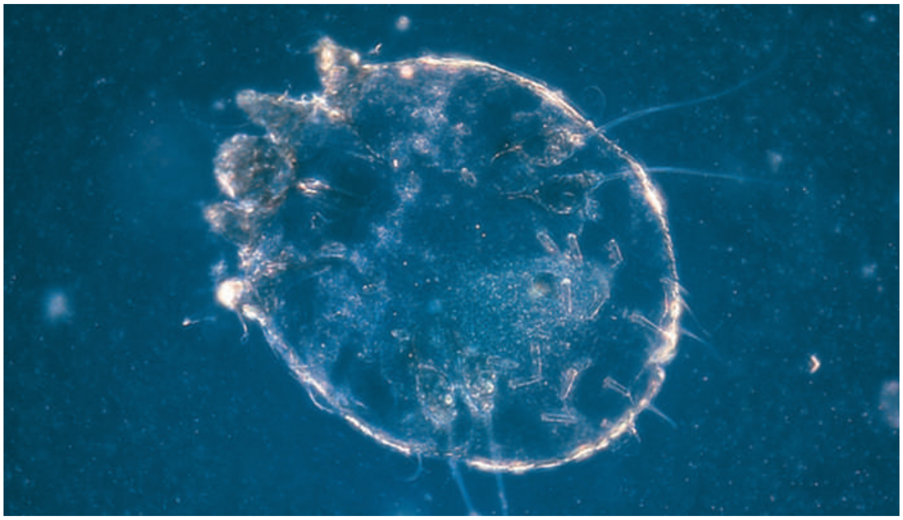
The commensal flora and fauna on the skin are dispersed into the environment when washed or sloughed off in some manner. This is important, because 10 to 40 percent of healthy individuals and up to 90 percent of hospital staff carry the bacteria *Staphylococcus aureus.* This bacteria is one of the most common causes of infection in wounds after surgery, and nearly all babies born in hospitals become colonized within a week.

Human eyes are covered with a specialized skin that is bathed in tears, and only a few microbes can survive these conditions. Corynebacteria such as *Corynebacterium xerosis* can establish themselves as resident commensals on human cornea.

Digestive Tract

The mouth provides a number of ecological niches where microscopic organisms can colonize. Dental caries (tooth decay) are caused by the interaction between commensal bacteria and sugar in the diet. *Streptococcus mutans* converts sugar into slime which sticks firmly to the enamel of the teeth, beginning the decay process. The crevices between the gum and teeth also harbor bacteria such as *Bacteroides* and *Fusobacterium* that can cause gum disease.

Commensal organisms usually do not colonize the stomach because it is highly acidic, although some acid-tolerant lactobacilli can live there. One bacteria, *Helicobacter pylori*, has recently been linked with ulcer formation in some people. The normal flora of the intestines, *Eschericia coli*, *Streptococcus*,



A microscopic image of a scabies mite.

and *Bacteroides* contribute to the normal functioning of the digestive system. The importance of the role of these organisms becomes more evident when the administration of antibiotics or laxatives kills them. Without these organisms, the digestive system may be colonized by pathogenic bacteria that are resistant to antibiotics.

Respiratory Tract

The respiratory tract is anatomically complex and constantly exposed to microorganisms in the air breathed in. The microflora of our nostrils resembles that of the skin, with colonies of commensal organisms such as micrococci, corynebacteria, staphlococci, and streptococci. *Streptococcus pyogenes* is part of the commensal flora of the nose in healthy individuals, but may cause tonsillitis and strep throat. The warm, moist environment of the upper respiratory tract provides a haven for commensal bacteria including *Streptococcus*, *Moraxella*, *Neisseria*, and *Haemophplus*, species. The lower respiratory tract is generally free from microorganisms, mainly because of the efficient action of the **cilia** that line the tract.

cilia hairlike projections used for moving

Roles of Commensal and Mutual Organisms

Nineteenth-century French microbiologist Louis Pasteur believed that animals cannot exist without a population of commensal and mutual organisms, and early experiments to raise germ-free animals met with failure. All germ-free animals have weak, poorly developed immune systems. This suggests that the roles of normal microscopic organisms are very important.

Commensal organisms play a significant role in preventing infections. This may be simply because they deny the invading organism access to the target site, or because the benign organism actively produces substances that inhibit the growth of, or even kill, other organisms.

Commensal flora and fauna may also "switch roles" and become an important source of infection for the human host. Infections caused by microscopic organisms derived from commensal organisms are known as endogenous infections. These infections range from minor conditions, such as boils, to life-threatening infections. For example, streptococcal bacteria

from the mouth or skin can gain access to the bloodstream and cause bacterial endocarditis, an infection of the interior of the heart.

equilibrium a state of balance

Commensal and mutual organisms are in a constantly changing dynamic **equilibrium** with their human host. Strains, or groups of these organisms, are constantly being replaced and displaced by other strains. In this way, the commensal organism adapts to changes that occur in the host. SEE ALSO INTERSPECIES INTERACTIONS.

Leslie Hutchinson

Bibliography

Dixon, Bernard. *Power Unseen: How Microbes Rule the World.* London, Freeman Press, 1994.

Heritage, J. E., G. V. Evans, and R. A. Killington. *Microbiology in Action: Studies in Biology.* Cambridge, U.K.: Cambridge University Press, 1999.

Postgate, John. *Microbes and Man*, 3rd ed. Cambridge, U.K.: Cambridge University Press, 1992.

Internet Resources

Medical Microbiology on the World Wide Web. Ed. Ayana Gibbs. University of Leeds. <http://www.Leeds.ac.uk/mbiology/fullproj/proj1.htm>.

Human Evolution

Human evolution is the lengthy process of change by which people originated from apelike ancestors starting nearly five million years ago. The modern scientific study of human evolution is called paleoanthropology. A subfield of anthropology, this discipline searches for the roots of human physical traits, culture, and behavior. It attempts to answer questions: What makes us human? When and why did we begin to walk upright? How did our brains, language, art, music, and religion develop? By approaching these questions from a variety of directions, using information learned from other disciplines such as molecular biology, paleontology, archaeology, sociology, and biology, we continue to increase knowledge of our evolutionary origins.

Most cultures throughout human history have myths, stories, and ideas about how life and culture came into existence. Although the current theory of evolution, based on the ideas of Charles Darwin, is accepted by a majority of scientists in our time, it is important to remember that many earlier ideas were recognized as well.

Darwin's books, *On the Origins of the Species by Natural Selection* (1859) and *The Descent of Man* (1872), expressed his theory of evolution and revolutionized the study of life and human origins.

Darwin presented evidence showing that natural species including humans have changed, or evolved, over long spans of time. He also argued that radically new forms of life develop from existing species. He noted that all organisms compete with one another for food, space, mates, and other things needed for survival and reproduction. The most successful individuals in this competition have the greatest chance of reproducing and passing these characteristics on to offspring. Over hundreds of thousands of generations, one form of life can evolve into one or more other forms. Darwin called this process natural selection.

> Darwin's theory of natural selection is commonly known as "survival of the fittest."

Modern science now understands that the mechanism for evolutionary change resides in **genes**, the basic building block of **heredity**. Genes determine how the body, and often the behavior, of an organism will develop over the course of its life. Certain information in genes can change, and over time this genetic change can actually alter a species' overall way of life.

genes segments of DNA located on chromosomes that direct protein production

heredity the passing on of characteristics from parents to offspring

In recent decades, biological and social scientists have made impressive strides in understanding our complex physical and cultural origins. Their research has revealed gradual alterations in our genetic structure, as well as shifts in culture and behavior, that have transformed humankind into the planet-dominant species.

Scientists estimate that our human ancestors began to diverge from the African primates between eight million and five million years ago. This figure is the result of studying the genetic makeup of humans and apes, and then calculating approximately how long it took for those differences to develop. Using similar methods of comparing genetic variation among human **populations** around the world, it is thought that all people living today share a common genetic ancestor.

populations groups of individuals of one species that live in the same geographic area

Early Life in Africa

The human story begins in one of the most geologically fascinating areas on Earth, the Great Rift Valley of Africa. It is an enormous split torn into Earth's crust that runs from the forests in Tanzania to the deserts of Ethiopia. In some places the rift is thousands of feet deep and exposes the last fifteen million years of the earth's history. Here, fossil remains of our earliest ancestors can be found. Humankind appears to have first evolved in Africa, and the fossils of early humans, or **hominids,** who lived between five million and two million years ago, come entirely from Africa.

hominids belonging to the family of primates

Starting with the modern human skull, it is possible to trace our ancestry back millions of years. As we travel back in time, our ancestors look less and less like us and begin to resemble our closest relatives, the African apes. Because our physical and genetic characteristics are similar, evolutionary theory offers evidence that ancestral humans had a very close relationship to a group of primates, the apes. Humans, chimpanzees, gorillas, and the large apes of Africa share a common ancestor that lived between eight million and five million years ago.

Humans, or hominids, belong to the scientific order named Primates, a group of more than 230 species of animals that includes the monkeys, lemurs, and apes. Modern humans have a number of physical characteristics resembling our ape ancestry. The social systems of humans also share similarities with the African apes and other primates, such as baboons, chimpanzees, and rhesus monkeys. Chimps live, groom, feed, and hunt together and form strong family bonds. Early humankind probably had a similar lifestyle.

Scientists now know that nearly 98 percent of the genes in humans and chimpanzees are identical, making chimps the closest living biological relative of humans. However, there are fundamental differences between modern humans and their primate relatives. The human brain is larger and more complex, giving humankind the ability to communicate through language, art, and symbols, to walk upright, and to develop a throat structure that makes speech possible.

One of the earliest defining human traits is bipedalism, the ability to walk upright on two legs. This characteristic evolved over four million years ago. Other important human characteristics, such as a large and complex brain, the ability to make and use tools, and the capacity for language and culture, developed more recently. Many of what we consider advanced traits, such as art, religion, and different expressions of cultural diversity, emerged during the past 100,000 years.

Most paleoanthropologists today recognize ten to fifteen different groups of early humans. They do not agree, however, about how they are related or which ones simply died out along the way. Researchers also disagree about how to describe, identify, and classify these early human species, and what factors influenced the evolution and extinction of each species.

Early Humans: Evolution of Australopithecines

bipedal walking on two legs

Nearly five million years ago in Africa, an apelike species evolved with two important traits that distinguished it from the apes. This species had small canine teeth (next to the four front teeth), and it was **bipedal**, meaning it could walk on two legs instead of four. Scientists refer to these earliest human species as australopithecines, or australopith for short.

fossil record a collection of all known fossils

The **fossil record** shows that there is not an orderly sequence leading from one form to another. Several groups lived at the same time and characteristics developed at different rates; therefore the human family tree suggests a long and complex past.

Fossils from several early australopith species that lived between four million and two million years ago clearly demonstrate a variety of adaptations that mark the transition between ape to human. Prior to four million years ago, fossil remains are scarce and incomplete; where available, however, they do show a primitive combination of ape and human features.

spinal cord a thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

Most of the key characteristics that stand out as distinctly human are related to their bipedal stance. The australopiths had an S-shaped spine that allowed for balance when standing. The opening through which the **spinal cord** attached to the brain was positioned more forward, allowing for the head to be balanced over the upright spine. The pelvic bone was shorter and broader than in apes, giving the pelvis a bowl shape that supported the internal organs when standing or walking upright. The upper legs angled inward allowing the knees to support the body while standing or walking. Shorter and less flexible toes functioned as rigid levers for pushing off the ground with each step.

Most early species had small canine teeth, a projecting face, and a small brain. They weighed between 22 and 37 kilograms (60 to 100 pounds), and were 0.9 to 1.5 meters (3 to 5 feet) tall. Males were generally larger than females. Both had curved fingers and long thumbs with a wide range of movement. The apes, in comparison, have longer, more curved, and stronger fingers that make them well adapted for hanging and swinging from branches. Apes also have short thumbs, which limits their ability to manipulate small objects.

There were at least two major groups of australopithecine, one with very large teeth and heavy jaw muscles referred to as robust, and another referred to as gracile. The main difference was in the size of the jaws and teeth. Beyond that, there was no appreciable difference in body size. The evidence suggests that the large-toothed robust group ate primarily plant foods, where as the gracile group concentrated on a more diverse diet that included meat. Details known about each group are delineated below.

The skeletal remains of "Lucy."

Early Australopiths or Gracile Group

- *Ardipithecus ramidus.* Discovered in 1994 and estimated at 4.4 million years old. This ancient line suggests a close relationship with apes and chimps because of the enamel found on the teeth. Whether or not it walked upright is unknown.
- *Australopithecus anamensis.* Discovered in 1995 and estimated at four million years old. Jaws were apelike but the legs were humanlike; it may have walked upright.
- *Australopithecus afarensis.* Discovered in 1974 by Donald Johanson and known as "Lucy." Estimated at 3.9 to 3.1 million years old. Thought to walk upright and bipedal, these may have left footprints in volcanic ash in Laetoli 3.7 million years ago. Fossils show sexual differences, and suggest that they were adept at climbing trees.
- *Australopithecus africanus.* First found in 1924 by Raymond Dart, this was the first known australopith. Dating from 3 to 2.4 million years ago, it had forelimbs longer than legs and walked upright. Many feel this is the best candidate as ancestor to early *Homo* species.

Later Australopiths or Robust Group

- *Australopithecus aethiopicus.* Found in 1985, this group dates from 2.7 million years ago. The skull, known as "the black skull," shows a possible relationship with *A. afarensis.*
- *Australopithecus boisei.* This group lived over a long period of time, between 2.3 and 1.2 million years ago. This skull has the most specialized features of the robust group, with a massive, wide face capable of withstanding extreme chewing forces.
- *Australopithecus robustus.* This group lived between 1.8 and 1.3 million years ago in the same region as *A. africanus.* This group had jaws, teeth, and **habitat** similar to *A. boisei*, but the groups appear to not be related.

habitat physical location where an organism lives in an ecosystem

Evolution of Modern Humans

Homo habilis. After researchers unearthed the australopithecines, the next major "missing link" to be found was *Homo habilis*, an early representative of modern humankind. Found by Louis and Mary Leakey at Olduvai Gorge in Tanzania, these fossils date to between 2.5 and 1.7 million years ago. This creature was bipedal, fully upright, and had the capacity to use forearms for handling tools and weapons.

These fossil specimens show an increased brain size of 600 cubic centimeters (37 cubic inches), and a jaw and tooth size more closely resembling modern humans. Any residual physical traits for climbing had also disappeared. Cut marks on bones suggest the use of tools to prepare meat. They probably retained some of the skeletal characteristics of the australopithecines that made them great climbers. They may have spent considerable

time in trees foraging, sleeping, and avoiding predators. They were the first of our relatives to have opposable thumbs, and the fossil skulls show physical traces of **asymmetrical** brain development, which is reflected in the way that stone tools were shaped.

asymmetrical lacking symmetry, having an irregular shape

Some researchers feel that *Homo habilis* had a large enough brain to have the rudimentary capacity for speech that may have encouraged cooperation and sharing amongst members of a group. That our distant *H. habilis* ancestors were able to produce such tools demonstrates that they had manual dexterity but also a capacity for planning, as well as knowledge about what kinds of stones to use and where to find them. The technology of these first toolmakers existed for more than 800,000 years.

Homo ergaster* and *Homo erectus. Next in the story of human evolution, we find a group represented by *Homo ergastor*, a recently recognized African link between *Homo habilis* and *Homo erectus*. This group lived from about 1.8 million to 1 million years ago, when *Homo erectus* and other forms replaced it. *Homo erectus* fossils found in Java and the Republic of Georgia at 1.9 million years old and 1.6 million years old, respectively, indicate an early migration of *Homo ergaster* from Africa followed by *Homo erectus* evolving in Asia and spreading to other areas.

A fossil skeleton of *Homo ergaster* found in Kenya in 1984 became popularly known as Turkana Boy. This skull led researchers to believe this group may have been the first "naked ape." This specimen suggested no body fur, a dark pigmented skin, and no evidence of living in trees. This species may have reached up to 1.8 meters (6 feet) in height; they appear to have had a near modern size brain and a striding gait. They may have been the first to make and wear clothing of some kind.

Homo ergaster made stone tools, including well-made hand axes and cleavers for the butchering and processing of hunted animals. This technology appeared in Africa and was later carried into western Asia and Europe by *Homo ergaster* or its descendants. This technology was widespread and used until the end of the Early Stone Age, only a few hundred thousand years ago.

It now appears certain that *Homo ergaster* was the direct ancestor to the first inhabitants of Eurasia, including *Homo erectus* in the Far East, as well as the predecessor of *Homo sapiens* and *Homo neanderthalensis* in Europe. *Homo ergaster* led to *Homo erectus*, the famous missing link, which is our first ancestor to occupy territory from what is now northern China in Asia, to southern Great Britain and Spain in Europe, and all of Africa.

Emergence of Modern Human Beings

Neanderthals and Modern *Homo sapiens.* The origin of modern humans is still controversial. The debate centers on whether modern humans have a direct relationship with *Homo erectus* or the Neanderthals, a well-known, more modern group of humans who evolved within the last 300,000 years. Some researchers feel that modern humans originated separately in Asia, Europe, and Africa. Others feel that modern humans originated in Africa and after migrating into Europe and Asia they replaced the Neanderthals or archaic *Homo sapiens* found there.

For many years, scientists believed that Neanderthals were the direct descendants of modern humankind. In the 1960s an interesting theory proposed that different groups of *Homo ergaster* gave rise to numerous groups of *Homo sapiens*, including a group known as Neanderthals. This theory suggested that the Neanderthals had disappeared because of being outcompeted by and having interbred with *Homo sapiens sapiens*, sometimes referred to as Cro-Magnon people. However, more recent evidence suggests a different story.

In a landmark study conducted in 1997, scientists examined the **mitochondrial DNA** of a Neanderthal fossil and a modern human. This analysis done by molecular biologists provides evidence about when two populations of people last had a common ancestor. The results concluded that it is unlikely that Neanderthals were related to modern humans. Instead it is thought that Neanderthals were a distinct species that evolved side-by-side with early *Homo sapiens* for hundreds of thousands of years. In addition, the earliest version of *Homo sapiens*, one with the characteristics that would link it with a common ancestor for Neanderthals and modern humans, *Homo sapiens sapiens*, had evolved in Africa from *Homo ergastor* at least 600,000 years ago.

mitochondrial DNA DNA found within the mitochondria that control protein development in the mitochondria

The scientists further calculated that, while Neanderthals and modern humans did indeed share a common ancestor, *Homo ergastor*, the two lineages had diverged sometime between 550,000 and 690,000 years ago. This established that the Neanderthals evolved in Europe and evolved from archaic *Homo sapiens* and go back perhaps nearly 300,000 years. It appears that the Neanderthals almost made it to the present, as they appear to have died out only 30,000-40,000 years ago, for reasons not fully understood at this time.

Compared with *Homo sapiens*, *Homo neanderthalensis* was barrel-chested with massive brow ridges, a nose that protruded forward, a low sloping forehead, a lower jaw without much of a chin, thick arm and leg bones, and heavier muscles in the shoulder and neck. The brain was actually larger than that of modern humans, possibly because of the additional capacity needed to control the extra musculature. Although the brain size of Neanderthals overlapped with early and modern *Homo sapiens*, the shape of the cranium was different, suggesting that perhaps the frontal cortex, which controls "higher thought," was restricted.

The Neanderthals also appear to have been culturally quite advanced. While most lived in caves, it is possible that some may have begun to build house-like structures. They manufactured a variety of stone tools, including spear points, scrapers, and knives. They used and controlled fire, which probably helped in cooking frozen meat and in keeping warm. Evidence that they buried their dead with flowers and tools suggests that perhaps they had a form of religion.

It appears, then, that modern human beings are direct descendants of a group known as Cro-Magnon *Homo sapiens* that appeared in Europe and Asia 100,000 years ago. Although they overlapped with the Neanderthals, they were physically unrelated. They appeared thoroughly modern, with a high forehead and a well-defined chin. Artifacts and stone tools demonstrate that they had mastered the art of making tools and useful instruments from stone, bone, and ivory, and they may have used spears. A number of colored paintings left on cave walls suggest an evolving, rich, and complex cultural life. They hunted cooperatively and were perhaps the first to have a language.

Conclusion

In March 2001 a new fossil, known as *Kenyanthropus platyops*, was added to the family tree of early humans. Thought to be 3.5 million years old, it is considered a new genus and species of an early human ancestor that lived in the same area and time of Lucy. This recent find is an example of the ways in which our long and complex past slowly reveals itself to us as we come to recognize and understand more about our human ancestors, piece by piece and fossil by fossil. SEE ALSO Biological Evolution; Primates.

Brook Ellen Hall

Bibliography

Conroy, Glenn. *Reconstructing Human Origins: A Modern Synthesis.* New York: W. W. Norton, 2000.

Ehrlich, Paul, E. *Human Natures, Genes, Cultures, and the Human Prospect.* Washington, DC: Island Press for Shearwater Press, 2000.

Gore, Rick. "The Dawn of Human: The First Steps." *National Geographic* 191, no. 2 (February 1997): 72–100.

Johanson, Donald, and Edgar Blake. *From Lucy to Language.* New York: Simon and Schuster, 1996.

Internet Resources

Becoming Human: Paleoanthropology, Evolution, and Human Origins. The Institute of Human Origins. <http://www.becominghuman.org>.

Human Populations

Modern humans (*Homo sapiens*) are grouped with the mammals (class Mammalia) in the subphylum Vertebrata. Within the mammals, humans are assigned by taxonomists to the primates (order Primates), along with lemurs, monkeys, and apes. Humans are grouped by most taxonomists together with the surviving species of Hominoidea, or great apes (the others include two species of gorilla, two species of chimpanzee, orangutans, and simangs). However, all members of the human family can stand upright with no difficulty and are naturally **bipedal**, whereas apes are naturally quadrapedal, only standing upright when necessary. Humans are also the only surviving members of the family Hominidae and genus *Homo*. Extinct members of the genus include *Homo habilis* and *Homo erectus*. The *Homo* sp. probably evolved from one of several species of australopithecines: *Australopithecus africanus*, *A. robustus*, *A. boisei*, and the recently discovered *A. garhi*. "Lucy" (*Australopithecus afarensis*) lived around 3.5 million years ago (abbreviated as mya) and may have been the ancestor of the evolutionary branch that led eventually to humans. It is not yet clear where the recently discovered *Kenyanthropus platyops* (who also lived around 3.5 mya) fits into the evolutionary sequence.

bipedal walking on two legs

Evolution

About 2.5 mya, the first humans, genus *Homo*, first appeared in the fossil record. For the first half million years, early representatives of *Homo* lived in loose association with *australopithecines*, from whom they differed in two important ways. First, they were somewhat larger and had much larger brains than australopithecines. Second, they used tools. Their tool use is the origin of the names for one species of these early humans, *Homo habilis*, or "handy" man. *H. habilis* lived in the dry savannas and forest edges, probably surviving for most of the year on roots, bulbs, and tubers. Although roots, bulbs, and tubers are very nutritious, digging them up from the hard, dry, savanna soils is difficult with only bare hands. Roots and tubers are also deficient in protein. So *H. habilis* would have needed to supplement the carbohydrate-rich diet of roots and tubers with high-quality protein, the best source of which is meat. *H. habilis* was a hunter and meat eater.

When you cannot run very fast and do not have big, sharp teeth, hunting large animals requires some form of social organization. So *H. habilis* individuals probably lived in small bands of closely related members. It is likely that some division of labor also existed, with the females doing most of the digging (something you could do while holding an infant) while the males hunted large game.

Fossils of another early member of our genus, *Homo erectus* ("upright" man) first appeared in Africa around 2 mya and spread rapidly into Asia. The fossils of *H. erectus* found in Asia were originally known as Java man or Peking man. *H. erectus* was as large as humans but had a heavier build. *H. erectus* also made another significant technological advancement, fire. They also had more sophisticated tools that were probably used for cleaning and cutting meat, for scraping hides, and as weapons. *H. Erectus* survived in many parts of the world until around a quarter million years ago.

The same evolutionary patterns established by the transition from *Australopithecus* to *Homo erectus* were extended even further with the evolution of *Homo sapiens.* The earliest members of our species had larger brains and smaller teeth than did *H. erectus.* Several types of (probably competing) *H. sapiens* existed at the same time. All were skilled big-game hunters, suggesting a high degree of social organization and, probably, language. Another distinctly human trait also appeared with *H. sapiens.* They apparently had religious practices and some concept of an afterlife. This led to burial rituals and the inclusion of tools, clothing, weapons, and food in the burial, presumably to aid the deceased in the afterlife.

One type of early *Homo sapiens*, Neanderthal, was widespread in Europe and Asia between 75,000 and 30,000 years ago. Neanderthals were short, robustly built, and had brains that were somewhat larger than modern humans. They used a wide variety of tools and were skilled hunters. However, an even more modern human, Cro-Magnon, appeared around 100,000 years ago. Cro-Magnon peoples and Neanderthals lived at the same time, but Neanderthals abruptly vanished from their range. Some biologists think Cro-Magnons exterminated Neanderthals, whereas others propose that interbreeding may have obliterated the differences. Cro-Magnon humans had even more sophisticated tools, modern language capabilities, and made extraordinary cave paintings.

Language

Larger brains led inevitably to the evolution of human languages. Language, and the sophisticated social organization it makes possible, offers enormous evolutionary advantages. Not only were humans able to organize themselves into sophisticated hunting parties, they were also able to

transmit information about other resources. Language also offers one other enormously important advantage. With language it is possible to transmit information from one generation to the next. The ability to pass along knowledge, traditions, rituals, and other information led to the development of culture. Cultural change can occur much more rapidly than genetic change. A cultural trait can spread through a **population** in less than one generation. The problem of cultural transmission is how to pass along cultural norms efficiently without being rigid and stifling the creativity necessary for a population to survive adverse changes in the environment.

population a group of individuals of one species that live in the same geographic area

Unique cultural traditions have been identified in the tools, weapons, and other implements found associated with human fossils. Along with cultural traditions, the domestication of plants and animals also spread rapidly. As a result most human societies eventually became sedentary. Agriculture and pastoralism (herding of domestic animals) replaced hunting and gathering. Agriculture and pastoralism led to cities, expanded food supplies, stratified societies, and the rapid growth of the human population.

Agriculture was independently invented three times at different places in the world. Agriculture was first discovered in the Middle East about 11,000 years ago and spread from there throughout Europe. From Middle Eastern agriculture we get cereal grains, grapes, and olives. European agriculture gave us rye, cabbage, celery, and carrots. Domesticated animals included cattle, sheep, goats, horses, pigs, dogs, cats, and chickens. Agriculture also developed in east Asia about the same time. From Asian agriculture we get rice, soybeans, citrus fruits, and mangoes.

When humans first entered the New World, they did not bring agriculture or domesticated animals with them, except for dogs. So agriculture developed a third time in the New World and gave us corn, tomatoes, kidney and lima beans, peanuts, potatoes, chili peppers, and squash. Domesticated animals were rare in the New World and included only llamas, alpacas, and turkeys.

Human Population Growth

Humans have successfully moved into every available nook and cranny on Earth. Our sophisticated technology allows us to survive comfortably where no other mammal or any complex organism could survive. Humans spend the winter at the South Pole. Humans live on mountaintops and in arid deserts. These are mere curiosities, but it is obvious that humans are able successfully to make a living in a wider variety of **habitats** and under a broader range of environmental conditions than can any other animal on Earth.

habitats physical locations where an organism lives in an ecosystem

For the first few million years of our evolution, humans lived in small groups and survived by hunting and gathering. The invention of agriculture allowed human populations to grow rapidly. They are still growing. If the number of humans on Earth is plotted against time, the curve stays essentially horizontal until about 1000 C.E. At that time, there were less than 100 million people in the entire world. From 1000 C.E. to 2000 C.E., the population growth curve turned sharply upward and now appears almost vertical. It took 2 million years to reach the first billion people, 130 years to reach the second billion, 30 years to reach the third billion, 15 years to reach the fourth billion, and only 12 years to reach five billion.

Two private farms butt up against a development of homes and businesses upon land that once contained fields of corn in York County, Pennsylvania.

The population of the world passed six billion in September 1999 and in March 2001 was over 6,137,748,000. By 2010 the world's population will pass seven billion.

This rapid population growth and the spread of humans to every part of the globe have profoundly altered the environment. Obviously the population of Earth cannot grow indefinitely. At some point, resources will run out and population growth will be limited. Biologists wonder what the **carrying capacity** of Earth is and what the quality of life would be like if the human population were to be allowed to increase to that point.

carrying capacity the maximum population that can be supported by the resources

Carrying Capacity

Carrying capacity is the maximum population of a given species that an ecosystem can support for an extended period of time. Every habitat, ecosystem, or **biome** has a carrying capacity of any particular species. Humans have moved into every portion of Earth and inhabit a variety of different ecosystems. Discussions of carrying capacity for human population must include the whole Earth as an ecosystem. There is much debate and discussion of Earth's carrying capacity. Many feel that Earth is already overpopulated and that drastic measures must be taken immediately to reduce the population and to reduce resource consumption.

biome a major type of ecological community

Humans have already transformed or degraded 40 to 50 percent of Earth's land surface. Humans use 8 percent of the total productivity of oceans. The percentage is much higher in the areas of concentrated productivity, such as continental shelves. Humans have already increased atmospheric carbon dioxide by 30 percent. On many islands, over one-half of the species have been introduced by humans, often devastating native populations. Over 20 percent of bird species have become extinct since 1800 as a result of human activity. Over 22 percent of marine fisheries are overexploited and are now in decline. Another 44 percent are at the limit of exploitation.

The biggest problem humankind may have to face in the near future is the availability of clean, fresh water. Humans already use over one-half of the available fresh water. Some experts predict that in the twenty-first century competition for water resources will come to dominate local, national, and international politics. These experts predict that the competition for water resources will be much more severe and dangerous than the present competition for energy resources.

Land resources are also limited and cannot support unlimited population growth. Cropland, rangeland, pasture, and forests are all under pressure. Most land suitable for farming is already being farmed. Increases in agricultural productivity through higher yield crops and more efficient farming practices have allowed agricultural production to increase more rapidly than the population. Most experts think that this cannot continue indefinitely.

Human Impact on the Environment

Humans interact with both the living and nonliving factors in our environment. Environmental degradation occurs when a potentially renewable resource such as soil, grassland, forest, or wildlife is used at a rate faster than the resource can be replaced. The resource becomes depleted and environmental degradation occurs. If the rate of use of the resource remains high, the resource can become nonrenewable on a human timescale or it can even become nonexistent (extinct). Worldwide, species are disappearing at a rate greater than the rate of species loss during any of the mass extinctions Earth has undergone.

biodiversity the variety of organisms found in an ecosystem

Sustainable development is a form of social change that includes recognizing that maintenance of natural resources is a basic human need. The idea of resource sustainability emerged in the late nineteenth century with regard to renewable resources such as forests and fisheries. At the start of the twenty-first century, the concept encompasses many other ideas, including population control as one of the keys to maintaining Earth's biosphere.

Not only are species being lost at an alarming rate, biodiversity is also being lost at the ecosystem level because of environmental degradation. Tropical forests are recognized as the most diverse ecosystems on Earth and are experiencing the highest rate of ecosystem loss, but temperate habitats are also suffering degradation. Because the temperate parts of the world were settled first, it is in these areas that the loss of **biodiversity** has been greatest.

Who is responsible for degrading the environment? We all are. Ordinary human activity from even the most responsible individuals inevitably pollutes and degrades the environment to some extent. We directly degrade the environment when we consume resources (burning wood in a fireplace, for example) and indirectly when resources are extracted and transformed into products we need or want. SEE ALSO BIODIVERSITY; POPULATION DYNAMICS; POPULATIONS.

Elliot Richmond

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Ehrlich, Paul R. *The Population Bomb.* New York: Ballantine Books, 1971.

Findley, Rowe "Will We Save Our Own?" *National Geographic* 178, no. 3 (1990):106–136.

Kohm, Kathryn A., ed. *Balancing on the Brink of Extinction: The Endangered Species Act and Lessons for the Future.* Washington, DC: Island Press, 1991.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth, 1990.

Odum, Eugene Pleasants. *Fundamentals of Ecology*, 3rd ed. Philadelphia, Saunders, 1971.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates, 1987.

Terborgh, John. *Where Have All the Birds Gone?* Princeton, NJ: Princeton University Press, 1989.

Hunter-Gatherers

"Hunter-gatherers" is a term generally used to describe people from ancient societies who survived exclusively by hunting, fishing, or gathering wild foods. There is controversy today among scientists, however, as to whether any societies in modern times can be considered to be true hunter-gatherer groups. Some scientists argue that no societies today dwell in isolation and that trade has existed between hunter-gatherers and neighboring societies for thousands of years. Others recognize the societal interaction but assert that the contact has done little to change the lifestyles of hunter-gatherers.

Despite varying opinions, one thing is clear: Until about 8,000 years ago, all people were foragers of wild foods. As recently as 3,000 years ago, the entire **population** of southern Africa depended on hunting game and gathering wild plants for their survival. Outsiders have given many names to the people in southern Africa who lived by hunting and gathering, including Bushmen, San, and Twa. Other notable hunter-gatherers, called the Soaqua, lived along the Western Cape coast of Africa, while others, known as Xam, thrived in the grassy plains of the semiarid Karoo region.

population a group of individuals of one species that live in the same geographic area

Basic Characteristics of Hunter-Gatherer Societies

While there is evidence that many differences existed among hunter-gatherer societies throughout the ancient world, there are also numerous uniting traits. The hunting and gathering lifestyle depended tremendously on large land areas where these ancient peoples could scout for adequate food. It has been estimated that people who depend on hunting and gathering must have approximately 20 to 1,500 square kilometers (10 to 700 square miles) of land per person, depending on the **climate**. Hunter-gatherer societies were generally very small. Large groups would have exhausted available food supplies rather quickly in any one area. These small groups were thought to be made up of individual family members or a number of related families collected together in a small band.

climate long-term weather patterns for a particular region

Hunter-gatherers usually moved in order to follow local food supplies. Possessions had to be carried from one camp to another. This suggests that permanent villages were rarely possible. Housing most likely consisted of crude lean-tos, huts, or primitive tents. A sedentary lifestyle may have been possible where food supplies were unusually abundant and reliable. Evidence suggests, for example, that the American Indians of the Pacific Northwest coast achieved high population densities and established permanent villages because resources were vast and reliable and food could be stored. Their main staples were dried salmon and flour made from acorns.

Ratio of Hunting to Gathering

Although hunting, fishing, or gathering of edible plants typically occurred together in hunter-gatherer societies, one activity sometimes prevailed. The Eskimos of Arctic Canada, Alaska, and Greenland, for example, traditionally relied on the hunting of whales and seals and on fishing for survival. By contrast, the San, or Bushmen, of modern-day South Africa tend to rely more on gathering than on hunting.

Varying Male and Female Roles

A bushman in Namibia gathers magnetti nuts.

While hunting and gathering activities were usually performed together, different social roles were often associated with each function. For example, the !Kung people of Botswana are regarded by many scientists as living examples of early hunter-gatherers. Hunting was done by males, and females strictly gathered edible plants. This was the most important activity because up to 80 percent of this society's diet consisted of plant foods. Though plant foods were seasonal, they were more substantial and dependable as a food source than game.

The women, who had the knowledge of the location and seasonal availability of edible plants in their area, went out collecting every day or every few days, depending on the circumstances. The !Kung people were relatively lucky, compared to other groups in the region, because they lived in an area where there are mongongo trees, which bear nutritious nuts. The nuts could be eaten raw, but evidence shows that the !Kung liked to roast them in a fire. Among the !Kung, role distinctions were also made on the basis of age and degree of leadership within a group or society.

Other Kalahari hunter-gatherers also practiced roles where the men hunted and the women gathered. The importance of hunting lay in its significance as a source of prestige for the men of the group. Hunting also provided sought-after delicacies, thus allowing the sharing of social ties within the band. Hunting in very small groups of between two and six individuals, the men would often stay away from camp for two or three days while following wounded prey. Large animals were slaughtered and cut up at the kill site so the meat could conveniently be carried back to the campsite.

Farming versus Hunter-Gatherer and Primitive Agricultural Societies

Scientists consider hunting and gathering to be among the two oldest professions in existence. Most societies living this lifestyle eventually began practicing primitive agriculture by preparing simple garden areas to supplement their hunting and gathering efforts. In contrast to modern farming practices, primitive agriculture was typically practiced in forests where the loose soil was easily broken up with a twig or fallen branch rather than on grassy fields with heavy sod.

Additionally, primitive agriculture probably did not use extensive fertilizers or modern techniques such as crop rotation, irrigation, or terracing.

Primitive agriculture is, therefore, much less productive than farming. Also, the size of the societies remained small with most being no larger than the hunting-gathering societies. The overall population densities of the primitive agriculture societies were also very low compared with farming regions.

Primitive agriculture societies that lived in forest areas often practiced "slash-and-burn" techniques. After about two years of cropping a plot, the land was left fallow for a number of years and allowed to revert back to secondary forest or brush. The brush was then burned. The most highly evolved slash-and-burn societies were the Maya of Guatemala and Yucatan. SEE ALSO FARMING; HUNTING.

Stephanie A. Lanoue

Bibliography

Barnard, A. *Hunters and Herders of Southern Africa.* Cambridge, U.K.: Cambridge University Press, 1992.

Creamer, W., and Jonathan Haas. "Pueblo: Search for the Ancient Ones." *National Geographic* 18, no. 4 (1991):84–99.

Schapera, I. *The Khoisan Peoples of South Africa: Bushmen and Hottentots.* London: Routledge and Kegan Paul, 1930.

Sitton, Thad. "Hunter-Gatherers and Human Ecology." *American Biology Teacher* 42 (1980):345–347.

Steyn, H. P. *Vanished Lifestyles.* Pretoria: Unibook Publishers, 1990.

Hunting

Hunting is the intentional act of tracking and killing wild animals for consumption or trophy. These animals are referred to as "game," quarry, or prey. Fishing is a type of hunting restricted to catching fish. As omnivores, humans require proteins and vitamins that are most easily provided by consuming meat. This is why hunting was a necessity for our human ancestors and preceded agriculture as a means of food procurement. Through the use of tools, Paleolithic humans hunted to ensure an adequate food supply and to obtain skins for use as clothing. Although agriculture became widely developed in the Neolithic period, game hunting remained prevalent and may have acquired cultural as well as biological significance.

Archaeological evidence for hunting is investigated today by examining patterns in the location of animal carcasses; the degree to which the skeleton is disassociated; cut or teeth marks on the bones; and the type, location, and wear of discarded hunting tools. These clues reveal aspects of the societal structure of prehistoric humans, such as gender roles, migratory habits, and nutrition. In ancient Greece, the sequence and style of killing and preparing the meat of an animal were highly ritualized under the laws and customs of polytheistic religion. Similar rituals were preserved through the Middle Ages, when boar and stag hunting became popular throughout Europe.

Game hunting today is still a strong pastime and a necessity of life for indigenous peoples living in remote areas. The decrease and disappearance of many large predators because of **habitat loss** and inbreeding has made hunting a necessity for controlling the population size of certain prolific

habitat loss the destruction of habitats through natural or artificial means

Three goose hunters walk with their kills at Langford Creek in Kent County, Maryland.

poaching hunting game outside of hunting season or by using illegal means

falconry a sport where falcons are used for hunting

species, such as deer and geese. However, overhunting and **poaching**, the illegal slaughter and sale of rare animals, can lead to further extinctions.

Humans rely on trained animals and specialized tools and weapons to hunt. Hunting with trained dogs is called coursing. Sporting breeds of dog have been bred for size, temperament, and intelligence, to aid the human hunter. For example, the harrier is always used in rabbit hunting, the fox hound in fox hunting, the pointer and retriever in wild foul hunting, and the Rhodesian ridgeback in lion hunting. In some cases, such as with the terrier, the dog is expected to seek out and attack the prey, whereas in others, such as the fox hound, the dog's task is to startle, or flush, the prey from its hiding spot. Retrievers, pointers, and setters may be called upon to retrieve the fallen carcass of a killed game bird without damaging it. Horses, likewise, may be highly trained in the maneuvers and tactics a hunter uses when in pursuit of prey, and are conditioned to withstand the noise and ruckus of the hunt. **Falconry** is a term describing the use of falcons, hawks, or eagles as trained hunters. Falconry originated several thousand years ago in China and has since been adopted by other cultures. Wild raptors are caught as chicks and trained to fly on command after being released from the falconer's wrist. They will attack and kill prey, and then abandon the corpse to the falconer. Although an uncommon practice, southern Asians have been training cheetahs for thousands of years to kill antelope, deer, and other fast-moving prey for humans.

Aside from animal-assisted hunting, there are many accessories and tools unique to the time of year, environment, and type of game that will be hunted. Camouflage clothing is necessary for concealment, and some hunters use species-typical calls or decoys to lure the game into their immediate vicinity. Firearms, crossbows, and the sling are often used on sport hunting excursions, whereas poisoned darts, arrows, and spears are common in hunting by African and South American natives. Traps are designed to ensnare, hobble, or injure prey. They can be made of a pair of metal jaws that snap shut when an animal's footstep depresses a switch or when bait is removed from a switch, a cage with a door that swings shut when the animal enters, or a pit that is thinly covered with debris so that animals fall through the debris to the bottom. Trapping is effective when covering large territories and for **nocturnal** prey. Unlike the use of weapons that leave holes in the coat, trapping preserves the integrity of the animal's hide because it affects primarily the lower limb. For this reason, the practice is popular with fur traders, who refer to it as fur harvesting. Whale hunting, or whaling, for blubber, meat, sperm, and bones and teeth, is an ancient practice common to many seaside civilizations. Harpoons are long barbed spears attached to ropes that are flung or shot at whales to injure and kill them. Australian aborigines rely on a unique hunting tool called the boomerang, which is thrown at game but returns to the hunter if it does not hit its mark.

nocturnal active at night

Hunting is also characterized by the type of game being sought. Big game hunting includes large animals such as moose, caribou, bear, reindeer, wolf, tiger, leopard, elephant, and wild goat. It can be very dangerous because the hunted animal is capable of counterattacking the hunter, and because these excursions take hunting parties to remote wilderness where immediate medical attention is unavailable. However, big game are the preferred sport for trophy hunting. Small-game hunting, known as shooting in Great Britain, focuses on smaller animals such as wild fowl, hare, rabbit, woodchuck, raccoon, and squirrel. These animals are more often destined for food than for trophy.

Animal carcasses and skins, both mammals and birds, may be taken to a taxidermist, where they are formed into a three-dimensional, lifelike representation of the animal for permanent display. The skin of the animal is fitted around a hard framework, such as polyurethane, the eyes are replaced with large glass beads, and the ears and hairless regions are sculpted in clay, epoxy, or wax. Taxidermy originated in the 1800s, when hunters began bringing their skins to upholsterers, who would stitch them up with rags and cotton. This is why taxidermized animals are sometimes referred to as stuffed.

Because of the dangers of overhunting and thereby unwittingly bringing about the extinction of the quarry, all fifty of the United States and many other countries enforce laws restricting sport hunting to certain periods of the year. These **hunting seasons** cover different periods for different game, different hunting techniques, and different locales. They are determined based on the natural breeding and migration periods of the game, and on its **relative abundance**, a measure of the species' well-being based on population size. Hunters must register their firearms and report the number and kind of game they have killed. Hunting licenses must be purchased annually, to document and limit the number of lawful hunters, and the income from their sale is often allocated to animal conservation organizations. Further benefits from hunting include the prevention of diseases that can be spread from wild animals to humans or livestock, for example, the spread of rabies through raccoon populations and tuberculosis through wild bison. Several programs currently exist to increase hunting of overpopulated wild game, such as white-tailed deer, that are becoming a nuisance near cities. The surplus of meat resulting from the kills is inspected, packed, and donated to homeless shelter food pantries.

hunting seasons a period of time during which hunting is permited

relative abundance an estimate of population over an area

Hunting does have some benefits, but the risk of hunting to extinction is well-documented in human history. Beginning with the likely prehistoric slaughter of all mammoths, overexploitation has also eliminated large birds such as the moa and the dodo, smaller birds like the passenger pigeon and Carolina parakeet, large marsupials such as giant wombats and giant kangaroos, and marine mammals such as Steller's sea cow. Many animals are becoming locally extinct and universally endangered owing to a lack of regulations in certain areas of the world. Many others, such as the gray whale and the Indian elephant, are currently at a high rate of decline.

Even with the presence of adequate hunting regulations, poaching undermines the conservation effort. Poaching is the unlawful hunting of protected game either outside the allotted hunting season or against a hunting ban. It is strictly opposed by all sport hunting associations and should not be confused with lawful hunting. Unfortunately, because of the law of supply and demand, poaching becomes increasingly profitable as the number of game animals declines. This increases the risk of extinction at a time when animals most need to be protected. Tiger pelts, elephant and rhinoceros ivory, and sea turtle eggs are examples of luxury items that unnecessarily cause the endangerment of a species. Poaching is most easily counteracted by refusing to buy animal products without first researching the legality of the sale. The effects of hunting and poaching are becoming stronger with the decrease in animals' natural environments and the increased human demand for food and luxury products. Destitute peoples in developing countries may depend on poaching for money or on hunting protected animals for food. A global effort is needed to end extinctions caused by the overexploitation of game animals. SEE ALSO Extinction; Farming; Hunter-Gatherers.

Rebecca M. Steinberg

Bibliography

Dorsey, Chris, and Matthew B. Connolly. *Wildfowler's Season: Modern Methods for a Classic Sport.* New York: Lyons and Burford, 1995.

Isenberg, Andrew C. *The Destruction of the Bison: An Environmental History, 1750–1920.* Cambridge, U.K.: Cambridge University Press, 2000.

MacKenzie, John M. *The Empire of Nature: Hunting, Conservation, and British Imperialism.* Manchester, U.K.: Manchester University Press; New York: St. Martin's Press, 1997.

Swan, James A., *The Sacred Art of Hunting: Myths, Legends, and the Modern Mythos.* Minocqua, WI: Willow Creek Press, 1999.

Walker, Adrian. *The Encyclopedia of Falconry.* Lanham, MD: Derrydale Press, 1999.

Ichthyology

Ichthyology is the science of animals that deals with fish. This field includes the study of fish growth, development, structure, characteristics, classification, geographical distribution, and the relationship of fish to their environment. The science of ichthyology was evolved in Europe during the eighteenth century. However, the Chinese were studying fish (with the intention to propagate them) at least ten centuries before the birth of Christ. There are also recorded observations on the varieties, habits, and qualities of various fish by the ancient Egyptians, Greeks, and Romans.

Today, ichthyologists strive to answer questions like, "How long can a fish live?" and "How big can a fish grow?" Although these questions may sound simple, the answers are based on a multitude of factors. And while it may be true that most fish live between sixteen and twenty years, it is much more difficult to predict size because fish growth never stops. Generally, fish get a little longer and a little thicker every year. One of the largest fish, a 13.7-meter (45-foot) whale shark caught off Florida's Atlantic coast in 1912, was recorded at a weight of 20 tons.

One of the best places to study fish is the national fish collection, housed at the Smithsonian National Museum of Natural History. The collection is the largest in the world and contains approximately eight million species from all over the world. The collection continues to grow as specimens are added from parts of the world where the fish **fauna** is poorly recognized or understood. Zoologists from the National Marine Fisheries Service and the U.S. Department of Commerce are permanently stationed at the museum, and they work closely with the specimens, focusing primarily on commercially important species.

Stephanie A. Lanoue

Bibliography

Lagler, Karl F., John E. Bardach, and Robert R. Miller. *Ichthyology.* New York: John Wiley & Sons, Inc., 1967.

Imprinting

Imprinting describes a process in which newborn animals rapidly develop a strong attachment to a particular individual, often the mother. It is associated particularly with precocious bird species (species that mature early) such as chickens, ducks, and geese, in which the young hatch fairly well-developed.

Imprinting is advantageous because once offspring imprint on their mother, they will try to remain close to her and follow her around, behaviors that are beneficial in terms of the offspring's survival. The young also indicate distress when the mother is absent.

Imprinting was one of the first matters tackled by the field of **ethology**. Konrad Lorenz, one of the founders of ethology, studied imprinting to determine what controls and limits the behavior associated with imprinting. Lorenz showed that newly hatched birds imprint on practically any moving object to which they are close during their first day of life.

ethology the study of animal behavior

In natural conditions, of course, this object is almost certainly to be the mother. However, in a famous experiment, Lorenz was able to get birds to imprint on him. Interestingly, male birds that imprinted on Lorenz subsequently courted human beings when they tried to find mates, rather than courting members of their own species. This suggests that imprinting not only provides **behavioral** instructions to young birds soon after they hatch, but has important implications for future behavior as well.

behavioral relating to actions or a series of actions as a response to stimuli

Further work on imprinting in birds has revealed that species may respond preferentially to the appropriate stimulus. Although baby birds imprint on any moving object, they are also more likely to imprint on objects that have certain head and neck features corresponding to those it

These Canadian goslings follow their mother through the water. Imprinting is the process by which newborn animals develop a strong attachment to one or both of their parents.

expects to find in an adult of its own species. This makes it more likely that, in the wild, baby birds will imprint on the correct individual.

Two characteristics of imprinting are essential. First, imprinting describes an innate, preprogrammed response that is released by the appropriate stimuli. In the case of the baby birds, the presence of any mobile entity close to the chicks in the first hours or day of life is sufficient to release the response. In other species, different stimuli are required. Baby shrews also imprint on their mother, and will hold onto the fur of either the mother or another sibling when the mother wishes to move, so that the entire family is able to travel in caravan style. In shrews, the releasing stimulus for imprinting is suckling: Babies imprint on the odor of the female who suckles them.

critical period a limited time in which learning can occur

A second feature of imprinting is that there is a very specific **critical period** when imprinting is possible. Goslings and other birds generally imprint in the first day of life and often within the first hours. For shrews, studies show that the critical period occurs between the fifth and fifteenth days of life. It is the female who nurses the babies during that time on whom they will imprint.

innate behaviors behaviors that develop without influence from the environment

learned behaviors behaviors that develop with influence from the environment

learning modifications to behavior from experience

Imprinting is an example of a behavior that has both innate and learned components. **Innate behaviors** are preprogrammed, and appear fully developed in individuals. Innate behaviors tend to appear in situations in which the environment is fairly predictable. **Learned behaviors** are shaped by the environment. The advantage of **learning** is that it is flexible. Learned behaviors are suited to changing or uncertain environments.

Imprinting requires learning because young animals use cues from the environment in order to learn who is the parent. The behaviors that result, however, such as following behavior in precocious birds, is largely innate. The largely preprogrammed behavior that follows imprinting is believed to

have evolved because it is more efficient than learning, and because the flexibility that comes from learned behaviors is not advantageous in situations where imprinting occurs.

Some authors have extended the notion of imprinting to include other instances of preprogrammed behavior that require a releasing factor. **Parental imprinting**, for example, describes the imprinting of parents on their offspring. Parental imprinting is believed to be responsible for the success of **brood parasites**, bird species that lay their eggs in the nests of other species. The adoptive parents imprint on brood parasite young when they hatch, and then feed and raise them. Song imprinting has been studied in some bird species. In white-crowned sparrows, for example, young males imprint on the songs of adult conspecifics (members of the same species) that they hear sung around them, and sing similar songs when they mature and begin to look for mates. SEE ALSO Behavior; Behavioral Ecology.

parental imprinting a process by which a gene's expression in a child depends on which parent donated it before development

brood parasites birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

Jennifer Yeh

Bibliography

Alcock, John. *Animal Behavior*, 4th ed. Sunderland, MA: Sinauer Associates, 1989.

Curtis, Helena. *Biology*. New York: Worth Publishers, 1989.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Halliday, Tim. *Animal Behaviour*. London: Blandford, 1994.

Krebs, John R., and Nicholas B. Davies. *Behavioral Ecology: An Evolutionary Approach*, 4th ed. Cambridge, MA: Blackwell Science, 1997.

Instinct

An instinct is an innate, preprogrammed behavior that is genetically determined. Instinctive behaviors do not vary much within a species and are usually performed in similar, often stereotyped, ways. The acquisition of instinctive behaviors is not dependent on the environment in which an individual is raised, or on interactions with other members of its species. For example, individuals that are removed from their natural habitat and placed in isolation nevertheless develop the instincts typical to their species. Behaviors in which instinct often plays a significant role include mate recognition, courtship rituals, predator avoidance or defensive behavior, food-gathering behavior, parental care behaviors, and self-grooming.

Instinct is often contrasted with **learning**. Learned behaviors are shaped by experience and by the environment. Practically no behaviors, however, are purely the result of either instinct or learning. Most behaviors are the product of both, involving contributions from both **genes** and environment. Many behaviors that seem instinctive can be modified by experience, and many supposedly learned behaviors show biases that can be accounted for only by innate factors.

learning modifications to behavior from experience

genes segments of DNA located on chromosomes that direct protein production

One type of instinctive behavior is called a **fixed action pattern**. A fixed action pattern describes a series of actions that is initially triggered by a stimulus, and then carried out to completion. Fixed action patterns are completed even though the behaviors are no longer necessary or no longer make sense.

fixed action pattern behaviors that are common to all members of a species

An African lioness instinctively knows to carry her cub through the wilderness. This action helps to protect the cub from predators.

The classic example is the egg-retrieval instinct of the gray lag goose. If a gray lag goose suddenly notices that one of her eggs is outside the nest, she rolls it back to her nest with a series of highly stereotyped head and neck motions. Even if the egg is removed (by a researcher) while the goose is in the middle of this behavior, she follows the sequence to completion. The trigger for a fixed action pattern is also called a releaser.

The advantage of instinctive behaviors is that they are much less costly than behaviors acquired through learning. Learning takes more time and energy, and also requires extensive nervous system resources. Generally, species with small brains behave more instinctively, where as those with larger brains rely more on learning. In addition, learning simply is not necessary or advantageous in many situations. It is helpful only where flexibility is important. In other circumstances, instinctive behaviors are highly adaptive and sufficient.

Instinctive behaviors are particularly suited to predictable aspects of the environment. An instinct of baby gull chicks, for example, is to peck at the red spot on the beak of adult gulls. This elicits feeding behavior from the parent. For the baby gull, there is no advantage to having to learn such a tactic.

Similarly, the fear of poisonous snakes in certain species of birds is instinctive. The motmot preys on small snakes, and young birds are attracted to these as potential food items. However, they also have an instinct to avoid snakes with a red and yellow banded coloration, which characterizes the highly poisonous coral snake. This highlights another big advantage of instinctive behaviors: Individuals know how to respond even if they are encountering a given stimulus for the first time. It is not surprising, then, that instinctive behaviors are often more prevalent in newborn or young individuals than in older ones.

Instinctive behaviors often weaken over time. In gull chicks, for example, it has been shown that newly hatched young are fairly undiscriminating. Food-begging behavior is triggered by any object that is long and narrow and that has a colored spot at the end. This object does not have to be a gull beak or even be attached to something that resembles an adult gull head. In older chicks, however, greater resemblance to an adult gull is required to elicit begging behavior.

brood parasites birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

Because of their relative simplicity, cues that trigger instincts can be taken advantage of by other species. **Brood parasites** are bird species that lay their eggs in the nests of other species, thereby sparing themselves the time and energy that would be required to raise those offspring. Examples of brood parasites include the cowbird and the cuckoo. The host parents feed the intruders because the baby cowbirds or cuckoos are able to produce the necessary triggers to elicit the parent's feeding instinct. These include making noisy hunger calls, stretching their necks high up out of the nest, and opening their beaks wide. In many cases, brood parasite offspring have evolved to produce triggers that are much more extreme and dramatic than those of the host's own young. As a consequence, the young brood parasites get fed preferentially in the nest.

Mating instincts are another category of innate behaviors that are frequent targets of the deceptive machinations of other species. In fireflies, for example, courtship typically consists of species-specific flashing by male fireflies followed by flashing replies from interested females. However, there is a certain species of predatory firefly that mimics the female reply of a different species in order to attract males as prey items.

pheromones small, volatile chemicals that act as signals between animals that influence physiology or behavior

In another species, the bolas spider, individuals release scents that resemble the **pheromones** (molecules that are used in chemical communication between members of a species) of female moths. Males who respond instinctively to this scent are caught as prey. Finally, certain flower species, including some tropical orchids, release female bee pheromones in order to attract male bees for pollination. This is one example in which learning can modify an instinctive behavior: Male bees that have encountered deceptive orchids repeatedly learn to avoid them. SEE ALSO Behavior; Behavioral Ecology.

Jennifer Yeh

Bibliography

Alcock, John. *Animal Behavior*, 4th ed. Sunderland, MA: Sinauer Associates, 1989.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Interspecies Interactions

populations groups of individuals of one species that live in the same geographic area

Populations of animals exist in cooperative and competitive relationships with each other. For any species to thrive it must find access to food resources and be able to successfully reproduce. Ecologists have identified many methods for survival among the species of animals and have, consequently, described many of the survival techniques. Three fascinating relationships exist that intrigue both the scientist and the layperson. They are mutualism, parasitism, and commensalism.

Mutualism

Mutualistic relationships may be the most fascinating because of the cooperation that exists between species. Competitive relationships in which two or more species compete for the same resource are quite common. However, when two species evolve a pattern of survival from which both benefit, it is an interesting scenario for biologists to consider.

mutualistic relationship symbiotic relationship where both organisms benefit

In a **mutualistic relationship** two organisms from entirely different species behave in a way in which both benefit. Most often, the two organisms are from species with very different lifestyles and nutritional needs. Often the need is not even nutritional, but rather one in which the offspring are assured a better chance for survival. No matter the reason or outcome, the dependency of the two organisms continues to grow with each passing generation until the two life cycles are dependent on each other for survival.

obligative mutualism an animal that must exist as part of a mutually beneficial relationship

Complete and total dependency is termed **obligative mutualism**. Obligative mutualists are found in the association between termites and their intestinal bacteria. The termites cannot digest the tough plant material cellulose. The bacteria can. Consequently the termite gut is full of these cellulose-digesting bacteria. The bacteria benefit by having a relatively safe place to live and reproduce, and the termite benefits by gaining access to the nutrition of the plant after the cellulose has been digested.

Another example of mutualism is the relationship between some large grazing animals like the rhinoceros and the small tick birds. The birds feed on the insects that cling to the skin of the rhinoceros. In turn, the size and reaction of the rhinoceros to predators helps the tick birds to remain safe and live a longer life.

Parasitism

Another interesting relationship between species is that of parasitism. In a parasitic relationship one species lives at the expense of another. There is a clear distinction between predation and parasitism. A predator will kill the prey outright and receive its benefit directly. A parasite will not kill its host (the organism on which it lives) outright. It is better for the parasite to have its host live as long as possible to ensure continued survival and reproduction for the parasite.

One of the most familiar parasitic relationships is that of a tapeworm. The tapeworm has no digestive or sensory (eyes, ears, nose) system. In fact, it does not even have a circulatory system (heart and blood vessels). The fact that tapeworms live in the digestive system of a host means they do not need to digest their own food. It is already done for them. They do not need

A cape buffalo grazes in a field while an oxpecker bird rests on the buffalo's back. Oxpeckers have developed broad, flattened beaks to better help them to pick their meals (ticks and embedded larvae) out of the skin of the buffalo.

to sense their environment because they are protected in the gut of the host. They are small, so nutrients are passed from one cell to another by simple **diffusion**. Unfortunately for the host, the nutrients it ingests are being absorbed instead by the tapeworm. Over a long enough period, the host will become malnourished, lose weight, and eventually die.

diffusion the movement of molecules from a region of higher concentration to a region of lower concentrations

Another example of parasitism is less deadly on the host, but may eventually affect populations. Interspecific (between species) and **intraspecific** (within the species) brood parasitism is often seen in birds. One female will lay her eggs in the nest of another. The unsuspecting nesting parents may not recognize the odd egg and will continue to sit and hatch all the eggs in the nest. After the eggs hatch, the parents will spend more resources feeding and caring for the unrelated offspring, sometimes at the expense of their own.

intraspecific involving members of the same species

Cuckoo birds have been known to lay their eggs and leave their young for others to care for. Often the baby cuckoo is larger and more demanding than the other babies. More food will go to raising the cuckoo than to the other nestlings. Sometimes the larger cuckoo will even kick the competing young out of the nest, duping the parents into raising the one single chick.

Purple martins are another species of birds in which brood parasitism occurs. The main difference is that the parasitism occurs within the species. This may not be as harmful a situation for the nestlings as it is with the cuckoo. In fact, some researchers suggest that this form of parasitism may even promote colonization and population growth.

Commensalism

Commensalism is a newer and more inclusive term for an older concept called **symbiosis**. The term "symbiosis" now more broadly describes the three types of relationships discussed in this article. Commensalism is a re-

symbiosis any prolonged association or living together of two or more organisms of different species

lationship in which one organism benefits and the other is unaffected. There is a very fine line in identifying a relationship as **commensal**. Some relationships may actually be long-term parasitism. Much study is needed before a relationship can be truly described as commensal.

commensal symbiotic relationship where in which one species benefits and the other is neither helped nor harmed

In one such relationship between a small crab and an oyster, the crab enters the oyster as a small larva. The inside of the shell provides a safe place for the crab to grow and develop. Once the crab has reached maturity, however, it is too large to leave through the oyster's narrow valve opening. It remains inside the oyster, feeding off floating particles of food that are siphoned by the oyster from the surrounding water. Neither animal is harmed, and the crab has a safe place to live and receive food.

Another commensal relationship exists between some species of ants and aphids, the sucking parasites of plants. The aphids secrete a sweet liquid substance that is consumed by the ants for food. The ants tend the aphids as a farmer would tend livestock. The aphids are not harmed and the constant attention by the ants keeps the aphid colonies fairly clean.

Scientists still do not completely understand why and how mutualism, parasitism, and commensalim evolved. Each of these types of relationships are distinct and specialized. They have evolved over time, and the survival of individual species is dependent on these highly evolved relationships. There is a great deal to be learned about each of them. SEE ALSO ENDOSYMBIOSIS; PARASITISM.

Brook Ellen Hall

Bibliography

Cody, Martin L., and Jeffrey A. Smallwood, eds. *Long-Term Studies of Vertebrate Communities*. San Diego: Academic Press, 1996.

Kawanabe, Kiroya, Joel E. Cohen, and Keiji Iwasaki, eds. *Mutualism and Community Organization: Behavioural, Theoretical, and Food-Web Approaches*. New York: Oxford University Press, 1993.

Levin, Simon A. *Fragile Dominion: Complexity and the Commons*. Reading, MA: Perseus Books, 1999.

Tokeshi, M. *Species Coexistence: Ecological and Evolutionary Perspectives*. Oxford: Blackwell Science, 1999.

Iteroparity and Semelparity

Success for an animal species does not only mean that it survives, but that it survives to reproduce. When a species or population of organisms is unable to reproduce enough offspring to keep the population numbers high, extinction is the result. However, reproduction is probably one of the most energy-depleting events a single organism may endure. Both plants and animals have a wide range of reproductive methods that result in repeated matings, **fertilization**, production of offspring, and survival of the next generation. However, for many groups, including some plants, all of the energy produced by the organism is directed to successful reproduction.

fertilization the fusion of male and female gametes

invertebrates animals without a backbone

Within the animal group, **invertebrates** have a wide variety of reproductive strategies that insure their survival. Many produce so many eggs and sperm that the sheer numbers of offspring make success of a few likely.

Feature	Texas	South Carolina	Ohio
Growth	rapid	intermed.	slow
Adult mortality	high	intermed.	low
Ave. size female	57	63	75
Ave. clutch size	9.5	7.4	11.8
Broods per year	3-4	3	2
Total offspring produced per year	33	22	24
Egg mass per egg	0.22	0.33	0.35

Proportions of births by age of female	Texas	South Carolina	Ohio
1	82	48	0
2	18	30	57
3	0	15	22
4	0	7	21

This chart demonstrates the results when there occurs an optimization of the tradeoff between growth and reproduction. The number of babies born yearly shows that an animal with a higher rate of mortality would benefit from a semelparous reproduction strategy since it may not survive until the next breeding season. Redrawn from the Association for Tropical Biology web site.

Vertebrates, however, tend to be more specialized in their reproductive habits. As a consequence, a great deal of energy is spent in assuring the most optimal conditions for survival of the young. Environmental pressures such as bad weather conditions or high predation rates call for species with the highest assurance of success. Two of the most successful types of reproductive styles are called iteroparity and semelparity.

vertebrates animals with a backbone

Iteroparity occurs when a parent breeds year after year. This means that the success of the parent's genetic material surviving to another generation is increased with every brood. For most plants and animals this works quite well. If for some reason conditions do not favor the survival of the young one year, there is a repeat chance the next year.

Sea turtles are an example of iteroparity. After mating, the females come out of the water, dig a large nest with their flippers, and deposit several dozen eggs. Should a predator uncover the nest and eat the young, it is not a disaster for the parent since she will return the next year to repeat the egg-laying cycle.

Semelparity is a type of reproduction that occurs less frequently, but is no less driven by the need for reproductive success. A common example of semelparity is found in salmon, a meaty and delicious food source for many animals, including humans, bears, and other water-living predators. Salmon eggs are a nutritious and desirable food source for marine-dwelling organisms. In the face of these facts, natural selection has driven salmon to a very ingenious but costly reproductive strategy.

Juvenile salmon begin the oceanic phase of their lives in massive schools that migrate around the world's major oceans. When they become adults and are ready for breeding, instead of laying their large nutritious eggs in the marine environment, where they are likely to be eaten, the salmon change their entire **physiology** to survive in freshwater. The breeding adults smell the river in which they were born and begin to swim up to their spawning grounds.

physiology the study of the normal function of living things or their parts

Many films show the intense and difficult trek adult salmon take to get to those grounds. They leap up and over waterfalls and swim against swift and strong currents. Many species actually change their color and the shape of their mouths. They do not feed during this time. Their body tissues are

Semelparous sockeye salmon bodies turn various shades of red, and their heads green, several days after reaching their fresh water spawning grounds.

converted to eggs or sperm. At the end of these breeding migrations, salmon look terrible. Their skin is peeling. They are wounded and damaged by accidentally hitting themselves against rocks and they are exhausted. Many fishermen do not eat breeding salmon because the conversion of body tissue to **gametes** makes the salmon meat soft and undesirable.

gametes reproductive cells that only have one set of chromosomes

Before bear populations decreased, the annual migration of salmon was a source of feasting for them. Many salmon simply died before reaching their breeding grounds or were eaten by predators, including some large birds of prey such as eagles. The survival of adult salmon traveling to individual breeding grounds was often very low. This low adult survivorship is another reason, in addition to the dangers of the marine environment, why semelparity is an advantage to the fish.

The large burst of energy that completely disables the fish ends with the laying and fertilization of the eggs. Afterward, the adult fish all die. However, the adults have provided the next generation a safe place to grow and hatch. When the offspring emerge from the eggs, they have an abundant food supply from **aquatic** insects and, eventually, minnows. The young have time to grow and develop to a larger size free from most predators. The sacrifice of the parent provides safety to the next generation.

aquatic living in water

Many spiders, some anguillid lizards, and certain amphibians also undergo semelparity. It is a type of reproduction found among animals whose environmental conditions may be too harsh for the young to survive. On the other hand, iteroparity favors repeated matings. **Iteroparous** plants and animals live for many years, breeding each season. Often their strategies are to produce high numbers of young. Another approach is found among mammals, who are iteroparous. Most of them give a great deal of adult protection to the young and ensure their survivorship in this manner.

iteroparous animals with several or many reproductive events in their lives

Basically, if the parent is at low risk of death when it is young, its species will be iteroparous. If the mortality rate is high for the young, semelparity might be observed. Both strategies work well as evidenced by the continuation of both reproduction styles. SEE ALSO Expenditure Per Progeny; Reproduction; Asexual and Sexual.

Brook Ellen Hall

Internet Resources

The Association for Tropical Biology. <http://atb.botany.ufl.edu/atb>.

Jawless Fishes *See Agnatha.*

Jellyfishes *See Cnidaria.*

Jurassic

The Jurassic period is the second of the three divisions of the Mesozoic era, "The Age of Reptiles." The Jurassic lasted for 64 million years, from about 208 to 144 million years ago. The period is named for rock strata found in the Jura Mountains on the border between Switzerland and France.

During the Jurassic, the supercontinent Pangaea began to break apart. This created two landmasses, a northern mass called Laurasia (North America, Europe, and Asia) and a southern mass called Gondwanaland (South America, Africa, Australia, Antarctica, and India). During the early Jurassic, North America separated from Africa and South America and moved northward, but still remained connected to Europe. By the late Jurassic, the North Atlantic was just beginning to appear between Europe and North America.

Widespread deposits of sand in western North America indicate that the region experienced a desert **climate** during the early Jurassic. Coral reefs and the remains of temperate and subtropical forests around the world provide evidence that the climate became moister and milder later in the period. Europe was covered with shallow seas throughout the Jurassic.

climate long-term weather patterns for a particular region

Jurassic vegetation consisted mainly of seed ferns, cycads, horsetails, conifers, and gingkoes. The Jurassic is sometimes called the "Age of Cycads" because of the variety and diversity of these seed-bearing, palmlike plants. Some cycads grew to be tall as trees; other forms were short and squat.

In the marine world, the great success story was that of the **ammonites**—the coiled, shelled relatives of modern squid. At the end of the Triassic (the period just before the Jurassic), nearly 47 percent of marine species went extinct, indicating a drastic rapid deterioration of the environment that results in a crisis for certain species and is known as an extinction event. Extinction events allow some species to adapt to different environmental conditions and fill new niches. This is known as **adaptive radiation**. Although only one family of ammonites survived an extinction event at the end of the Triassic, this family radiated into an astonishing array of forms, some of which attained sizes of 2 meters (6 feet) or more.

ammonites an extinct group of cephalopods with a curled shell

adaptive radiation a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

This reptile fossil from the Jurassic era was found in Solnhofen, Germany.

bipedal walking on two legs

carnivorous animals that eat other animals

quadrupeds animals with four legs

The Jurassic period is known for an increase in the numbers and diversity of dinosaurs. At the beginning of the period, dinosaurs such as the **bipedal** and **carnivorous** theropods were small and lightly boned, feeding on insects or other small dinosaurs. By the close of the period, massive predators like *Allosaurus* and *Ceratosaurus* had appeared. These dinosaurs had heavy bodies, powerful hind legs, front limbs used for grasping and holding prey, and long, sharp teeth for spearing and stabbing. The largest of all dinosaurs, the plant-eating sauropods, also developed during the Jurassic. The sauropods include *Apatosaurus* (formerly called *Brontosaurus*), *Brachiosaurus*, *Diplodocus*, *Seismosaurus*, and *Suprasaurus*. These animals were **quadrupeds**, with pillarlike legs (like the legs of an elephant) that supported their enormous body weight, which was often 18 metric tons (20 tons) or more. The large size of the sauropods may have helped them maintain a consistent body temperature. The *Stegosaurus* is known for a distinctive row of heavy, triangular, bony plates, known as scutes, which were arranged along its back. Paleontologists (scientists who study dinosaurs) believe these plates helped the *Stegosaurus* regulate its body temperature and protected it from being eaten. Several sharp, bony spikes on the end of the tail of *Stegosaurus* probably served as a weapon against attack.

The debate continues as to whether birds most likely evolved from small, bipedal dinosaurs or other ground-dwelling reptilian ancestors. *Archaeopteryx* is one of the earliest undisputed bird fossils. It exhibits features of both dinosaurs and birds, including a long, bony tail; small, sharp teeth; feathers; and a "wishbone" that allowed for the attachment of flight muscles.

Jurassic and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Mesozoic	Cretaceous		144
	Jurassic		208
	Triassic		245

Mammals continued to diversify during the Jurassic, but remained small and **nocturnal**, possibly to avoid competition with the dinosaurs. These early mammals were almost all **herbivores**, **insectivores**, and **frugivores** (fruit eaters). SEE ALSO Geological Time Scale.

nocturnal active at night

herbivores animals who eat plants only

insectivores animals who eats insects

frugivores fruit-eating animals

Leslie Hutchinson

Bibliography

Lane, Gary, A., and William Ausich. *Life of the Past*, 4th ed. Upper Saddle River, NJ: Prentice Hall, 1999.

K/T Boundary

Toward the end of the Cretaceous period, many species of marine organisms became extinct. Land dinosaurs completely disappeared, along with flying reptiles, sea reptiles, and ichthyosaurs. Other land reptiles were little affected. Most species of turtles, crocodilians, lizards, and snakes survived. Amphibians and mammals were only mildly affected.

Overall there was a major, worldwide decrease in the number of species of plants and animals. This drop in the number of species is one of the events that signaled the end of the Cretaceous period and the beginning of the Tertiary period. The transition between the two periods is known as the K/T boundary ("Cretaceous" in German is *die Kreidezeit*).

Determining whether all the species died out in a few years or over millions of years has proved to be a difficult problem for geologists and paleontologists. Attempts to pinpoint the time of the K/T boundary event result in a margin of error of at least one million years, which means that it could have taken place one million years earlier or one million years later. Although one million years is a very short time on the geologic time scale, such a margin of error indicates that all the species may not have died out at the same time. In any case, instantaneous events are very rare and usually do not affect more than a small region. For these reasons, most geologists assumed the K/T event resulted from a gradual process, such as global cooling.

An alternate to the hypothesis of extinction by a gradual process has been suggested. A group of paleontologists has proposed that the extinction may have been due to a single, catastrophic event. The American geologist Walter Alvarez first discovered evidence for this event. While conducting research near Gubbio, Italy, in the late 1970s, Alvarez discovered an abnormally high concentration of the rare element iridium in a layer of rock at the K/T boundary. The iridium anomaly, or spike, has been found all over the world in layers of rock dating to the same time. It is called an iridium spike because on a graph of iridium concentration versus time, the concentration near the time of the K/T boundary is sharply higher than in adjacent rock layers. The iridium concentration is at least twenty times more than normal and is even greater at some locations. The iridium spike seems to mark one of those rare, catastrophic events that took place worldwide.

Because meteorites often contain high concentrations of iridium, Alvarez and his father, American physicist Luis Alvarez, suggested an extraterrestrial origin for the iridium. If the iridium concentration at the K/T boundary resulted from a collision at that time between Earth and an asteroid, the dust from the collision would have substantially reduced the amount of sunlight available for plants to carry out **photosynthesis**. The plants would eventually die, the large plant-eating dinosaurs would starve, and the meat-eating dinosaurs that preyed on the plant-eaters would also starve.

photosynthesis the conversion of sunlight to food

However, the fossil record does not show a sharp decrease in the number of large land dinosaurs, as would be expected after an impact large enough to produce global cooling. Instead, the fossil record indicates a gradual decrease in the number of species of large land dinosaurs over millions of years. There is also no marked decrease in the number of land plants. Therefore, the asteroid impact theory may be inadequate in explaining the decrease in large land dinosaurs.

The asteroid theory is generally accepted as the most likely explanation of the iridium spike and may be the best explanation for the extinction of marine organisms. The foraminifera, ammonites, coccolithophores, and other species did disappear suddenly at precisely the right time. However, there are several competing hypotheses and it is not certain that the asteroid impact alone can account for dinosaur extinction. A major difficulty of all hypotheses is the selectivity of the extinctions. Why were dinosaurs wiped out while other land reptiles were little affected?

It is possible that the mass extinctions at the K/T boundary may be due to a combination of asteroid impact and other factors. The land animals may have died out as a result of seafloor spreading, **continental drift**, and volcanism occurring around the same time; while the marine organisms were affected by the impact. Shifting oceanic circulation patterns due to continental drift may have caused climatic changes and changes in sea level. SEE ALSO CRETACEOUS; GEOLOGICAL TIME SCALE; TERTIARY.

continental drift movement of the continents over geologic time

Elliot Richmond

Bibliography

Alvarez, Luis W., et al. "Extraterrestrial Cause for the Cretaceous-Tertiary Extinction: Experimental Results and Theoretical Interpretation." *Science* 208 (1980):1095–1108.

Gore, Rick. "Extinctions." *National Geographic* 175 (1989):662–699.

Russell, Dale A. "The Mass Extinctions of the Late Mesozoic." *Scientific American* 246 (1982):58–65.

Stanley, Steven M. "Mass Extinctions in the Ocean." *Scientific American* 250 (1984):64–72.

Keratin

Keratin is a highly durable protein that provides structure to several types of living tissues. It is a major component of mammalian hair and hooves, mammalian and reptilian nails and horns, reptile and fish scales, bird feathers, bird beaks, and the outermost layer of skin in most animals. Keratin provides a tough, fibrous **matrix** to these tissues. An important quality of keratin is its ability to flex in multiple directions without tearing.

matrix the nonliving component of connective tissue

Keratin's microscopic structure is the key to its durability and flexibility. The molecules of this protein twist into coils called alpha helices and

The beak of a bald eagle contains keratin.

contain many disulfide bonds (bonds between pairs of sulfur ions). Disulphide bonds are particularly stable and can resist the action of proteolytic enzymes, which specialize in breaking apart proteins. Keratin is also insoluble in water. When human hair is straightened or curled in a beauty salon, special chemicals must be used to break the disulfide bonds. The breaking and subsequent reconfiguration of these bonds allows the hair to change shape. The final shape depends on the relative positions of the sulfur ions in the new bonds.

The protective structures containing keratin form through a process called keratinization. In keratinization, precursor cells to the specific tissue types first migrate from the germinal layer to their target location. Then fibers of keratin gradually invade the precursor cells, displacing cell **organelles** such as the nucleus and **mitochondria**. These organelles are **resorbed** and are not present in the mature tissue type. The differentiated, mature keratinized tissue is nonliving and incapable of sensory perception. Keratinized structures grow through the additional migration of differentiating **germ cells**, not through the division of the existing tissue cells.

organelles membrane bound structures found within a cell

mitochondria organelles in eukaryotic cells that are the site of energy production for the cell

resorbed absorption of materials already in the body

germ cells egg or sperm cells; gametes

Keratinized tissues can form onto a base of skin or bone. Keratinized structures such as hairs and fingernails are embedded in the skin. Calluses on hands or feet are mounds of keratin which have been created in response to repeated stress on a particular region of skin. Other structures, such as the horns of a bull, are rooted onto a bony core.

Keratinized structures take on a wide range of characteristics depending on the thickness of the protein layers. Hair is thin and flexible, whereas scales are often tough and inpenetrable. Keratin is also present in sharp structures such as spines and porcupine quills. SEE ALSO BONE; CHITIN.

Judy P. Sheen

Bibliography

Balin, Arthur K., Loretta Pratt Balin, and Marietta Whittlesey. *The Life of the Skin: What It Hides, What It Reveals, and How It Communicates.* New York: Bantam Books, 1998.

Fraser, R. D. B., T. P. MacRae, and G. E. Rogers. *Keratins—Their Composition, Structure and Biosynthesis.* Springfield, IL: Charles C. Thomas, 1972.

Keystone Species

ecosystems self-sustaining collections of organisms and their environments

equilibrium a state of balance

All **ecosystems** on Earth are formed of a delicate balance of species. When an ecosystem is at **equilibrium**, the relative numbers of organisms within each species remain stable. A food web is a graphical representation of the trophic (food-based) interactions between species. Arrows are drawn between every species and its prey, and the sum of these interconnections forms a complicated tangle of lines. In 1966 Robert Paine, an American ecologist, conceived of the idea that not every interaction in the food web is equally important in maintaining the equilibrium of the ecosystem.

population a group of individuals of one species that live in the same geographic area

Some species can dramatically increase or decrease in **population** and have little effect on the gradual return of a static-state ecosystem. This means that if this species propagates or dies off in large numbers, the relative population sizes of other species in the community will be skewed, but the community will eventually return to its original state.

habitat physical location where an organism lives in an ecosystem

Alternatively, some species have much greater importance to the community. A sizable change in the population of this type of species causes a cascade of direct and indirect effects leading to the collapse of the food web and possible loss of **habitat**. The few web links that hold such a critical importance are called strong interactions, and the species responsible for this effect are keystone species.

For example, one species of shore crab in the tropical dry forest of Costa Rica feeds primarily on tree saplings. The saplings that are distasteful to crabs grow into mature trees and eventually dominate the landscape. The environment provided by a forest of these trees is relatively open compared to the denser off-coastal forest, and this environment attracts particular animal species that like open forests, such as howler monkeys, coatis, and tapirs.

If the crab colony were to suddenly become extinct, the forest would recover its dense heterogeneous character because the saplings of invasive trees would no longer be cut back. Those animals that depend on the open forest ecosystem would languish, and could undergo local extinction.

Keystone species were considered by Paine to be top predators. He based this definition on the observation of a tidal ecosystem at Mukkaw Bay on the coast of Washington, in which the diet of a particular species of starfish included several secondary predators (when a carnivore feeds on other carnivores, these prey are called secondary predators). In Paine's example, the secondary predators were in direct competition. Paine observed that removing the dominant starfish from an experimental plot increased competition among these secondary predators. Their populations increased because the top predator was no longer killing them off, and thus they were able to kill off more of their own prey, which were lower on the food chain.

As a result, the populations of the remaining species fluctuated rapidly. After two years, the species diversity, defined as the number of species per area of land, had decreased from fifteen to eight. This effect showed how the top predator's existence was keeping the other species in check. By feeding on the competing secondary predators, the keystone starfish had prevented them from devastating populations of species lower down the food chain.

When the starfish was removed, the food web was thrown into chaos. Note that the keystone species is not the dominant species—it does not have the largest number of individuals in the ecosystem. By definition its influence must be far larger than its population can account for.

Since Paine's landmark study, species of other **trophic levels** have been described as keystone, and many of them are not top predators. Animals such as beavers are considered to be keystone because they engineer the environment. Beavers build dams in rivers and streams that create large bodies of still water. Pond-dwelling animals and plants may then colonize the new environment. If beavers were removed, the environment they created would collapse. The dam would eventually break apart and the entire pond food web would be disrupted.

trophic levels division of species in an ecosystem by their main source of nutrition

Another type of keystone species is an exotic, or introduced, species. This is a foreign organism that enters a new habitat and disrupts the existing food web. One example of this is the spread of introduced kudzu in the Atlantic region of the United States. Kudzu is a vine native to desert habitats that is known to decrease erosion of sand dunes. After being imported into the United States in 1876 for ornamental gardens, kudzu was adapted to control erosion during the Great Depression of the 1930s. Kudzu quickly

adapted to the plentiful water and rich soil of the southern United States, in the process choking out native shrubs, flowers, and trees. Because trophic interactions with other plants and animals in the area were so greatly affected, kudzu is considered to be keystone.

pathogens disease-causing agents such as bacteria, fungi, and viruses

Alternatively, some consider certain **pathogens** to have a keystone effect, such as the canine distemper virus's effect on lion populations in Serengeti National Park in Africa. This occurred in 1994, when the domesticated stray dogs living along the park boundaries in Tanzania and Kenya transmitted canine distemper virus to the wildlife. This resulted in thousands of deaths within the lion population. The disease also affects leopards, cheetahs, tigers, raccoons, coyotes, wolves, foxes, ferrets, skunks, weasels, mink, badgers, hyenas, and jackals.

Paine's narrow definition has since been broadened to include mutualists (animals that provide benefits for and receive benefits from another species), pathogens (disease-causing microorganisms), parasites, and many more feeding strategies than merely top predator. Also in the 1960s, researchers defined "functional group," a collection of many species that collectively perform the role of a keystone species.

Human beings cannot be called a keystone species because our influence on nature is not disproportionately large compared to our abundance (population size). Our cities, roads, and technologies, however, have altered nearly every ecosystem on Earth. Because species diversity is a strong signifier for a healthy habitat, it is important for humans to understand how to preserve the greatest species diversity within remaining natural habitats. This requires knowledge of how to stabilize a high species diversity in parklands and nature preserves.

The largest grouping of endangered species in the United States consists of primary predators, such as large predatory cats, bears, and eagles. If, as Paine suggested, many of these top predators are keystone, then their extinction will create turmoil in the relative numbers of remaining species. The overabundance of deer and raccoons in urban areas of the United States reflects this destructive trend. SEE ALSO ECOSYSTEM; INTERSPECIES INTERACTIONS.

Rebecca M. Steinberg

Bibliography

Diamond, Jared, and Ted J. Case, eds. *Community Ecology*. New York: Harper and Row, 1986.

Nabhan, Gary Paul, and John L. Carr. *Ironwood: An Ecological and Cultural Keystone of the Sonoran Desert*. Washington, D.C.: Conservation International, 1994.

Power, Mary E. et al. "Challenges in the Quest for Keystones." *Bioscience* 46 (1996):610–620.

Roughgarden, Jonathan. *Primer of Ecological Theory*. Upper Saddle River, NJ: Prentice Hall, 1998.

Kingdoms of Life

Life on Earth originated between 3.5 and 4 billion years ago. Since then millions of different organisms have evolved (and most have gone extinct). Faced with such a multitude and diversity of organisms, biologists have looked for ways to classify all these organisms into different groups to make it easier to study them. But what criteria should they use for grouping? And how big or small should the groups be?

The most meaningful way of grouping organisms is based on how they are related. In this way, group membership will reflect the organisms' common evolutionary history. This means that scientists want to group organisms that share a common ancestor. In addition, they want to show characteristics that unite all group members with each other but that also distinguish group members from nongroup members. For example, all mammals have hair and milk glands, characteristics unique to mammals. The number of groups and the number of organisms within a group depends on the grouping criteria and whether the emphasis is on how organisms are different or how they are the same (this is often referred to as the "splitters" vs. "lumpers" approach). There is really no incorrect way of grouping organisms as long as the grouping criteria are clearly stated and strictly followed.

Systematists (scientists that study the classification of organisms) have traditionally considered the kingdom to be the highest and most inclusive category. However, deciding exactly how many kingdoms to recognize had been a source of controversy until 1969, when Robert H. Whittaker of Cornell University introduced a five-kingdom system that became popular with most biologists. Whittaker's five kingdoms are Monera, Protista, Plantae, Fungi, and Animalia. One kingdom, Monera, contains all the **prokaryotes**, and the other kingdoms contain different groups of eukaryotes. However, work done in the 1980s by Carl R. Woese of the University of Illinois on the genetic makeup of cells seems to favor a six-kingdom system that divides Monera into two kingdoms, Bacteria (Eubacteria) and Archae (Archaebacteria).

prokaryotes single-celled organisms that lack a true cell nucleus

Bacteria and Archae are both prokaryotes, but when researchers compared their ribosomal RNA sequences, they found that Archae are more closely related to eukaryotes than they are to other prokaryotes. It appears that eukaryotes evolved from an Archae-like ancestor and subsequently took up **genes** from Bacteria (e.g., purple bacteria, cyanobacteria), thus acquiring **mitochondria** and chloroplasts.

genes segments of DNA located on chromosomes that direct protein production

mitochondria organelles in eukaryotic cells that are the site of energy production for the cell

Bacteria live in many different environments. This kingdom includes many **pathogens**, including *Salmonella*, which causes food poisoning, but also many economically important species such as *Lactobacillus*, which is used to make yogurt; *Rhizobium*, which "fixes" atmospheric nitrogen for plants to use; and *Streptomyces*, which is a source of many antibiotics. In contrast, Archae, including the methanogens, halophils, and thermophiles, live in extreme environments that are hot, salty, or **acidic** such as hot springs or deep sea vents. One Archae, a thermophil, is the source of a heat-resistant **enzyme** that is widely used in molecular biology.

pathogens disease-causing agents such as bacteria, fungi, and viruses

acidic having the properties of an acid

enzyme a protein that acts as a catalyst to start a biochemical reaction

The eukaryotic Plantae, Fungi, and Animalia kingdoms contain mostly multicellular eukaryotes that differ in their structures, modes of nutrition, and life cycles (before reproduction). For example, Plantae (mosses, ferns, conifers, flowering plants) have cell walls containing cellulose and are **autotrophs**, which means they make their own food from carbon dioxide and an energy source such as sunlight. In contrast, both Fungi (yeasts, mushrooms, truffles, bread molds) and Animalia (jellyfishes, sponges, worms,

autotrophs organisms that make their own food

Kingdom	Type of Organism	Characteristics
Monera	Bacteria	Spherical, rodlike, or spiral forms
	Blue green algae	Photosynthetic
Protista	Diatoms	Single-celled; photosynthetic
	Silicoflagellates	
	Coccoliths	
	Dinoflagellates	
	Animal flagellates	Similar to euglenoids but lack chlorophyll
	Ciliated protozoan	
Fungi	Slime molds	Multinucleated organisms; parasitic; heterotrophic; have cell walls
	Schizomycophyta bacteria	
Plantae	Mosses	Have cell walls containing cellulose; autotrophic
	Ferns	
	Conifers	
	Flowering plants	
Animalia	Jellyfishes	Heterotrophic; no cell walls
	Sponges	
	Worms	
	Snails	
	Insects	
	Fishes	
	Amphibians	
	Reptiles	
	Birds	
	Mammals	

Five-kingdom classification system.

heterotrophs organisms that do not make their own food

snails, insects, fishes, amphibians, reptiles, birds, mammals) are **heterotrophs**, which means they get their energy by eating other organisms. Fungi and Animalia differ in that Fungi secrete digestive enzymes and then absorb the digestive juices, while Animalia ingest other organisms. In addition, Fungi have cell walls, Animalia do not.

The kingdom Protista contains a wide variety of organisms, ranging from single-celled autotrophs (diatoms, dinoflagellates) and heterotrophs (amoebas, ciliates) to colonially living heterotrophs (slime molds) and large multicellular autotrophs (algae such as kelp and seaweed). Protists were the first eukaryotes to evolve, and members of this group gave rise to the other eukaryotic kingdoms. The diversity that we find among the organisms in the kingdom Protista stems partly from the fact that Protista is what systematists call a "wastebasket" kingdom. This means that any organism the systematists cannot assign to one of the other kingdoms (using the above grouping criteria) is assigned to the Protista. This also means that with further work and the establishment of new grouping criteria, we may see a further division of the Protista into several new kingdoms in the not-too-distant future. Science is an ongoing process! SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Kathrin F. Stanger-Hall

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman Inc., 1999.

Purves, William K., Gordon H. Orains, and H. Craig Heller. *Life: The Science of Biology*, 4th ed. Sunderland, MA: Sinauer Associates Inc., 1995.

Doolittle, W. Ford. "Uprooting the Tree of Life." *Scientific American* 282, no. 2 (2000):90–95.

Lamarck, Jean-Baptiste

Botanist
1744–1829

Jean-Baptiste Lamarck was born on August 1, 1744, in Bazentin-le-Petit, France. He died on December 18, 1829. He is best known for his theory on evolution, which stated that acquired traits can be inherited. Charles Darwin later challenged this theory. Lamarck also was the first scientist to define animals as either vertebrates (having backbones) or invertebrates (those without).

Lamarck came from a long line of military horsemen. At the age of nineteen he left a school run by Jesuits (a religious order) to join the army. While serving he became interested in the plants along the Mediterranean Sea. Resigning from the army after an injury, Lamarck began to study medicine, but then switched his interest to **botany**. He studied under the French botanist Bernard de Jussieu at the royal botanical gardens in Paris. After years of studying and collecting, he published a three-volume work on the plants of France in 1778. This gained him recognition, and in 1781 he was put in charge of the royal gardens in Paris.

botany the scientific study of plants

In the 1790s Lamarck changed his interest from plants to animals and soon developed a system for classifying invertebrates. He appears to have been the first scientist to relate fossils to the living creatures to which they are most similar. When the Museum National d'Histoire Naturelle was founded in 1793, Lamarck was placed in charge of the invertebrates. Lamarck was one of the founders of the modern concept of the museum collection.

genetics the branch of biology that studies heredity

From his studies on plants and animals, Lamarck developed his theory of evolution. He believed that plants and animals change their forms to adapt to their environment, and that their young inherit these changes. He thus believed, for example, that the forelegs and necks of giraffes have become longer due to the way they eat. These acquired traits would be passed on to following generations. Lamarck presented his ideas in the famous *Philosphie Zoologique* (1809). His theory, not unreasonable for its time, was later disproved by discoveries in **genetics** in the early 1900s and rejected by most scientists. However, the Soviet Union embraced Lamarck's theory in the Stalin era. This set that nation back in genetics until the 1960s.

Jean-Baptiste Lamarck's theory of evolution was later challenged by Charles Darwin.

Another area of interest for Lamarck was the weather. He was the first scientist to try to forecast it. He published an annual weather report from 1799 to 1810. He is believed to have named the various types of clouds: cirrus, stratus, cumulus, and nimbus. SEE ALSO ADAPTATION; BIOLOGICAL EVOLUTION.

Denise Prendergast

Internet Resources

Jean-Baptiste Lamarck (1774–1829). Museum of Paleontology, University of California, Berkeley. <http://ucmp.berkeley.edu/history/lamarch.html>.

Leakey, Louis and Mary

Anthropologists
Louis Leakey 1903–1969
Mary Leakey 1913–1996

Louis and Mary Leakey were a husband-and-wife anthropology team that contributed much to the modern understanding of human origins. Louis Seymour Bazett Leakey was born in 1903 outside Nairobi, Kenya. He was sufficiently integrated into the local life there that he was accepted as one of the tribe of the Kikuyu people and learned their language first. To fulfill the foreign-language requirement at Cambridge University, Leakey was permitted to test himself on Kikuyu, as nobody else was qualified. At Cambridge, he specialized in archaeology and anthropology, receiving a Ph.D. in 1930. He discovered what he considered to be the oldest known human fossils in 1931, but a combination of poor notes and a shoddy understanding of geology prevented him from reliably identifying them.

This error precipitated a series of strong criticisms of Leakey's methods from a number of sources. His former colleague Martin Pickford suggested Leakey "broke records in misreporting the discovery context of important fossils and stone tools" over the course of forty years. Nevertheless, Leakey conducted numerous significant digs at Olduvai Gorge and was the first to characterize *Homo habilis*, a human ancestor. Mary Leakey discovered "Zinjanthropus" (*Australopithecus boisei*), an extinct hominid species that brought them worldwide fame. Louis disdained what he perceived to

The Leakeys work at an excavation site in central Africa in 1961.

be unnecessary measuring and statistical analysis by his contemporaries; he was much more interested in experiments of an occasionally crackpot nature. Naked, he charged a pack of hyenas to steal their prey and chewed off a hunk of the carcass to see if a modern human could do so. He thought zebra fat could cure tuberculosis; he wanted to flood the Sahara and make an ocean.

By contrast, Mary, who never earned an advanced degree, was a much more meticulous scientist and eventually gained greater respect in the field. They had met while she was illustrating his *Adam's Ancestors*. As a couple they encouraged Jane Goodall and Dian Fossey in primate research. Together the Leakeys established that the upright posture of later protohumans led to free hands, and therefore to tool making. Louis began to travel more from Africa, lecturing and womanizing despite being in poor health, while Mary stayed behind in Olduvai Gorge and Nairobi. The pair grew distant. Louis died in 1969, and Mary died in 1996 at the age of 83.

Ian Quigley

Bibliography

Leakey, Mary. *Disclosing the Past.* Garden City, NY: Doubleday, 1984.

Pickford, Martin. *Louis S. B. Leakey: Beyond the Evidence.* London: Janus, 1997.

Learning

The need for experimental proof is a key part of the scientific definition of learning. As outside observers of animal behavior, humans are practically incapable of understanding which cognitive processes, if any, lead to the production of a certain animal behavior. For example, a pigeon may be trained to type the letters "f-o-o-d" on a typewriter when it is hungry.

Although we may be tempted to conclude that the pigeon has learned a new word, this is unlikely. There may be many explanations for the pigeon's behavior. Only with carefully designed experiments and a general learning theory, we can begin to dissect exactly what motives cause the animal to behave this way. Although we may observe animals performing complex tasks in the wild, we cannot conclude that the animal has learned without rigorous experimental tests in a controlled setting.

Even in a strictly monitored experiment, the results of a learning test can be inconclusive. The general model for such experiments was to train an animal to perform a task. This training was accomplished by choosing a natural behavior of an animal and modifying or encouraging that behavior with a treat and a signal. Eventually, the signal will cause the animal to perform that behavior in order to receive the treat.

In other words, the unconditioned **stimulus**, or natural behavior of the animal, is paired with a conditioned stimulus, the chosen signal. When the animal responds to the conditioned stimulus with the appropriate behavior, it is rewarded with a treat, which leads to an eating reward. Thus, a rat that displays the normal ratlike behavior of rearing on its hind legs is suddenly rewarded with a piece of fruit every time it performs the behavior. At the

stimulus anything that excites the body or part of the body to produce a specific response

Two young male hippopotamuses play fight. The lessons learned through play will benefit them in their adult lives.

same time that it rears, a red light flashes at the side of the cage. Eventually, flashing the red light will cause the rat to rear on its hind legs, supposedly because it expects to receive its treat. In this case, the rearing behavior is the unconditioned stimulus, the red light is the conditioned stimulus, and the fruit is the reward.

Psychologists and cognitive biologists have long argued over what exactly this hypothetical rat is learning. It is possible that the rat equates the conditioned stimulus, abbreviated as CS, with the treat reward, abbreviated as R. If this is true, then the rat learns that the flashing light means that treats are coming.

Alternatively, the rat may understand that rearing, which is the unconditioned stimulus (US), leads to a treat reward; in this case the light tells the rat when to rear, but has no real meaning with regards to the treat. Both of these examples assume that the rat is associating the stimulus, S, with the reward, R. This is called S-R learning. Another explanation is that the rat learned that one stimulus—rearing or the light—leads to another stimulus, the appearance of the treat.

The subtle difference between this interpretation and S-R learning is that in this case, appearance of the food is not the rat's reward. Instead, appearance of the treat is merely another stimulus that causes the rat to eat, and the actual consumption of the food is the rat's reward. Because the treat is considered another stimulus in this theory, it is referred to as S-S learning.

A class of scientists known as behaviorists believed that animals are defined solely by their behaviors, and that behaviors are determined entirely by environmental cues. Thus every animal is born with the ability to learn any new task. Two of this field's main proponents were the psychologists B. F. Skinner and Ivan Pavlov. Pavlov discovered what was called classical conditioning, a method of pairing a conditioned and an unconditioned stimulus so that eventually the conditioned stimulus alone elicits the response.

His famous experiment tested a dog salivating when food is presented. If a bell is rung at the same time the food is presented, every time, eventually the dog will salivate to the sound of the bell even in the absence of food. Skinner used similar principles to describe the behavior of humans. He proposed the theory of operant conditioning. According to this theory, the animal performs a wide variety of activities in its daily life, and some of these activities are rewarded by a reinforcing stimulus. This reinforcement increases the effect of the operant, the behavior directly preceding the reinforcing stimulus. Operant conditioning is widely used to train animals, but it is also a theory on their methods of learning.

Ethologists such as Nikolaas Tinbergen disagreed with the behaviorists' opinion that the mechanisms of learning are the same for all animals. Ethologists believe that natural animal behaviors are innate, meaning that the animal is born with a neural system that promotes certain species-specific behavior. This is why animals tend to produce species-specific **vocalizations** and behaviors, even when they are raised in very foreign environments.

vocalizations sounds used for communication

Tool use is one example of an innate behavior for several organisms, such as the male satin bower bird of Australia and New Zealand, which constructs elaborate abstract designs out of twigs, leaves, and dirt to attract the female. He decorates these sculptures by crushing berries and fruits for their pigmented juice and then painting the structure using a wad of bark as a paintbrush. Elaboration of tool use is more easily taught to those species that have the innate tendency to use tools.

The combination of behaviorist and ethologist influences on the study of learning have shaped modern psychology. Animals are still used to test how humans learn, but unique species traits are now taken into consideration when interpreting the data. SEE ALSO Behavior; Tool Use.

Rebecca M. Steinberg

Bibliography

Dachowski, Lawrence, and Charles F. Flaherty. *Current Topics in Animal Learning: Brain, Emotion, and Cognition*. Hillsdale, NJ: Lawrence Erlbaum Associates, 1991.

Lutz, John. *An Introduction to Learning and Memory*. Prospect Heights, IL: Waveland Press, Inc., 2000.

Schmajuk, Nestor, and Peter C. Holland, eds. *Occasion Setting: Associative Learning and Cognition in Animals*. Washington, DC: American Psychological Association, 1998.

Levi-Montalcini, Rita

Italian-American neurologist
1909–

Rita Levi-Montalcini, born in Turin, Italy, is a prominent neurologist who discovered nerve-growth factor (NGF), a substance that controls how many

Rita Levi-Montalcini discovered nerve-growth factor.

regeneration regrowing body parts that are lost because of injury

cells make up the adult nervous system. This 1952 discovery has become an important clue to how life starts as a single embryonic cell and then marvelously differentiates into a complex organism made up of many different cell types. Levi-Montalcini's work has also contributed to the understanding of neurological diseases such as Alzheimer's and Parkinson's, tissue **regeneration**, and the mechanisms of cancer.

Before the discovery of NGF, little was known about how organs signal developing nerve cells to link up with them or how messenger chemicals tell nerve cells when to grow and when to stop growing. Scientists now know of several hundred signals that affect cells and organs, and growth factors can be used to speed up burn healing and to diminish the side effects of the chemotherapy and radiation therapy that are used to combat cancer.

Levi-Montalcini's discovery of NGF and her other scientific work are nothing short of remarkable considering her tumultuous life circumstances. Her childhood was dominated by an unreasonable father who refused to acknowledge her love of science. Rather than encouraging her to pursue science and math courses, he insisted Levi-Montalcini attend finishing school where, much to her disgust, she had to study childcare, etiquette, and marriage. After completing finishing school, and largely against her father's wishes, Levi-Montalcini hired a tutor to teach her math, science, Latin, and Greek for eighteen months until she was able to pass the entrance exam to the University of Turin medical school. In 1936 she completed medical school, specializing in neurology and psychiatry.

After graduation, Levi-Montalcini accepted a research position at the university. After only three short years, she was forced to leave when the fascist anti-Semitic laws that governed Italy at the time drove her away. Not to be deterred, Levi-Montalcini constructed a crude home laboratory using scrap materials and continued her research under secretive conditions. After World War II, she moved to the United States where she continued her research at Washington University in St. Louis, Missouri, from 1947 to 1981. In 1981 she returned to Italy, where she still lives.

In 1986 Levi-Montalcini was awarded the Nobel Prize for physiology or medicine, an award she shares with her American coworker at Washington University, the biochemist Stanley Cohen. She is also the founder of the Laboratory of Cellular Biology, one of the largest biological research centers in Italy.

Stephanie A. Lanoue

Bibliography

McGrayne, Sharon. *Nobel Prize Women in Science.* Chicago: Birch Lane Press, 1996.

Random House Webster's Dictionary of Scientists. New York: Random House, 1997.

Life History Strategies

Among biological organisms, there is a continuum in life history strategies between what are referred to as *r*-selected species and *k*-selected species. Life history strategy is correlated with many aspects of an organism's reproductive strategy and life history, as well as with demographic variables such as generation time and life span, and **population parameters** such as **population density** and **population dynamics**. Where individual species fall on the *r*-*k* continuum is largely determined by the environment in which they live.

The variables *r* and *k* in *r*- and *k*-selection come from the logistic equation for population growth. This equation describes how population density changes over time. In the initial phase, population growth is very rapid and largely dependent on the variable *r*, which represents the intrinsic rate of natural increase of a species. Mathematically, *r* is the birth rate plus the immigration rate, minus the **death rate** and the emigration rate. A population grows rapidly in its initial phase because there are abundant resources, and consequently little or no competition between individuals. Thus, *r*-selected species exist in circumstances where they are often at this stage of rapid growth.

population parameters a quantity that is constant for a particular distribution of a population but varies for the other distrubutions

population density the number of indiduals of one species that live in an given area

population dynamics changes in a population brought about by changes in resources or other factors

death rate a ratio of the number of deaths in an area in a year to the total population of the area

The *k* refers to the maximum density at which a population is able to exist in a given environment, and is called the carrying capacity of that environment. The value of *k* depends on the resources available. Once population densities are close to the **carrying capacity**, growth slows and population density levels off at or around *k*. Because resources are no longer in abundant supply in this saturated environment, there is significant competition between the individuals of a population. Species that are *k*-selected describe those for which the population density is usually close to the carrying capacity. Differences between *r*- and *k*-selected species exist over a wide variety of traits.

carrying capacity the maximum population that can be supported by the resources

Those species that are *r*-selected exist well below the carrying capacity of their environment. This may be a consequence of either **biotic** or **abiotic** qualities of the environment. For example, many *r*-selected species are associated with unstable environments that alternate between periods of abundance and periods of high mortality. So long as resources are abundant, populations grow exponentially. Then, the population is decimated and the cycle begins again. On the other hand, population densities may remain well below the carrying capacity of an environment as a consequence of biological factors such as predation.

biotic pertaining to living organisms in an environment

abiotic nonliving parts of the environment

Because *r*-selected species exist well below the carrying capacity of the environment, there is generally little competition between individuals. In addition, mortality may depend largely on chance. Under these circumstances, the production of high-quality offspring may not necessarily pay off. It is more important to produce a large number of offspring as quickly as possible, thus increasing the probability that at least a few of them will survive long enough to contribute to the next generation. The emphasis is on the quantity of offspring produced rather than on their quality.

Features associated with *r*-selected species include small size, a short generation time, reproduction early in life, and the production of large numbers of offspring in which comparatively little investment is made. Some *r*-selected species are **semelparous**, meaning that individuals reproduce in one big reproductive bout and then die. This is sometimes referred to as big-bang reproduction.

semelparous describes animals that breed only once and then die

In terms of life history, *r*-selected species exhibit what is called a Type III survivorship pattern, with very high mortality in the early stages of life,

and only a very small proportion of individuals surviving into adulthood. The population patterns of *r*-selected species often show periods of rapid, **exponential growth**, followed by sudden crashes. Often, *r*-selected species are the first colonizers of a new habitat.

exponential growth a population growing at the fastest possible rate under ideal conditions

K-selected species, on the other hand, generally occupy comparatively stable environments. Because there are long periods of environmental stability, populations are able to increase in size until population densities are close to the carrying capacity *k* of the environment.

In these saturated environments, crucial resources are in short supply, and there is intense competition between individuals of the population. As a result, competitive ability becomes very important. The number of offspring produced becomes less important, while the quality matters more. (There is a necessary trade-off between the quality and quantity of offspring produced, because of the limited resources that a parent is able to acquire and process.)

In *k*-selected species, individuals produce fewer, high-quality offspring that will perform and survive better in a competitive world. This is associated with such traits as larger body size, longer generation time, slower development, and reproduction later in life. *K*-selected species also often exhibit parental care.

K-selected species are more likely to be **iteroparous**, that is, to reproduce in numerous bouts. They also tend to invest in survival more than *r*-selected species, and may generally be more intelligent. Unlike *r*-selected species, *k*-selected species have a Type I survivorship curve, where survival early in life is relatively high and most individuals live to a comparatively late age. Population sizes in *k*-selected species are relatively stable, at or near the carrying capacity of the environment. Unlike *r*-selected species, *k*-selected species are not effective colonizers. Instead, they tend to be found in climax communities (stable, long-established ecological communities).

iteroparous animals with several or many reproductive events in their lives

It is important to remember that there is a continuum between *r* and *k* strategies among biological organisms, and that it sometimes does not make sense to try to pigeonhole species as one or the other. Mice, for example, seem to be *k*-strategists compared to clams, which are perpetually emitting tiny eggs. Mice are also characterized by parental care.

However, when compared to other species of mammals, mice are closer to the *r*-strategist extreme. Their generation time is shorter than that of most other mammals, as is their life span and time to reach reproductive maturity. In addition, mice have much larger litters than most mammals.

Small mammals such as rodents and rabbits are often closer to the *r*-selected extreme, while larger mammals such as humans and elephants are more *k*-selected. Among plants, weedy species are *r*-selected, while larger species with longer life spans, such as trees, are *k*-selected.

Jennifer Yeh

Bibliography

Alcock, John. *Animal Behavior*, 4th ed. Sunderland, MA: Sinauer Associates, 1989.

Gould, James L., and William T. Keeton, with Carol Grant Gould. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Krebs, Charles J. *Ecology: The Experimental Analysis of Distribution and Abundance.* New York: Harper Collins College Publishers, 1994.

Pianka, Eric R. *Evolutionary Ecology.* New York: Addison Wesley Longman, 2000.

Linnaeus, Carolus

Botanist
1707–1778

Carolus Linnaeus was the founder of modern scientific methods for naming plants and animals.

Carolus Linnaeus was born on May 23, 1707, in Råshult, Sweden. He died on January 10, 1778. Linnaeus was the founder of the modern scientific method of naming plants and animals. He was the first person to name each living thing with two names: the genus (group) and the species (kind). It was Linnaeus who first gave humans the scientific name *Homo sapiens.* Linnaeus, the son of the parish pastor, showed an early love of flowers. By the age of eight he was nicknamed "the little botanist." Linnaeus studied at the universities of Lund and Uppsala. He was appointed lecturer in botany at Uppsala in 1730. Two years later, with fifty dollars given to him by the Royal Society of Science, he explored Lapland, walking nearly 1,600 kilometers (1,000 miles) over a five-month period. From this experience, he wrote *Flora Lapponica* (1737), a book that firmly established his reputation. In 1735 he received his degree in medicine from Uppsala. While in medical school, he had a small botanical garden and wrote careful descriptions of its plants. These notes formed the basis for his later books. In Holland, he published his work on classifying and naming various plants in *Systema Naturae* (1735), *Fundamenta Botanica* (1736), *Genera Plantarum* (1737), and *Critica Botanica* (1737). Linnaeus created a revolutionary advance by introducing a Latin binomial (two-name) system: each species received a Latin name with two parts (the genus and the species). Linnaeus also recognized other, broader classification groups that are still used today: order, class, and kingdom. His system allowed plants to be placed rapidly in a named category, which was extremely useful during the eighteenth century, when new plants were being discovered at a very fast rate. Linnaeus classified not only plants and animals but also minerals and the kinds of diseases known in his day.

In 1738 Linnaeus returned to Sweden, settling in Stockholm, where he was very successful as a practicing physician. In 1739 he married Sara Moraea, the daughter of a physician. Two years later, he was appointed to the chair of medicine at Uppsala, but after a year he transferred to a chair of botany there. His later years were spent teaching and writing books. In 1761 he was knighted by the Swedish government in recognition of his work. SEE ALSO BINOMIAL (LINNAEAN SYSTEM).

Denise Prendergast

Bibliography

Muir, Hazel, ed. *Larousse Dictionary of Scientists.* New York: Larousse Kingfisher Chambers Inc., 1994.

The New Encyclopedia Britannica, 15th ed. Chicago: Encyclopedia Britannica, Inc., 1993.

Internet Resources

Carl Linnaeus (1707–1778). University of California, Berkeley, Museum of Paleontology. <http://www.ucmp.berkeley.edu/history/linnaeus.html>.

Livestock Manager

Livestock managers take care of livestock on farms and ranches. Livestock include animals such as beef cattle, swine (pigs and hogs), goats, and sheep. The animals are raised and sold for food, their hides, or breeding purposes. On farms and ranches, the animals may graze in open pastures and be housed in barns or pens.

Animals need to be taken care of every day. Unless they are grazing, they must be fed and watered daily. Livestock managers must be sure their herds are healthy. They routinely examine the animals and may give them vaccinations and medicines. Barns and pens must be repaired and kept clean, and fences around grazing areas must be maintained. The livestock manager may be involved in the planting, harvesting, and storage of different food crops for the livestock. Other activities include branding animals for identification purposes and rotating animals from one pasture to another. Sheep must be routinely sheared so that their wool can be sold.

Livestock managers may also breed animals. This involves picking the best livestock to be bred, artificially inseminating the animals, assisting with the births of the offspring, and feeding and caring for both the parents and offspring. Records must be kept regarding the animals' weights, diets, birth records, and pedigrees. Computers are important for managing this type of data.

Becoming a livestock manager does not necessarily involve formal training or education. A person may acquire the necessary practical knowledge by working under more experienced persons on a farm or ranch. In grade and high school, it is good training to participate in livestock programs run by organizations such as 4-H. A livestock manager would benefit from a university degree. A bachelor's degree in agricultural sciences (the study of farming, producing crops, and raising livestock) with an animal science major provides a thorough understanding of raising livestock. Courses include those in animal sciences (breeding, nutrition, **genetics**), agriculture (entomology, natural resources, veterinary science), and business (economics, accounting, marketing).

genetics the branch of biology that studies heredity

Denise Prendergast

Bibliography

Internet Resources

Institute of Agriculture and Natural Resources. University of Nebraska at Lincoln. <http://www.ianr.unl.edu/ianr/anisci/anscdept.htm>.

Occupational Outlook Handbook 2000–01. <http://stats.bls.gov/ocohome.htm>.

Living Fossils

The history of life on Earth is deciphered through the examination of fossils. Fossils are inorganic remains of plants and animals that reveal the structure of certain parts of the organism. By examining the way structures change in certain organisms over time, the natural history of a particular group can be reconstructed. Many organisms do not have structures suitable for fossilization, like the soft body of a snail. However, some portions of the snail's body (the shell) are easily turned into fossils over time. Snail shells, millions of years old, are discovered when they are exposed near the surface of Earth. By studying these fossils it is possible to partially deduce what snails, or any other fossilized lineage of organisms, looked like over millions of years of change. Living fossils are divided into two categories. The first includes organisms that are believed to have changed very little over time and that still retain a close resemblance to their older extinct relatives. Examples of these types of organisms are found all over the world. A familiar example of a living fossil of this type is the **horseshoe crab**. The structure and body of the horseshoe crab is very similar to ancient fossils of **arthropods**. Arthropods evolved to become several distinct and large groups of organisms. Insects, **crustaceans** (crabs, shrimp, and lobsters), and a wide variety of additional animals are all descendants of the early arthropods. Although the living arthropods share several features of the ancient arthropods, they are also quite different in major body structures and functions.

horseshoe crab a "living fossil" in the class of arthropods

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

The horseshoe crab, however, is still very similar to the ancient forms of arthropods and helps us to understand how ancient arthropods looked and lived. This is why crabs are called living fossils. In the continental United States, the horseshoe crab is found only on the Atlantic seaboard.

Another example of this type of living fossil is the shark. Sharks do not appear to have changed very much over hundreds of millions of years. The rare fossils of sharks and their relatives show that they had bodies very similar to the species living today. Shark teeth are more commonly found as fossils since they are the only true bony part of the animal. By comparing the teeth of ancient and modern sharks it is possible to see that sharks also qualify as living fossils.

In the plant kingdom, the horsetail rush and the palmlike cycad are considered the last living relatives of their extremely ancient ancestors. The relatives of these plants are often found as fossils in regions where dinosaurs are discovered. They are believed to have been the food of some of these giant **herbivores**.

herbivores animals who eat plants only

In the marginal areas of the sea that are adjacent to the land there is a single remnant of a once flourishing group of **bivalves** called the **brachiopods**. They once lived in the oceans by the millions. There were numerous species and they were distributed over the coastal regions of the entire planet. The brachiopods lived for many millions of years and were as common as clams are today. However, only one simple species has survived. It is a small brachiopod called Lingula.

bivalves mollusks that have two shells

brachiopods a phylum of marine bivalve mollusks

The brachiopods appear initially to be similar to clams. In truth, however, they are quite different. Their soft tissues (internal organs) are nothing like those of a clam. In fact, brachiopods are so different from clams that they do not even belong in the same phylum, Molluska. If Lingula were not still living it is possible we would know very little about how the brachiopods lived, reproduced, or what their internal structure was like. This living fossil helps biologists to know a great deal about an ancient group that may have been a mystery.

The second category of living fossil is more exciting for researchers to discover. They are examples of species of plants or animals that were

A coelacanth is an example of a living fossil.

believed to have been extinct, but have been rediscovered in modern times. They are truly living fossils in that they are species of ancient organisms that have survived extinction by living in small pockets of land or ocean in which conditions may have been marginal, but livable. They have lived and reproduced continuously for hundreds of millions of years, but managed to escape notice until the last century. These organisms may once have been found throughout the world, but live today in very specific, geographically small areas.

vertebrates animals with a backbone

pectoral of, in, or on the chest

One of the most famous examples of this type of living fossil is the coelacanth. The coelacanth is a member of a group of fish called the Sarcopterygians, which are believed to be the ancestors of the land **vertebrates**. They are commonly referred to as the lobe-finned fish because their **pectoral** and pelvic (front and back) fins are very thick and sturdy and look more like heavy lobes than fins. These fish are long and round and often use these fins to rest the weight of their heavy bodies on the seafloor. The structure of the fins of the Sacropterygians is very similar to that of the bones of all land vertebrates, including humans, leading researchers to believe that these ancient fish were the ancestors of the amphibians and all other tetrapods.

Until the early part of the 1900s, all that was known about the coelacanths was derived from the study of fossils. However, on a winter day in 1938, fishermen in a boat near the mouth of the Chalumna River, off the coast of South Africa in the Indian Ocean, found a strange fish tangled in their nets. As the story goes, a British woman living in the region recognized the fish as rare and unusual. The woman purchased the fish and sent it back to Britain where it was declared a marvel. A lineage of fish believed to have been extinct for over 65 million years was still alive! Examining this extraordinary fish was like looking into the past. It had all the characteristics of the fossil species, but was different enough to be given its own species name. The scientific name for this fish is now *Latemeria chalumnae*.

The excitement from the discovery of this fish has still not subsided. About 200 additional *Latemeria* have been discovered since the first one

was caught. Scientists do not believe their **populations** are very large, and they apparently live in very deep water, which makes it difficult for researchers to study them. First, they are hard to find. Second, they are very difficult to keep in captivity for study because they require a high-pressure environment in order to remain alive. However, scientists are gradually **learning** more about this living fossil and are successfully keeping it alive in newly designed aquariums. In addition to this advance, another species, *Latemeria menandosis*, was recently discovered off North Sulawesi Island in Indonesia.

population a group of individuals of one species that live in the same geographic area

learning modifications to behavior from experience

One of the important things scientists have learned by studying these living fossils is that they apparently hatch their young inside their bodies which is unusual for most fish. This piece of information has lead to speculation about how these early ancestors of amphibians may have reproduced. This may have led to the ability to possibly breed out of water without endangering or drying out their eggs. Unfortunately for the coelacanth today, this means that they cannot reproduce in large numbers and need all the help from conservationists they can get.

It is believed that there are only a few hundred of these fish alive at present. They are still in danger of extinction and in need of protection. However, if any animal qualifies for the title of "living fossil," the coelacanth is probably the most famous.

Another living fossil was discovered during the last century. This fossil was of a plant believed to have been extinct since the demise of the dinosaurs. The plant belongs to a group called the gymnosperms, or naked seed plants. They are part of a group that includes plants that make seeds without a seed coat. The living fossil we are talking about is called *Gingko biloba*.

For hundreds of years this small tree was known only from fossil impressions in clay. Its **fossil record** extends back in time almost 200 million years and the tree was once common all over North America and Europe. The Ice Age is believed to have made environmental conditions too harsh for the plant's survival. In more recent times, the gingko was considered a sacred tree in China, and a group of Buddhist monks cared for and nurtured the tree in a remote valley in China. This small group of trees was discovered by explorers and reintroduced to the world. Unlike the coelacanth, the gingko has flourished since being rediscovered and today gingkoes are found flourishing all over the world. They are a link to the days of the dinosaurs and can be found as ornamental trees in many communities. The gingko has become so popular it is even included in some botanical medicines.

fossil record a collection of all known fossils

Additional examples of living fossils exist in many groups of animals and plants. Some **mollusks**, such as the *Nautilus*, were another amazing discovery of a remnant species of an ancient group of cephalopods. Other modern relatives of the cephalopods include the octopus and squid. It too was discovered in deep ocean waters off the coast of Indonesia. One of the intriguing aspects of the nautilus is that it represents a very primitive form of the ancient cephalopods. Animals derived from this ancient group are called ammonites and have extremely complicated and beautiful shells. Some grow to extremely large size compared to the nautilus and measure several feet across. They are believed to be carnivores of the deep oceans and able to

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses swim up and down columns of water in the ocean feeding on fish they encounter.

Until the nautilus was discovered, the Nautiloids were considered extinct and people knew very little about the soft tissue structure of these amazing animals. Biologists have created special environmental aquariums, and the nautilus has been successfully kept and bred. These specimens are providing scientists with increasing information about the life history of this group of mostly extinct animals.

No matter what the type, living fossils provide scientists with a window to the past. They help us understand how life on Earth evolved and what kinds of plants and animals inhabited the planet before humans. It is hoped that we will continue to discover more living fossils and learn more about the inhabitants of this planet. SEE ALSO GEOLOGICAL TIME SCALE; MORPHOLOGICAL EVOLUTION IN WHALES.

Brook Ellen Hall

Bibliography

Carroll, R. *Vertebrate Paleontology and Evolution.* New York: W. H. Freeman, 1982.

Stewart, W. *Paleobotany and the Evolution of Plants.* New York: Cambridge University Press, 1987.

Locomotion

Animals have evolved an amazing variety of ways to get around. There are animals with no legs; animals with one appendage that serves as a "leg" (snails, clams); animals with two, four, six, or eight legs; animals with dozens of legs; even animals with hundreds of legs. There are animals that move constantly, and animals that stay in one place for their entire adult life. There are animals that swim purposefully and animals that drift wherever the currents take them. Animals slither, crawl, flap, glide, and swim. Some animals spend their entire life underground, whereas others spend almost their entire life in the air. All of these are different modes of animal locomotion.

ethology animal behavior

sessile immobile, attached

Locomotion is not the same as movement. All animals move, but not all animals locomote. In **ethology**, or the study of animal behavior, locomotion is defined as movement that results in progression from one place to another. Animals that spend all or nearly all their entire adult life in one place are called **sessile**. Animals that move around are called motile.

Locomotion has evolved to enhance the animal's success at finding food, reproducing, escaping predators, or escaping unsuitable habitats. Typically, the animal uses the same mode of locomotion for all these functions, but there are exceptions. For example, a squid normally swims forward or backward by undulating (rhythmically waving) finlike flaps on the sides of its body. However, when startled, the squid expels water through a nozzle and jets backward. Shrimp have a similar behavior. They normally swim using modified appendages called swimerettes. When avoiding a predator, they contract their powerful tail muscles and rapidly move backward through the water. Even some normally sessile animals use crude forms of locomotion to escape predators. Scallops can clap their shells together to produce a sort of jet propulsion. Some **cnidarians** (such as sea anemones) can break free from their attachment point and then use an undulating motion to swim away from a slow-moving predator.

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

Principles of Locomotion

Locomotion can be passive or active. Each has its advantages and disadvantages. Passive locomotion is the simplest form of animal locomotion. This behavior is exhibited by jellyfish and a few other animals. In this form of locomotion, the environment provides the transportation. The advantage is that no muscular effort is required. The disadvantage of this type of locomotion is that the animal is at the whim of wind and wave. It goes where the current takes it. A somewhat different form of passive locomotion is exhibited by the remora (the name for various species of fish in the family *Echeneidae*). Remora attach themselves (harmlessly) to a larger fish or sea turtle and thus go wherever the larger animal goes. However, remora are perfectly capable of swimming on their own.

Most animals exhibit active locomotion at some stage of their life cycle. To move purposefully from place to place, animals must have a means of providing propulsion and a means of controlling their movement. In most cases animals use some sort of muscle tissue attached to a structure to contract and generate the force required to move. This muscle could be attached to a leg bone, causing the animal to jump, as in a frog, or it could contract a chamber, causing a jet of water to propel the animal, as in a squid. The amount, type, and location of contractions are controlled by a nervous system. The nervous system can be as simple as the nerve web in hydra or as complex as the elaborate and highly specialized human nervous system. Nervous system control produces rhythmic movements of the appendages or body that result in locomotion.

Active locomotion can be **appendicular** or axial. In appendicular locomotion, various appendages such as legs, wings, and flippers interact with the environment by pushing or flapping to produce the propulsive force. Axial locomotion occurs when the animal modifies its body shape to achieve motion. For example, squid contract their large body cavity and forcefully expel water through a nozzle, producing a form of jet propulsion. Eels produce rhythmic ripples down the lengths of their bodies. Leeches stretch out their bodies, extending their **anterior** ends forward. They then anchor and draw their **posterior** ends forward by shortening and thickening their bodies.

appendicular having to do with arms and legs

anterior referring to the head end of an organism

posterior behind or the back

Whether passive or active locomotion is used, the physical environments occupied by animals fall into four broad categories, each requiring unique forms of locomotion. The four environments are fossorial (underground), terrestrial (on the ground), aerial (in the air, including **arboreal**, on tree-dwelling), and aquatic (in the water). Each environment has similar restraints on motion: mass or inertia, gravity, and drag. Drag is any force that tends to restrict movement.

arboreal living in trees

In fossorial locomotion, drag is the most important factor restricting forward motion. If the soil is very loose, some animals (insects and lizards) can "swim" through. This form of locomotion is quite rare. Most fossorial animals must burrow or dig tunnels. Some dig as they go, pushing the soil behind them. However, most fossorial animals build permanent tunnels.

Once the tunnel is constructed, the mode of locomotion in the tunnel is indistinguishable from terrestrial locomotion.

Animals that spend part of their time in the air (bats, birds, flying insects) need powerful muscles to maintain flight against the force of gravity. Animals that burrow underground or that move about on the surface also require strong muscles to balance the force of gravity. Thus animals that live in aerial, fossorial, or terrestrial environments have evolved strong skeletal systems. Muscles must also overcome inertia to propel the animal forward. The more massive the animal, the more inertia it has.

buoyancy the tendency of a body to float when submerged in a liquid

Many aquatic animals are weightless in water. The **buoyancy** of the water exactly balances their weight. So muscular effort is not required to maintain their position. However, these animals must still exert muscular effort to initiate motion. Because water has substantial drag, muscular effort is also required to maintain motion. Some animals have negative buoyancy. They sink to the bottom if they stop swimming. Animals with negative buoyancy must expend muscular energy to remain at a given level in the water. An animal with positive buoyancy floats to and rests on or near the surface and must expend muscular energy to remain submerged.

Because the amount of drag due to movement through water is substantial, animals that need to move quickly must have a very streamlined shape. Drag results mainly from the friction of the water as it flows over the surface of the animal. Drag is also caused by water sticking to the surface of the animal. Many fish have evolved a special mucous coating that protects the skin and also reduces friction. The flow of water over the skin of the animal is usually lamellar, which means different layers of the water flow at different speeds relative to the animal. The slowest layer of flow is the one next to the body surface. Moving away from the surface, each layer moves a little faster until the speed of the water flow over the animal is matched at the last layer. Turbulence reduces lamellar flow and increases drag, ultimately limiting the speed of the animal through the water. Dolphins have evolved a gel-like layer just under the skin that tends to absorb turbulence and restores lamellar flow, thus allowing them to swim at a higher speed.

The viscosity of air is much lower than that of water, producing much less drag. However, lamellar flow of air, especially across the wing surfaces, is even more critical. Lift is provided by the shape of the wing. Lift results from air flowing faster across the upper surface than across the lower surface of the wing. Turbulence eliminates lamellar flow and lift is reduced.

Fossorial Locomotion

Fossorial animals dig burrows, bore into the soil, or construct tunnels. Constructing tunnels or burrows requires that the material be compact and stick together. Semisolid mud or loose sand will not support a burrow. Lizards that "swim" through loose sand or amphibians that swim through mud do not leave tunnels or burrows. While these behaviors could be considered fossorial, they are not discussed here.

invertebrates animals without a backbone

Fossorial invertebrates. Burrowing **invertebrates** have evolved a number of ways to dig through material. Some worms use the contract-anchor-extend method of locomotion. Contraction of the muscles in the rear half

of the body pushes the body forward and causes the proboscis to protrude. When the proboscis is fully extended, the worm anchors the proboscis in the soil and pulls the rest of its body forward. This process is repeated, producing a slow and erratic forward motion.

Clams and some other burrowing **mollusks** use a variation of the contract-anchor-extend method. They extend a muscular "foot" into the soil. Blood is pumped into the foot, causing it to swell and thus forming an anchor. Then the muscle contracts, pulling the clam down into the soil.

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

Many worms, such as earthworms, use peristaltic locomotion. This form of locomotion is generated by the alternation of longitudinal waves and circular-muscle-contraction waves flowing from the head to the tail. The movement is similar to the contract-anchor-extend method, but each peristaltic wave produces separate anchor points. So several segments of the worm may be moving forward at the same time.

Fossorial vertebrates. Fossorial **vertebrates** include amphibians, reptiles, and mammals. Locomotion of fossorial amphibians and reptiles is usually axial. Fossorial locomotion of mammals is appendicular. Moles are a good example of fossorial mammals. They have strong, flat forelegs with large, strong claws. Moles dig by extending a foreleg straight ahead in front of the snout and then sweeping it to each side. The loosened soil is pushed against the sidewalls of the burrow. Many rodents dig burrows for nesting but forage above ground. These animals dig by alternately extending their forelegs forward and downward. The loosened soil is pushed backward under the body. The animal may back up through the burrow, pushing the soil out to the surface.

vertebrates animals with a backbone

Terrestrial Locomotion

This is the form of locomotion humans use to get around. However, few species use the pure **bipedal** locomotion of humans. Most animals use four or more legs. Only **arthropods** and vertebrates have evolved the ability to move rapidly on the ground using legs. Both groups of animals raise their bodies above the ground and use their legs to propel themselves forward. The legs provide both support and propulsion, so the animal must maintain balance as it moves. The sequence and patterns in which the various legs move is determined by the need to maintain balance. More legs create greater stability, but the fastest vertebrates and invertebrates use six or fewer legs.

bipedal walking on two legs

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

Walking. Both arthropods and vertebrates use a similar pattern of walking or gait. A foot is planted on the ground and the body is pushed or pulled forward over the foot. The foot remains stationary as the body moves forward. Then the body remains stationary as the foot is lifted and the leg moves forward. For walking and slow running, gaits are generally **symmetrical**. The footfalls are regularly spaced in time. Fast-moving vertebrates, such as horses, have an **asymmetrical** but regularly repeating gait.

symmetrical a balance in body proportions

asymmetrical lacking symmetry, having an irregular shape

Insects tend to move their six legs in a simple pattern, lifting and replacing each leg in turn followed by the leg in front of it. Then the legs on the other side are moved. Forward motion always begins with the posterior legs. In slow walking, only one leg is lifted at a time. The limb movements of centipedes and millipedes are similar to those of insects, but with many

more legs and simultaneous waves of movement that progress from the posterior end to the anterior end on both sides of the animal.

Four-legged vertebrates must synchronize leg movements to maintain balance. The basic walking pattern of all four-legged vertebrates is left hind leg, left foreleg, right hind leg, and right foreleg. This cycle is then repeated. The faster symmetrical gaits of vertebrates are obtained by overlapping the leg-movement sequences of the left and right sides.

Running. Verterbrates that can run are known as cursorial. They have short, muscular upper legs and thin, elongated lower legs. This adaptation reduces the mass in the lower leg, allowing it to be brought forward more quickly. For slow, steady-running, cursorial vertebrates use a gait known as trotting. All-out running is known as galloping. The gallop is an asymmetrical gait. When galloping, the animal is never supported by more than two legs. Horses at full gallop have all four legs off the ground at the same time during part of the gait. This fact was first demonstrated by Eadweard Muybridge, the American photographer and motion picture pioneer, using high-speed photography involving multiple cameras. His groundbreaking, eleven-volume work, *Animal Locomotion*, was published in 1899.

Cursorial birds and some lizards use bipedal locomotion. These animals have evolved large feet to increase support. The axis of the body is held perpendicular to the ground. Cursorial birds and lizards have long tails for balance, so that the center of gravity of the animal always falls between its feet. The running gait is, of course, a simple alternation of left and right legs. Lizards begin with four-footed locomotion and switch to bipedal as speed increases.

Hopping. The locomotor pattern of hopping is found in both invertebrates and vertebrates. Invertebrates include a few insects, such as grasshoppers and fleas. Vertebrates include tailless amphibians, kangaroos, rabbits, and a few rodents. All hopping animals have hind legs that are approximately twice as long as the forelegs.

Frogs jump by first flexing their forelegs and tilting their bodies upward. The hind legs are swung out from the sides of the body. When the upper hind leg is perpendicular to the body, the hind leg is forcefully straightened out and the animal is launched upward at a 30° to 45° angle.

quadrupedal describes an animal with four legs

Rabbits, kangaroos, and all other mammals move their legs vertically when they jump, instead of horizontally. The hopping gait of rabbits is **quadrupedal**. A jumping rabbit stretches forward and lands on its forefeet. As the forefeet touch, the back flexes, and the hind end rotates forward and downward. The hind feet touch down next to the forefeet, and a new jump begins. Kangaroos take off and land on their hind feet. The back is not arched and the front legs are used only for balance. All of the muscular effort required for jumping is provided by the powerful hind legs.

Crawling. Invertebrates that crawl use either peristaltic or contract-anchor-extend locomotion. Limbless vertebrates use serpentine, rectilinear, concertina, or sidewinding locomotion. The most common pattern is serpentine locomotion, used by snakes, legless lizards, and a few other species. Rectilinear locomotion is used by most snakes, occasionally by large snakes all the time, and by fossorial limbless vertebrates when burrowing. Concertina and sidewinding locomotion are largely confined to snakes.

Serpentine. In serpentine (snakelike) locomotion, the body moves in a series of curves. In serpentine motion the entire body moves at the same speed. All parts of the body follow the same path as the head. Propulsion is by a lateral thrust in all segments of the body in contact with projections of the surface.

Concertina. Concertina locomotion is used when the surface is too slick for serpentine locomotion. The snake moves its body into a series of tight, wavy loops. These provide more friction on the slick surface. The snake then extends its head forward until the body is nearly straight or begins to slide backward. The snake then presses its head and upper body on the surface, forming a new frictional anchor, and pulls the posterior regions forward.

Sidewinding. Sidewinding locomotion is a specific adaptation for crawling over loose, sandy soils. It may also have the added advantage of reducing contact with hot desert soils. Like serpentine locomotion, the entire body of the snake moves forward continuously in a series of sinuous curves. These curves are sideways to the direction of motion of the snake. The track made by a sidewinding snake is a set of parallel curves roughly perpendicular to the direction of movement. The unique feature of sidewinding is that only two parts of the body touch the ground at any instant. The remainder of the body is held off the ground. To begin, the snake arches the front part of the body forward and forms a loop leaving only the head and the middle of the body in contact with the ground. The snake then moves in a sinuous loop, causing the contact point to move backward along the snake's body as each body segment loops forward. As soon as enough body length is available, the animal forms another loop and begins the next cycle. Each part of the body touches the ground only briefly before it begins to arch forward again.

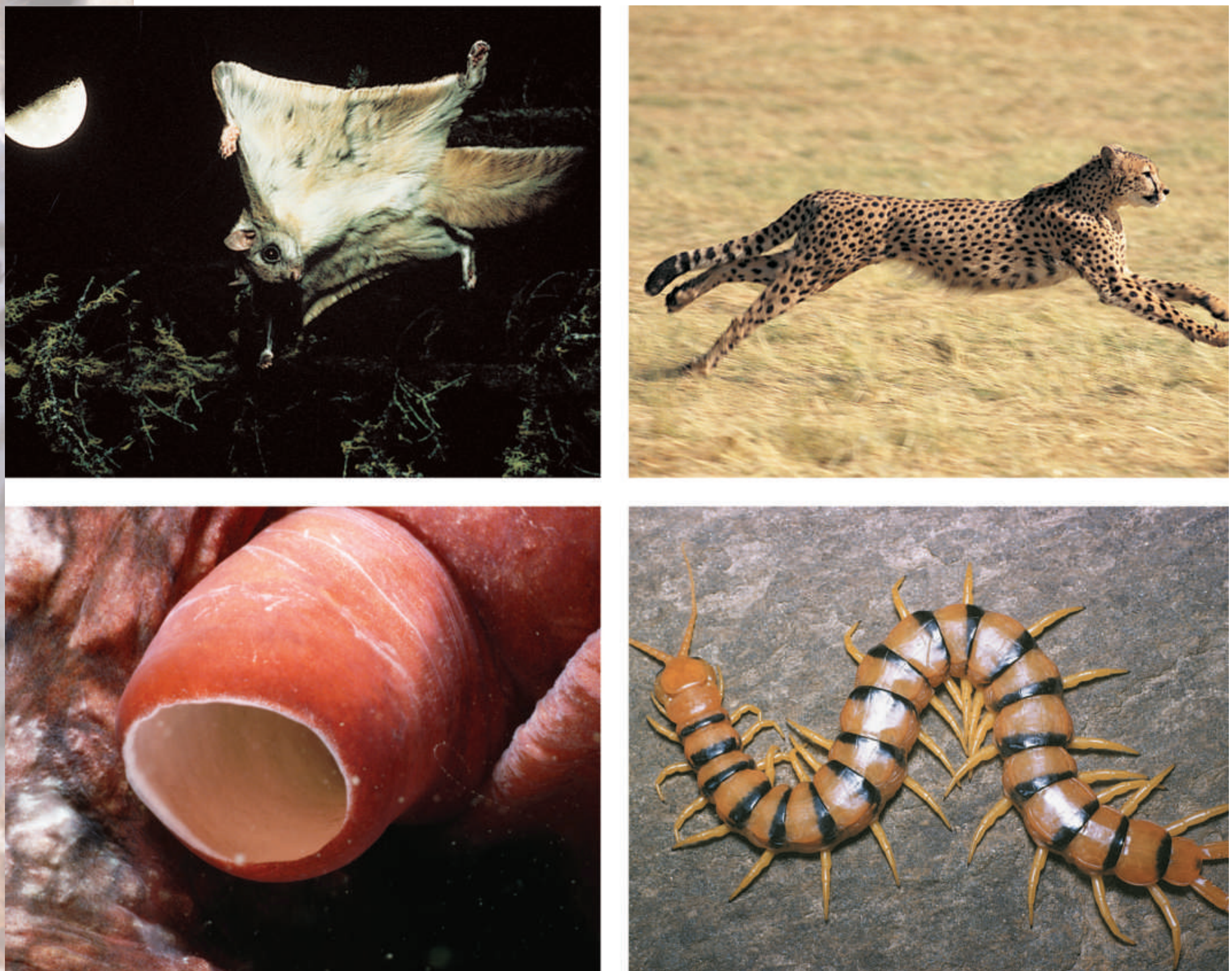
Rectilinear Locomotion. In snakes, rectilinear motion is completely unlike the other forms of locomotion. The body is held relatively straight and glides forward in a manner similar to the motion of snails. The belly of the snake is covered by rows of wide, overlapping scales. Each scale is attached to two pairs of muscles, both of which are attached at an angle to ribs ahead of and behind the scale. Waves of contraction move from the front of the snake toward the back, lifting and moving each scale forward in turn. Then the scale is pulled rearward, but the edge of the scale digs into the surface, propelling the snake forward.

Aerial and Arboreal Locomotion

Animals have evolved many ways of moving without touching the ground. Aerial locomotion includes gliding, soaring, and true flight. Animals who move through trees are known as arboreal.

Climbing. Each group of arboreal animals has a unique adaptation for climbing. Arthropods weigh little so they show few specialized climbing adaptations. Most arthropods, especially insects, can climb. The heavier vertebrates have many climbing adaptations.

Arboreal frogs and lizards are slender-bodied animals whose climbing gait is essentially the same as their terrestrial gait. The tips of the toes on arboreal frogs are expanded into large, circular disks, which increase the contact area. The digits of arboreal lizards are spread out. On the bottom



Many different types of locomotion exist in nature. *Clockwise from upper left:* The flying squirrel glides, the cheetah uses its four legs to run over the earth, the centipede coordinates its multiple legs, and the mollusk pushes water through this body part to propel itself through the ocean.

of each of these spatula-shaped digits are claws and one or two rows of elongated scales. Chameleons have two more specialized adaptations. Their tails are able to grasp objects (prehensile), and their digits have fused into two groups of opposable digits. Chameleons can tightly grasp a thin limb.

Brachiation and leaping. Most arboreal animals must occasionally leap across a gap between trees or branches. The leaping motion is essentially the same as terrestrial leaping, although landing is trickier. Brachiation is using the arms to swing from limb to limb. A few primates have developed highly specialized adaptations for brachiation, although all monkeys brachiate to some extent. Primates that use this form of locomotion have extremely long, powerful arms or forelimbs.

Gliding. In gliding, the animal coasts from a high point to a low point, losing elevation constantly. Gliding animals include amphibians, reptiles, and mammals. The small animals known as flying squirrels demonstrate this behavior. A flying squirrel will climb to near the top of one tree and launch itself into space, gliding to a lower branch on the next tree, then climbing to the top and repeating the process as often as necessary. Gliders have adap-

tations that allow them to increase the width of their bodies. In the flying squirrels flaps of skin extend from the front limbs to the back. Frogs, snakes, and lizards are able to flatten their bodies. Some gliding lizards have elongated ribs that open like a fan.

Soaring. Soaring is a very different process. Birds who are able to soar are much better gliders than any of the gliding animals. They are able to soar because of their instinctive or learned ability to take advantage of columns of rising air to gain altitude. A vulture will soar in circles in a rising column of air to a high altitude, then glide to the next rising air column. In this way, vultures are able to stay aloft for hours with almost no muscular effort.

True flight. Three living groups of animals possess true flight: insects, birds, and mammals. They can propel themselves upward and forward by flapping their wings. Each of these groups evolved this ability independently of the others. A fourth group, the extinct winged reptiles known as pterosaurs, may have been capable of true flight or only of soaring and gliding. The aerodynamics of flight are basically the same for all flying animals. However, the mechanical details are quite different among the groups. While all three groups propel themselves forward by flapping their wings, many species of birds also include extensive gliding and soaring to conserve energy.

Aquatic Locomotion

Animals that live in aquatic environments exhibit many different forms of locomotion. Some animals crawl or burrow into the bottom of a body of water. Others swim through the water using a variety of different appendages. Still others float freely, following the currents wherever they go. Aquatic organisms range in size from microscopic to the blue whale, the largest animal that has ever lived.

Invertebrates. Aquatic invertebrates swim through the water, crawl along the bottom, or burrow into the bottom. In swimming, muscular activity propels the animal by pushing against the water. On the bottom, muscular activity moves the animal around by interacting with the bottom. Some bottom dwellers simply crawl around on the bottom in a manner exactly like terrestrial locomotion. Others take advantage of the weightless environment to move in ways unique to the water environment.

Aquatic invertebrates have developed two distinct modes of swimming. One mode uses hydraulic propulsion. Jellyfish are a good example of this type of locomotion. They have umbrella-shaped bodies, with the "handle" of the umbrella containing the digestive system. The outer margin of the top of the umbrella, or medusa, is a band of muscles that can contract rapidly. As the muscles contract (just like closing an umbrella) water is expelled forcefully and the jellyfish is propelled along. Scallops use a similar locomotion. They are the best swimmers among bivalves, but at its best, the motion is jerky and poorly controlled. It is used mostly to escape predators. Rapid clapping movements of the two shells create a water jet that propels the scallop.

Cephalopods, such as the squids and octopi, are also mollusks that use water-jet propulsion. Adult cephalopods have lost most of their heavy shell. Many squid are excellent swimmers and can swim forward or backward by undulating flaps along each side of their bodies. All cephalopods are much

mantle the tissue in mollusks that drapes over the internal organs and may secrete the shell

better swimmers than any other species of mollusk. The **mantle** of cephalopods encloses a cavity that contains the gills and other internal organs. It also includes, on its bottom surface, a narrow opening called a siphon. When the circular muscles surrounding the cavity simultaneously contract, water is forced through the siphon. This propels the cephalopod in a direction opposite to the direction of the siphon. Thus the siphon also provides directional control.

Fishes. Some fishlike animals use a purely undulatory motion to move themselves. Almost all fish use undulatory movement to some extent and supplement that motion with muscular effort by fins.

An eel swims by undulating its entire body in a series of waves passing from head to tail. This type of movement is called anguilliform (eel-like) locomotion. During steady swimming, several waves simultaneously pass down the body from head to tail. The waves move faster as they approach the animal's tail.

While eels have a body with a fairly blunt anterior and constant diameter for the rest of the length of the body, most fish have a body that tapers at both anterior and posterior ends. For these fish, undulatory motion is not the most efficient. So most fish exhibit carangiform locomotion, in which only the rear half of the body moves back and forth. The fastest swimming fish use this method of locomotion, so it is apparently the most efficient one. In contrast, ostraciiform locomotion uses only the tail fin to sweep back and forth. This is slower and apparently less efficient.

dorsal the back surface of an animal with bilateral symmetry

Whales and other cetaceans use undulatory body waves, but the waves move the whale's body up and down instead of from side to side. The elongated tail region of whales produces a form of carangiform locomotion apparently as effective as that of the swiftest fish. Fish, whales, and other aquatic vertebrates have some arrangement of fins distributed around their bodies. They all have a caudal (tail) fin, vertical in fish and horizontal in cetaceans. Aquatic vertebrates also have a large **dorsal** fin and a pair of large fins (or flippers) on the sides of their bodies close to the front. The caudal fin is the primary means of locomotion. The lateral fins do most of the steering. The dorsal fin or fins provide stability.

Tetrapodal vertebrates. Tetrapodal vertebrates (four-legged vertebrates) that use undulatory locomotion include crocodilians, marine lizards, aquatic salamanders, and larval frogs. However, adult frogs and other tetrapods primarily use appendicular locomotion. Many aquatic tetrapods move primarily by using the hind legs. However, sea turtles, penguins, and fur seals have evolved short hind legs with webbed feet used primarily as rudders. These animals use their powerful forelegs, which have evolved into flippers.

Diving birds, such as cormorants and loons, are propelled by their webbed hind feet. Loons are the best adapted for diving. Their body, head, and neck are elongated and slender; the hind legs have moved far back to the posterior end of the body; the lower legs are short; and the feet are completely webbed.

Frogs and some freshwater turtles have elongated rear legs with enlarged, webbed feet. Other aquatic turtles (such as snapping turtles) are relatively poor swimmers. These turtles walk on the bottom of the lake or stream with limb movements very similar to those used on land except that they can move faster in water than they can on land.

Many mammals have swimming movements identical with their terrestrial limb movements. Most aquatic mammals—such as sea otters, hair seals, and nutria—use their hind legs and frequently their tails for swimming. The feet have some degree of webbing. Fur seals and polar bears swim mainly with forelimbs. SEE ALSO Flight; Skeletons.

Elliot Richmond

Bibliography

Alcock, John. *Animal Behavior: An Evolutionary Approach*. Sunderland, MA: Sinauer Associates, 1997.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishers, 1989.

Gould, James L., and Carol Grant Gould. *The Animal Mind.* New York: W. H. Freeman & Company, 1994.

Gray, James. *Animal Locomotion.* London: Weidenfield and Nicolson, 1968.

Hertel, Heinrich. *Structure, Form, and Movement.* New York: Reinhold, 1966.

Muybridge, Eadweard. *Animals in Motion.* New York: Dover Publications, 1957.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates, 1987.

Tricker, R. A. R., and B. J. K. Tricker. *The Science of Movement.* New York: American Elsevier Publishing Company, 1967.

Lorenz, Konrad

Zoologist and Ethologist
1903–1989

Konrad Lorenz shared the 1973 Nobel Prize in physiology.

Austrian zoologist, ethologist, and Nobel Prize winner Konrad Zacharias Lorenz was born in Vienna in 1903, the son of a fabulously wealthy orthopedic surgeon. He spent his childhood roaming the forests and marshes of the family estate on the banks of the Danube in the company of the teeming wildlife of the area and a neighbor, Gretl Gebhardt. It was at play, splashing in the marshes pretending to be ducks, that the two seven-year-olds discovered what would become Lorenz's lifelong work. Newly hatched ducklings saw the children and followed them as though they were the ducklings' parents. This phenomenon, now called imprinting, is an example of a genetically programmed pattern of behavior that is innate in all members of a species but is dormant until triggered by some crucial experience. In the case of the ducks, imprinting stimulated them to follow and mimic the first thing they saw upon hatching. Lorenz went on to establish that birds and mammals imprint upon birth, by sight, sound, touch, or smell.

Lorenz obtained a medical degree in 1928 from the University of Vienna, where he reunited and married his childhood friend Gebhardt, who had become a gynecologist. He then immersed himself in his lifelong passion: observation of animals in their natural **habitat**.

habitat physical location where an organism lives in an ecosystem

After World War II (1939–1945) Lorenz moved his family to his childhood estate, Altenberg, and surrounded by animals both domestic and wild, he began a series of popular books. *King Solomon's Ring*, published in 1949, consisted of lively stories about his pets and their behavior as well as about Lorenz's relationships with a number of wild birds. *Man Meets Dog*, published in 1950, discussed the ancient and intimate bonds between human beings and dogs.

That same year, Lorenz and Erich von Holst established the Max Planck Institute for Behavioral Physiology at Altenberg. For the next twenty years Lorenz concentrated on the study of waterfowl, particularly investigating the process of instinct: how and why animals behave in appropriate and complex ways without human reasoning.

ethology the study of animal behavior

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

physiology study of the normal function of living things or their parts

Lorenz dramatically shaped the way in which scientists approached the study of animal minds and behavior. In the mid-twentieth century, scientists tended to observe animals isolated in cages and to believe that all behavior was learned. Lorenz popularized **ethology**, the more difficult study of animal behavior in the field under natural conditions. His years of observations along with colleagues Nikolas Tinbergen and Karl von Frisch established the existence of many genetically inherited behavior patterns in animals, all subject to **natural selection**. Their work led to a shared Nobel Prize in 1973 in the field of **physiology**. Konrad Lorenz was also awarded the Gold Medal of the New York Zoological Society, was elected to the Royal Society of London and the American National Academy of Sciences, and received numerous honorary degrees worldwide.

Toward the end of his life in 1989, Lorenz said of his duckling discoveries with Gebhardt, "What we didn't notice is that I got imprinted on ducks in the process. I still am, you know. And I contend that a lifelong endeavor is fixed by one decisive experience in early youth. And that after all, is the essence of imprinting." (Wolf 1983, p. 32–34). SEE ALSO Ethology; Imprinting.

Nancy Weaver

Bibliography

Concise Dictionary of Scientific Biography. New York: Charles Scribner's Sons, 2000.

Wolf, Michael. "The Mind of Konrad Lorenz." *World Press Review* 30 (1983):32–34.

MacArthur, Robert Helmer

Canadian-Born American Biologist
1930–1972

Robert Helmer MacArthur was born in Toronto, Canada. MacArthur was an important scientist in the field of ecology, the study of the relation between living creatures and their natural environment. When MacArthur started his studies in ecology, it was a merely descriptive science. Under his influence, ecology developed into a science based on quantitative, or measurable, data.

genetics the branch of biology that studies heredity

MacArthur moved to the United States at the age of seventeen to study at Marlboro College in Vermont, where his father was a professor of **genetics**. In 1951 he earned a bachelor's degree, in the field of mathematics, from Marlboro. Two years later, in 1953, he achieved his master's degree in mathematics from Brown University. While pursuing a Ph.D. at Yale,

MacArthur switched from mathematics to zoology, with a concentration on ecology. After receiving his Ph.D. in 1957, MacArthur spent a year in England studying birds. In 1958 he was appointed as an assistant professor of biology at the University of Pennsylvania. In 1965 he became a professor of biology at Princeton. He held this position until his death from cancer at the age of forty-two.

MacArthur's first studies were on five similar species of birds called warblers that were living together in a spruce forest in New England. Some scientists believed that these birds might be an exception to the generally accepted **competitive exclusion principle**, which states that in stable environments, no two species occupy the same **niche** (the specialized role of an animal in its environment). However, MacArthur's studies showed that the birds occupied different parts of the trees, and thus did indeed follow the principle. This work earned for MacArthur the Mercer Award of the Ecological Society of America (1959).

competitive exclusion principle the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

niche how an organism uses the biotic and abiotic resources of its environment

MacArthur used his background in mathematics to focus on **population** biology. He studied how the population sizes of bird species varied with the size of their **habitats**. MacArthur and biologist Edward O. Wilson studied populations of birds living on islands. Their findings were published in 1967 in the book *The Theory of Island Biogeography*.

biogeography the study of the distribution of animals over an area

population a group of individuals of one species that live in the same geographic area

habitats physical locations where an organism lives in an ecosystem

MacArthur and Wilson also developed the idea of life history strategies. They noted that some species have short lives characterized by very fast growth and high reproductive rates, then a sudden and drastic decline in numbers. An example of this type of species—called ***r*-selected species**—is the lemming. MacArthur and Wilson compared these animals to species that have slow growth and stable populations. An example of this type of species—called a ***k*-selected species**—is the elephant.

***r*-selected species** a species that shows the following characteristics: short lifespan; early reproduction; low biomass; and the potential to produce large numbers of usually small offspring in a short period of time

***k*-selected species** a species that natural selection has favored at the carrying capacity

In 1971, when MacArthur learned that he had cancer and might live only a few more years, he decided to compile his many ideas into a single book. This book, *Geographic Ecology: Patterns in the Distributions of Species*, was published in 1972 shortly before his death. SEE ALSO LIFE HISTORY STRATEGIES; WILSON, E. O.

Denise Prendergast

Bibliography

McMurray, Emily J., ed. *Notable Twentieth-Century Scientists.* Detroit: Gale Research Inc., 1995.

Millar, David, Ian Millar, John Millar, and Margaret Millar. *Chambers Concise Dictionary of Scientists.* Cambridge, U.K.: The Press Syndicate of the University of Cambridge, 1989.

Muir, Hazel, ed. *Larousse Dictionary of Scientists.* New York: Larousse, 1994.

Malaria

Malaria is one of the oldest known infections. It is also the world's most deadly tropical parasitic disease. It kills more people than any other communicable disease except tuberculosis. The disease was first described in ancient Sanskrit and Chinese documents. **Hippocrates** also described the

Hippocrates a central figure in medicine in ancient Greece, he is considered the father of modern medicine disease in his writings. It is believed that the army of Alexander the Great was wiped out by the disease during its march across India.

Malaria is thought to have been introduced into the United States by European colonists and African slaves in the sixteenth and seventeenth centuries. It is now endemic in ninety-two countries worldwide. With approximately 41 percent of the world's population at risk, the disease poses a serious health threat globally. As many as two million people die annually; half of the deaths occur in children under five years of age. According to the World Health Organization, this amounts to one child dying every thirty seconds.

Malaria is characterized by both acute and relapsing infection in humans. Hallmark symptoms include periodic episodes of chills and fever, spleen enlargement, and **anemia**. The disease is caused by microscopic one-celled organisms called **sporozoa**, which belong to the genus *Plasmodium*. These parasites are transmitted to humans by several species of anopheles mosquitoes. Malaria is also found in apes, monkeys, birds, bats, reptiles, and rodents. While humans can be infected only by Anopheles mosquitoes, birds and other animals are known to have become ill after being bitten by mosquitoes from the genus *Culex*.

anemia a condition that results from a decreased number of red blood cells

sporozoa a group of parasitic protozoa

Four species of *Plasmodium* are known to cause human malaria: *P. falciparum*, *P. vivax*, *P. malariae*, and *P. ovale*. Diagnosis can be determined by a blood smear. The most common type, *P. falciparum*, requires relatively high environmental temperatures for development and is usually found in tropical areas such as western Africa. *P. vivax* malaria accounts for 43 percent of all cases and is widespread globally. It is known to occur even in cold-winter areas of Korea, Manchuria, and south Russia. The less common *P. malariae* malaria occurs in about 7 percent of all cases and is confined to the Mediterranean, while *P. ovale* malaria is rather rare and isolated within a small area of eastern Africa and the islands of the western Pacific.

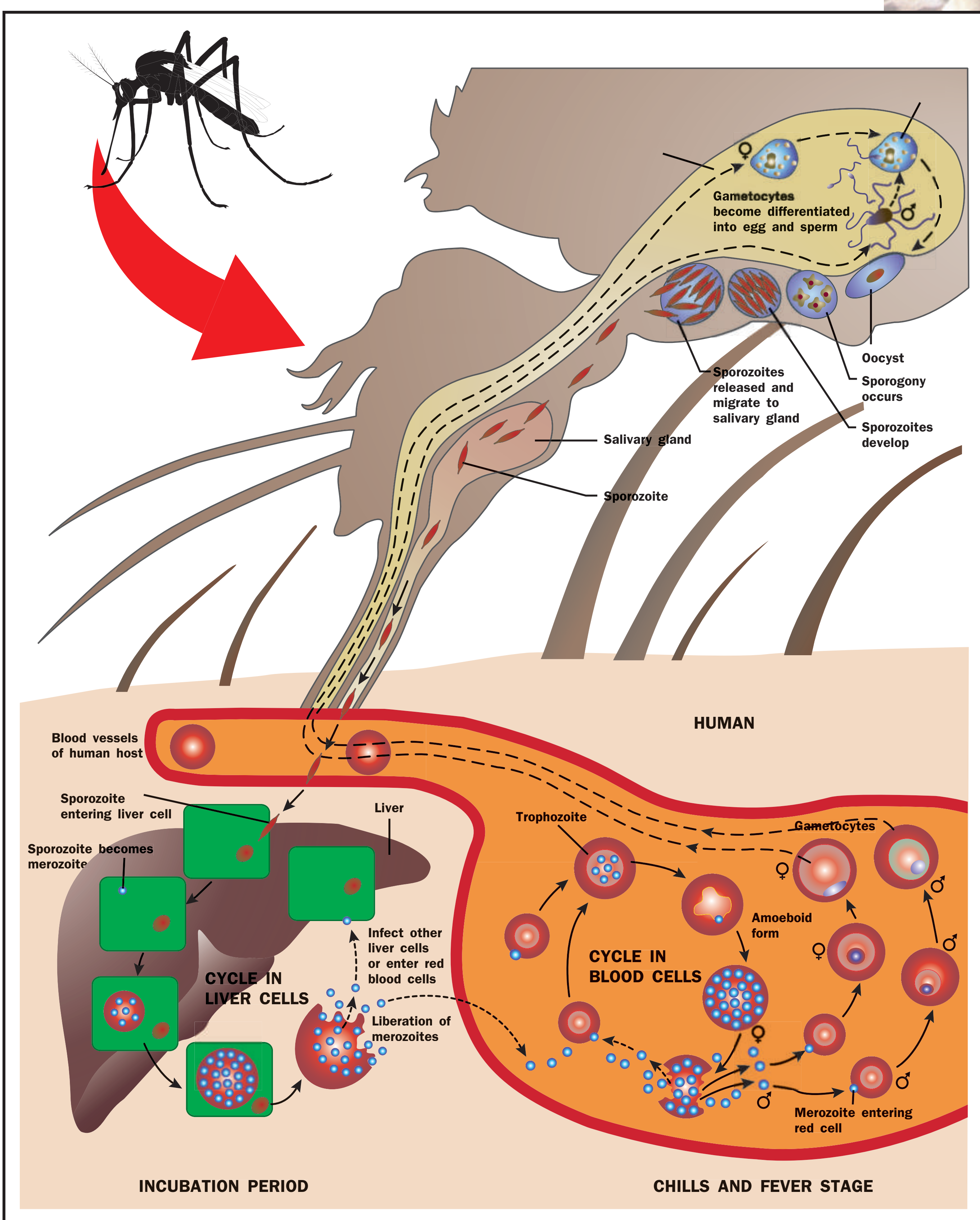
Malarial attacks typically last four to ten hours during which a person experiences successive stages of chills, high fever, severe headache, and then profuse sweating. Between attacks, body temperature may be normal. The intervals between attacks are usually either forty-eight hours or seventy-two hours. The first attack typically occurs seven to nine days after a person is bitten by a disease-carrying mosquito.

Mosquito Transmission

Though malaria can occur in temperate regions, it is most common in the tropics and subtropics, where climatic conditions favor mosquito development. Mosquitoes lay their eggs in water where larvae mature and hatch into flying adults. Newly hatched female mosquitoes are especially bloodthirsty and require a blood meal to produce fertile eggs. When these mosquitoes bite a human who is already infected, they ingest the malarial parasite and the disease transmission cycle begins.

The life cycle of the *Plasmodium* starts in the stomach of the female mosquito. The organism's double life cycle has two phases—a sexual reproductive cycle and an asexual reproductive cycle. While the parasite is in its asexual, free-swimming stage, it is known as a **sporozoite**. When an infected mosquito bites, the sporozoite is injected along with saliva into the human bloodstream.

sporozoite an infective stage in the life cycle of sporozoans



The life cycle of the virus that causes malaria.

merozoites a motile stage in some parasitic protozoa

Once inside the bloodstream, the sporozoite enters a red blood cell. Inside the red blood cell, it changes shape and divides into smaller forms called **merozoites**. The red blood cell containing these merozoites ruptures, releasing them into the blood. The merozoites infect other red blood cells, and the life cycle is repeated. The rupturing of red blood cells causes the symptoms of fever and chills.

gametocytes cells that produce gametes through division

zygote a fertilized egg

oocyst a cyst in sporozoans that contains developing sporozoites

A mosquito biting an infected host at this stage can ingest merozoites. If this happens, the merozoites enter the mosquito's stomach and become male and female **gametocytes**. This kicks off a sexual reproductive life cycle where the separate male and female gametocytes unite together to form a single-celled **zygote**. This zygote grows to become an **oocyst** or large egglike sac, which eventually divides, releasing a multitude of asexual, free-swimming sporozoites.

These sporozoites move to the mosquito's head and salivary glands from which they can be injected into a human during the mosquito's next bite. This asexual cycle is repeated. During the asexual life cycle, the parasites grow and divide synchronously. The resulting merozoites produce the regularly occurring fever and chill attacks that are typical of malaria.

Early Cases and Treatments

quinine a substance used to treat malaria

The first documented treatment of the disease occurred in 1630 when "Jesuit's bark," from a cinchona tree, was used to ease the fever of a Spanish magistrate in Peru. Amazingly, the magistrate recovered and eventually the substance **quinine** was isolated from the bark and processed commercially as a treatment. The *Cinchona* genus includes about forty species of plants, mostly trees, native to the Andes of South America. Certain species are also known to grow in India and Sri Lanka.

chloroquine a drug commonly used to treat malaria

In the 1940s, the antimalarial drug **chloroquine** was introduced as an effective additional treatment. Chloroquine is a member of an important series of chemically related antimalarial agents, the quinoline derivatives. A global eradication program was initiated in the 1950s and 1960s by the World Health Organization (WHO), in Geneva, Switzerland, which led to a significant decrease in malaria cases in Asia and South America.

Drug Resistant Strains and Reemergence of Disease

habitat physical location where an organism lives in an ecosystem

Drug resistant strains of malaria began to emerge in the 1970s, making the disease harder to control. During the 1990s the prevalence of malaria escalated at an alarming rate, especially in Africa where control efforts have typically been piecemeal and uncoordinated. Additionally, the phenomenon of "airport malaria," or the importing of malaria by international travelers, is becoming commonplace. Persons who are not normally exposed to this mosquito in its natural **habitat** can acquire "airport malaria" through the bite of an infected mosquito that has traveled far from its home.

In one study, random searches of airplanes at Gatwick Airport in London found dozens of airplanes from tropical countries containing mosquitoes. After a mosquito leaves an aircraft, it may survive long enough to take a blood meal and transmit the disease, usually in the vicinity of the airport. Incidents of malaria transmitted this way are expected to become more common, since airport travel has increased by almost 7 percent a year since 1980 and is predicted to increase by 5 percent a year for the first twenty years of the twenty-first century.

Resurgence and increased risk of the disease appears to be linked to several factors. Changes in land use, such as mining, logging, and agricultural projects, particularly in the Amazon and Southeast Asia frontier area, are providing new mosquito breeding sites. Other reasons for the disease's spread include global climatic changes, disintegration of health services, armed conflicts, and mass movements of refugees into areas of high malaria transmission.

Reemergence of malaria through mobility occurred in Brazil, for example. Malaria had been practically eradicated from most areas of the Amazon region until massive population movements began to colonize new territories. New highways were built, linking the Amazon to the rest of the country and attracting laborers to work on road construction. In 1970, prior to new road construction in these new areas, there were approximately 50,000 cases of malaria reported; by 1990, reports had increased to more than 500,000, representing 10 percent of the world's reported cases outside Africa.

As a result of the explosion of international travel, imported cases of malaria are now showing up more in developed countries such as the United States Malaria is also reemerging in areas where it was previously under control or eradicated, such as in Korea. According to the WHO, **global warming** and other climatic events such as **El Niño** also play a role in increasing the disease. Malaria has now spread to highland areas of Africa, where El Niño effects such as increased rainfall have influenced mosquito breeding sites and hence the transmission of the disease. The emergence of multidrug-resistant strains of parasites is also exacerbating the situation.

global warming a slow and steady increase in the global temperature

El Niño a periodic condition characterized by a warming of the central Pacific Ocean and the changes in global weather patterns

Disease Prevention

Prevention of malaria encompasses a variety of measures. Some may protect against infection—these are directed against mosquitoes—whereas others focus on stopping the development of the disease in human beings. Although only a limited number of drugs are available, if these are used properly and targeted to those at greatest risk, malaria can be reduced.

Since the early 1990s, considerable progress has been made in the search for a malaria vaccine. More than a dozen candidate vaccines are currently in development; some of them are in clinical trials. An effective vaccine could be available within the first twenty years of the twenty-first century. In the meantime, there are a number of prescription drugs available on the market in developed countries that can help prevent malaria, especially in individuals traveling to high incidence areas. Some of the best-known preventatives include Mefloquine, Malarone, and Primaquine.

Medical researchers continue to discover new drug therapies. Most recently, Chinese scientists discovered a drug called artemether that is derived from the Chinese herb qinghaosu. The new drug appears to be as effective as quinine although much slower acting. It may even kill resistant strains of malaria. SEE ALSO Interspecies Interactions; Parasitism.

Stephanie A. Lanoue

Bibliography

Noble, Elmer R., Glenn A. Noble, Gerhard A. Schad, and Austin J. MacInnes. *Parasitology.* London: Lea & Febiger, 1989.

Turkington, Carol, and Bonnie Ashby. *Encyclopedia of Infectious Disease.* New York: Facts on File, Inc., 1998.

Economist Thomas Robert Malthus advocated controlling population growth to avoid food shortages.

Malthus, Thomas Robert

Economist
1766–1834

Thomas Robert Malthus, English economist and demographer, proposed a theory suggesting that **population** growth generally tends to outrun the food supply and that therefore population growth should be curbed. Although most of his work was centered on social conditions and economics, Malthus had a significant impact on the theory of evolution.

population a group of individuals of one species that live in the same geographic area

Born February 13, 1766, in Surrey, England, Malthus was the sixth child of seven born to Daniel Malthus and Catherine Graham. The young Malthus was educated primarily at home until his admission to Jesus College in Cambridge, England, in 1784. He was graduated with a degree in mathematics, but was well read in French and English history, English literature, and Newtonian physics. A master of arts degree followed in 1791, and in 1797 he was ordained a minister in the Anglican Church. In 1804 the East India Company founded a new college to provide general education to staff members before they went on service overseas. Malthus was asked to join the faculty as professor of history and political science.

The Industrial Revolution encouraged rapid population growth in part to provide an accessible pool of cheap labor for the emerging spinning and textile industries. Public policy during Malthus's time supported the notion that population growth was desirable and that assistance should be given to poor people. Malthus, on the other hand, suggested in *An Essay on the Principle of Population, As It Effects the Future Improvement of Society* (1798) that overpopulation tends to be a drain on resources and that state welfare should be curtailed so that the population would level off. He argued that if it was not possible to maintain the production of food to satisfy the population, then the population must be kept down to the level of available food. He felt that individuals should marry late and practice "natural restraint" so as to have few or no children.

In addition to its relevance for the social policy of the times, Malthus's work made an important contribution to the development of ideas and theories concerning the evolution of plants, animals, humans, and Earth. In 1859 Charles Darwin published his theory of evolution in a book entitled *On the Origin of Species.* In this book, he agreed with Malthus's speculation that competition for resources such as food, **habitat**, and mates would have a cumulative effect on the evolution of different species of plants and animals. This principle became known as **natural selection** and was considered a primary factor in the evolution of new species. Alfred Russel Wallace, a geologist and contemporary of Darwin, also constructed and published a theory of evolution. He, too, acknowledged that

habitat physical location where an organism lives in an ecosystem

natural selection the process by which organisms best suited to their environment are most likely to survive and reproduce he was influenced by Malthus's work on population and competition for resources.

Malthus was elected to the Royal Society in 1819, the Political Economy Club in 1821, and the Royal Society of Literature in 1824. He was also admitted to the Statistical Society of London in 1834, the French Academy of Sciences in 1833, and the Royal Academy of Berlin the same year. Malthus died on December 23, 1834. SEE ALSO Biological Evolution; Darwin, Charles; Wallace, Alfred Russel.

Leslie Hutchinson

Bibliography

Darwin, Charles. *On the Origin of Species by Means of Natural Selection.* New York: Penguin, 1987.

Muir, Hazel, ed. *Larousse Dictionary of Scientists.* New York: Larousse, 1994.

Winch, Donald. *Malthus.* New York: Oxford University Press, 1987.

Mammalia

Mammals are a group of animals (of the class Mammalia) found throughout the world. Even in regions where the most extreme climatic conditions exist, there are likely to be mammals. Seals, walruses, and whales survive in the cold Arctic and Antarctic. Small pikas live near the tops of high mountain ranges. Arid deserts are home to a wide variety of rodents and their coyote predators. Camels and their amazing ability to survive for long periods without drinking water are an almost universal symbol of the desert. Mammals have successfully survived in so many environments that it is no wonder scientists call this the Age of Mammals.

Mammals, however, did not always exist over such a wide geographical range. They have an evolutionary history going back to the dinosaurs. The history of mammals may surprise people, because mammal fossils have been found in rock deposits similar in age to the fossils of dinosaurs. Fossils identified as belonging to mammals have been found in rocks of the Late Triassic, about 200 million years ago. Early mammal fossils have been discovered in Europe, Great Britain, southern Africa, the Turkestan Range of southern Russia, China, North America, and South America.

Although widespread, the fossils of early mammals are actually rare. Many of the fossils are incomplete skeletons and isolated teeth. By the Middle Jurassic era (208 to 144 million years ago), however, mammals were flourishing, and the numbers of various species and groups had increased dramatically. At the end of the Cretaceous era (144 to 66 million years ago), when the large dinosaurs faced their final extinction, mammals survived to become the group that would produce the largest animals remaining on Earth.

Characteristics of Mammals

What is a mammal? How is it recognized from other **vertebrate** animals? Some body shapes and features of mammals are shared with other groups of animals that have backbones. These shared characteristics are vertebrae, an internal skeleton, and a four-chambered heart.

vertebrate animal with a backbone

On the other hand, several characteristics of mammals are unique and help distinguish a mammal from something else. The most familiar of the unique mammal characteristics is that their bodies are covered with hair or fur. Hair is a form of scales and indicates a shared ancestry with reptiles. In fact, scales are still found on some mammals, as on the tails of rats. In some mammals, such as whales, the amount of hair is greatly reduced. This is a secondary characteristic and is considered an evolutionary loss from an ancestor who had hair.

The skin of mammals is unique in that it contains sweat, scent, sebaceous oil, and mammary glands. The skin of all vertebrates is an important aspect of their health and survival, but few have developed such an elaborate variety of specialized glands as the mammals. Sweat glands help to cool the animals. Scent glands help species to recognize one another. Sebaceous glands provide a special type of oily substance for the maintenance of healthy hair and the prevention of bacterial infection. Mammary glands are unique to mammals and are, in fact, the characteristic for which the group is named. The mammary glands in females secrete the nourishing milk that helps the young to grow. There are very few other groups of animals in which so much maternal care is given as is the case with mammals.

The skeletal features of mammals are similar to those of other vertebrates—fish, amphibians, reptiles, and birds—but are easily distinguishable as mammalian. Some of the more obviously distinctive features of mammals are found in the skull. It is difficult to indicate a skeletal feature completely unique to mammals, especially because there are a variety of modifications.

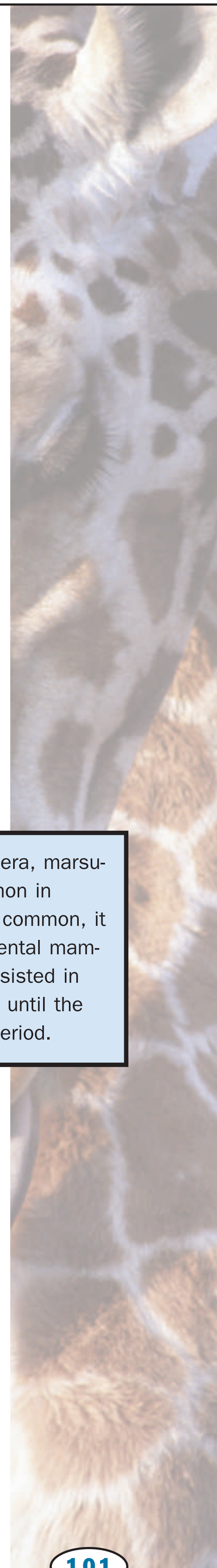
However, the general structural pattern of mammals is easily identified. Their teeth, which many consider to be part of the skeletal system, are what most scientists rely upon to identify mammals. Individual molar teeth have many cusps, or points. Reptiles, amphibians, and fish usually have simple cone-shaped teeth that are often replaceable throughout the life of the animal. Birds have no teeth at all. Mammals have only one set of replacement teeth, and when the second set is worn out, the animal may starve.

The heart of mammals is very efficient because it is four-chambered. Only birds and possibly dinosaurs share this characteristic. There are two atria and two ventricles for increased circulation. The great efficiency of this type of structure is important for high-energy animals, who need a great deal of oxygen to support their high rate of metabolism. Reptiles have a three-chambered heart and, consequently, have less efficient bodies because of the mixing of unoxygenated and oxygenated blood. This increased circulation pressure in mammals is the primary reason they are considered warm-blooded, or **homeothermic**.

Perhaps the most significant characteristic of mammals is the **placental** uterus. While many animals keep their eggs inside their bodies until the young hatch, the young are still living off a yolk inside an enclosed egg. The egg may hatch inside the parent, but it receives no nourishment from the parent throughout its development. Mammals, on the other hand, are often simply described as placental animals because of the remarkable temporary organ called the placenta.

homeothermic describes animals able to maintain their body temperatures

placental having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus



Once internal **fertilization** has occurred within the female, the egg attaches to the placenta, a blood-rich and nourishing lining of the uterus. The egg stays there and continues to develop into a fetus. The young mammal receives all its nourishment from the mother and is completely dependent on her even after it leaves the uterus.

fertilization the fusion of male and female gametes

Classifying Mammals

The classification of mammals is complicated and always changing. The natural world does not always fit neatly into schemes of classification. The **monotremes** are one example. The most famous monotreme is the duck-billed platypus. The spiny anteater, or echidna, is also a monotreme. The monotremes are the only group of mammals that are **oviparous**, which means they lay eggs that hatch outside the body. Their ancestry is not well-known and no monotreme fossils have been dated before the Pleistocene epoch (1.6 million years ago). Scientists continue to debate whether monotremes should be placed in the mammal group, but an agreement has not been reached.

monotremes egg-laying mammals such as the platypus and echidna

oviparous having off-spring that hatch from eggs external to the body

Marsupials. Yet there are numerous agreements about classification. For example, one of the many agreed-upon criteria for deciding which groups of mammals are more primitive is based on placental care. The most primitive mammals that are fully accepted into the group are marsupials. Marsupials all have an abdominal pouch, the marsupium, in which they raise their young. The young are initially nourished in the uterus, but only for a short time, and a placenta-like organ is not very well developed.

Perhaps these mammals represent the first type of true mammal. It is believed that the early fossil mammals were marsupials. Fossils with marsupial-like skulls are found in rocks over 100 million years old. Many of today's marsupials are small, rodent-looking mammals like the brown four-eyed opossum or the ashy-mouse opossum. It is easy to imagine that mammals similar to these small creatures lived in the debris of forest floor alongside the mighty dinosaurs. They would have been hard to see and too quick for predators. Insects were in abundance and would, as they do today, compose the major diet of these tiny primitive mammals.

During the Mesozoic era, marsupials were very common in North America, more common, it is thought, than placental mammals. Marsupials persisted in this part of the world until the mid- to late-Tertiary period.

It is believed that marsupials reigned in the mammal world for many millions of years. Fossils of marsupials, and even filmed footage of now-extinct marsupials, like the Tasmanian devil, show that, without competition from the large dinosaurs and reptiles, they grew to very large sizes. Many became large **carnivorous** marsupials, like the saber-toothed *Thylacosmilus*. This mighty predator was the size of a jaguar and very dangerous in appearance.

carnivorous animals that eat other animals

Marsupial-type fossils are found over most of the planet, with the exception of the oceans. Fossil opossums have even been found on Antarctica. They are believed to have survived on this vast expanse of land when the **climate** there was more comfortable for life. When South America split from the large supercontinent of Pangea, it became a type of continental raft on which species of marsupials evolved in isolation from their cousins in Africa and Europe.

climate long-term weather patterns for a particular region

During the Ice Age, when tremendous amounts of water were tied up in ice sheets, the **Isthmus** of Panama was exposed, enabling marsupials to travel north into North America. Although many have since become extinct, it is still possible to see frequently the hardy opossum, *Didelphis*, in most regions of Mexico and the United States. In South America many marsupials still live in the forests, although their numbers are dwindling.

isthmus a narrow strip of land

The last stronghold for marsupials is the continent of Australia. Because of its isolation from the other continents after the split-up of Pangea, the more evolved and efficient placental mammals never reached Australia. It is as though time was frozen for the marsupials in Australia. Delightful animals, like the kangaroo, koala, wombat, and numbat, still exist in this remote continent. However, as in the rest of the world, they are under threat from the placental mammals. True mammals, like house cats and rabbits, are making it hard for the small marsupials to survive. Rabbits and other grazers are competing for grasslands. The eucalyptus forests necessary for the survival of the koala are threatened. However, many human steps are being taken to help preserve these mammals in the wild and there are still many marsupials found in Australia.

Placental mammals. In every corner of the world, placental mammals thrive. They exist as two major types of animals, carnivores and herbivores. The story of the **herbivores** is as complicated as is that of the smaller groups of these mammals.

herbivores animals who eat plants only

Rodents are often considered a nuisance, but their success at survival under the most extreme conditions is undisputed. They are hardy and reproduce quickly. Despite the efforts of many farmers, home dwellers, and urban developers, rodents have managed to live side by side with humans and even have secured an entire means of survival from the waste of humans, another highly successful placental mammal. Rodents are at the base of many food chains in the wild and in cities.

Around forty million years ago, an evolutionary adaptation of grasses provided the stimulus for a burst of evolution among the herbivores. Grasses developed a metabolic way to survive in more arid conditions. These new species are called the C4 grasses. These grasses, like crabgrass, are a type of grass that can survive in hostile environments. As these tougher species of grass became available in regions like flat plains and plateaus, the animals that ate the grass ventured into more open space. While this was good for herbivores because it expanded their food resources, it also became easier for predators to see them.

The animals that survived this evolutionary explosion were those with increased running ability. Grazing mammals evolved longer and narrower legs which they used to elude predators. Groups such as the gazelle, antelope, and horse became the fastest long-distance runners on Earth. They still exist and show no signs of slowing down.

In response, the predators also became faster. The large cats are unanimously considered the fleetest predator on land. The amazing speed of the cheetah has been recorded many times. It is heralded as the fastest land animal alive. Before their extermination by humans, many species of large cats roamed over most of the planet. The American lion and saber-toothed cats were only recently, in geologic terms, eliminated from Earth.

A ten-day-old grizzly bear cub attempts to nurse. The mammary glands that produce the milk for this cub characterize mammals alone.

Bears, many of whom are actually omnivores, are considered by most to be the mightiest land predator on the planet today. The strength of the grizzly, kodiak, and polar bear is legendary. They are surprisingly fast runners, and very few animals are prepared to withstand combat with them.

Mammals survive not only on land but in the ocean as well. Whales, dolphins, seals, walruses, otters, and other marine mammals are very successful in their ways of life. The killer whale may be the largest predator on Earth. They feed on other marine mammals and are especially fond of seals.

The largest animal on Earth is a mammal. The blue whale is estimated to weigh around 150 tons and is almost 27 meters (89 feet) long as an adult. It feeds on tiny **krill**, a shrimplike animal that it catches with a the help of a **baleen**, a sievelike structure in its mouth.

krill an order of crustaceans that serves a food source for many fish, whales, and birds

baleen fringed filter plates that hang from the roof of a whale's mouth

Many species of whales had been hunted to extinction by the 1960s. Fortunately, an international ban was placed on the hunting of these magnificent mammals and many species are increasing in number.

It is surprising to read that the ancestors of whales were land dwellers, a group of mammals called creodonts. Fossil evidence indicates that these animals may have become increasingly adapted to a marine environmment until they evolved to a completely water-based existence. They are still mammals, however, as evidenced by the formation of a placenta, live birth, and young that suckle for breast milk. Baby whales, although quite large, are completely dependent on their mothers for a long time.

One may find a mammal just about anywhere on Earth. They have evolved to fill almost every possible **niche** and continue to flourish despite harsh environmental and climatic changes. The current loss of mammals,

niche how an organism uses the biotic and abiotic resources of its environment

however, continues at an alarming rate and, over the last 20,000 years, the loss of mammal species, like the mammoth, is staggering. It is hoped this trend will not only halt but, in cases of endangered mammals, be reversed.

Ellen Brook Hall

Bibliography

Hickman, C., L. Roberts, and F. Hickman. *Integrated Principles of Zoology.* St. Louis, MO: Times Mirror/Mosby College Publishing, 1984.

Lillegraven, J. A., Z. Kielan-Jaworowska, and W. Clemens. *Mesozoic Mammals: The First Two-Thirds of Mammal History.* Berkeley: University of California Press, 1979.

Macdonald, David. *The Encyclopedia of Mammals.* New York: Facts on File, 1984.

Marine Biologist

Marine biology is a field of study encompassing all oceanic life, including representatives from each of the taxonomic kingdoms (plants, animals, blue-green algae, fungus, and single-celled microorganisms called protists). **Taxonomy** is a system used to name organisms based on their evolutionary relationships. Specializations within this field include **ecology**, environmentalism, **parasitology**, reproduction, ocean farming, and anatomy. Many ocean-dwelling organisms have yet to be discovered and assigned a taxonomic nomenclature (scientific name). Other specializations are based on ocean regions, such as coastal, coral reef, deep-sea trench, arctic, and open ocean marine biology. This field is strongly rooted in international research and cooperation because ocean wildlife does not necessarily belong to any one government or country. It necessitates a love of the outdoors, and of the ocean in particular, a willingness to work independently at distant locations, good analytical skills, excellent writing skills, and environmental awareness. Strong swimming skills and certification in scuba (a word derived from the acronym for self-contained underwater breathing apparatus) are also mandatory. Marine biologists may seek employment as a teacher, researcher, resource manager for a governmental agency, field biologist in a consulting company, advocate in an environmental organization, or technician in an aquarium or zoo.

taxonomy the science of classifying living organisms

ecology the study of how organisms interact with their environment

parasitology the study of parasites

For those who have a strong interest in fishes, marine mammals, marine ecology, or any other related field, it is best to obtain a strong background in basic biology and oceanography. Look for colleges with large marine biology departments, preferably located along the coast of an ocean environment that interests you. Search the Internet for information on the field and make contacts with specialists at other institutions. It is extremely important that you join a research lab or intern at an aquarium or on a research boat during your undergraduate college education. Training marine mammals, for instance at a theme park or for biopsychology or communications research, requires knowledge of psychology and possibly of veterinary science. For a career in academics or college professorship, a doctoral degree from a high-level research institute is necessary. If you wish to work at a zoo or teach high school, a master's degree will suffice.

Rebecca M. Steinberg

Marine biologists diving in Bermuda use the quadrat—an ecological sampling unit that consists of a square frame of a known area—to help them count the number of a given species within a given area.

Bibliography

Moyle, Peter B., and Joseph J. Cech. *Fishes: An Introduction to Ichthyology.* Upper Saddle River, NJ: Prentice Hall, 2000.

Nybakken, James Willard. *Marine Biology: An Ecological Approach.* San Francisco: Benjamin Cummings, 2001.

Mayr, Ernst

American Biologist and Ornithologist

1904–

Ernst Mayr, one of the cofounders of the "Modern Synthesis" in evolutionary biology (along with Theodosius Dobzhansky, George Gaylord Simpson, and G. Ledyard Stebbins), is a naturalized American citizen born in Kempten, Germany. The Modern Synthesis sought to integrate Charles

Ernst Mayr attempted to synthesize the natural selection theory and population genetics.

Darwin's theory of **natural selection** with the recent development of **population** genetics by R. A. Fisher, Sewall Wright, and J. B. S. Haldane.

natural selection a process by which organisms best suited to their environment are most likely to survive and reproduce

population a group of individuals of one species that live in the same geographic area

Mayr showed an ardent interest in birds from an early age and took only eighteen months to complete his doctoral program in ornithology at the Berlin Natural History Museum (1926). In 1928 he began leading a series of ornithological expeditions to New Guinea, the Philippines, and the Solomon Islands. His field guides to the birds of these areas continue to be used by scholars of ornithology.

After his Pacific forays, Mayr joined the staff of the American Museum of Natural History (AMNH) in New York City in 1931 and was appointed curator of its ornithology collection in 1932, a position he would hold for over twenty years. During this time, he described twenty-six new bird species and 410 subspecies. In the style of Darwin, his intellectual hero, Mayr used his accumulated knowledge of natural history to gain insight into broad evolutionary questions. His work at AMNH focused on systematics: the classification, genealogy, and defining boundaries of species and populations. Mayr's classic "biological species concept" won wide acceptance among scientists in its time, and continues to structure many scientist's thinking about species: "species are groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups." This definition has led to the identification of many previously unknown species. Mayr's contribution to systematics is reflected in two seminal works: *Systematics and the Origin of Species* (1942), where the biological species concept was presented, and *Methods and Principles of Systematic Zoology* (1953).

Mayr left AMNH in 1953 to become the Alexander Agassiz Professor of Zoology at Harvard's Museum of Comparative Zoology, a position he still holds today as emeritus faculty; in 1961, he was appointed director of the museum. At Harvard, Mayr shifted his intellectual focus from systematics to speciation (how species are formed) and other general questions in evolutionary biology. He published *Animal Species and Evolution*, a major synthesis of evolutionary theory, in 1963. Mayr has been a leading advocate of population thinking—the notion that species are best understood by taking into account the fact that traits vary among individuals—in the classification and study of living things. According to Mayr, speciation typically occurs as a result of geographic separation, and therefore from a reduction of gene flow, between large parent populations and small founder populations.

Mayr is an eminent scholar in the history of evolutionary biology, and his recent career is marked by two major works on the subject, *The Growth of Biological Thought* (1982) and *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought* (1991).

Mayr's accomplishments have earned him numerous honors, including the National Medal of Science (1970), the U.S. government's highest award for scientific research, and the Royal Swedish Academy of Science's Crafoord Prize (1999).

Gil G. Rosenthal

Bibliography

Mayr, Ernst. *Evolution and the Diversity of Life: Selected Essays.* Cambridge, MA: Harvard University Press, Belknap Press, 1997.

Medical Doctor

The long and sometimes bizarre history of Western medicine can be traced as far back as an Egyptian surgical papyrus of the seventeenth century B.C.E., which advises treating a head wound by "first softening the head with grease, then pouring milk into both ears" (Swierczynsky 2000, p. 115). Despite diagnoses and cures that might seem laughable or horrendous to us, doctors have always intended, as do medical students today, to "make a difference in people's lives, to relieve pain and suffering." From the bloodletting of the Middle Ages, where surgeons got their nickname "leeches," to the miracle antibiotics and technological advances of the twentieth century, doctors have seen their job as the treatment of illness, injuries, and other adverse conditions.

Any degree holder can apply to medical school upon qualifying through the Medical Colleges Admission Test. The four-year graduate program includes two years of work in the areas of anatomy, biochemistry, biology of healthy organisms, pathology, immunology, writing skills, and clinical studies. The third year is a forty-hour hospital workweek divided into intensive sections of internal medicine, surgery, psychiatry, obstetrics and gynecology, and pediatrics. In the fourth year, the student takes electives focusing on an area of interest and applies for a residency with a hospital. Generalists, including family practice and internal medicine interns, take a three-year residency. Surgeons and specialists require up to five years.

The old catastrophic view of medicine is expanding to include preventive care. Diet, exercise, herbal remedies, healing touch, and techniques such as acupuncture are being added to the repertoire of tools for staying healthy as well as for recovering from serious illness. And doctors would probably still agree with Galen, the ancient Greek, concerning the patient's participation: "confidence and hope do more than the physic."

Nancy Weaver

Bibliography

Health Reference Center. Medical History. Info Trac. Gale Group. Central Texas Library System subscription service.

Health Reference Center. Medical School. Info Trac. Gale Group. Central Texas Library System subscription service.

Swierczynsky, Duane. "You're Lucky to be Alive." *Men's Health* 15 (2000):115.

Mendel, Gregor

Botanist
1822–1884

Gregor Mendel, the father of **genetics**, was born on July 22, 1822, in Heinzendorf, Austria. He died on January 6, 1884. He was the first person to propose the idea of **genes** and to apply mathematics to genetics. Although his work was initially ignored by scientists, it proved to be the basis of modern genetics.

genetics the branch of biology that studies heredity

genes segments of DNA located on chromosomes that direct protein production

Mendel's interest in natural science developed early. He studied at the Philosophical Institute at Olmütz for two years. In 1843 he entered the

Gregor Mendel was a pioneer in the field of genetics.

artificial pollination manual pollination methods

recessive hidden trait that is masked by a dominant trait

monastery in Brünn, becoming a priest in 1847. Then he went to the University of Vienna, where he studied science from 1851 to 1853. In 1854 Mendel returned to Brünn and taught natural science in the technical high school there until 1868.

Seeking to learn how plants inherit different traits, Mendel began his experiments with garden peas in the small monastery garden in 1856. From 1856 to 1863 Mendel grew almost 30,000 specimens of garden peas. These plants had sharply contrasting characteristics (tall versus short, smooth seed versus wrinkled seed, and so on). He studied seven pairs of alternative characteristics, making hundreds of crosses by **artificial pollination**.

Mendel kept very careful records of the plants that he crossed and the resulting offspring. He noted that the occurrence of the alternative characteristics in the crossed varieties of plants followed simple statistical, mathematical laws. For example, Mendel crossed species that produced tall plants with those that produced short plants. Then, he counted the numbers of tall and short plants that appeared in subsequent generations. In the first generation, all of the plant offspring were tall. The next generation had some tall plants and some short plants in proportions of three (tall) to one (short). This showed that no blending of traits occurred (no medium-height plants). Further, if allowed to self-pollinate (fertilize themselves), the short plants always had short offspring. Mendel proposed that each plant received one character from each of its parents. Tallness was dominant and shortness was **recessive**, appearing only in later generations. Mendel also showed that when several pairs of alternative characteristics are observed, the several pairs enter into all possible combinations in the subsequent generations. In the pea plants he studied, he observed that the seven alternative characteristics recombined at random. He worked out the statistics of these combinations and confirmed his predictions by experiment.

Mendel developed three theories to explain the results of his experiments. His first law is the principle of segregation. It states that during the formation of sex cells (egg and sperm), paired factors are segregated (separated). Therefore, a sperm or egg may contain either a tallness factor or a shortness factor, but cannot contain both. The second law, the principle of independent assortment, states that characteristics are inherited independently of one another. Thus, the fact that the tallness factor is inherited does not determine which alternative of any other pair of characteristics is inherited. The law of dominance, which is the third theory, states that each inherited characteristic is determined by the interaction of two hereditary factors (now called genes). One factor always dominates the other (for example, tallness always dominates shortness). Mendel was the first to understand that trait units are physical particles passed from one generation to another by reproduction. This is remarkable, since at that time knowledge about cell structure was limited.

hybrid offspring resulting from the cross of two different species

It is now known that Mendel's second principle applies only to genes that are transmitted in different linkage groups. Also, the appearance (or dominance) in **hybrid** offspring of one of the alternative characteristics has now been proven not to be true for all alternative characteristics. However, these limitations do not affect the fundamental truth of Mendel's findings. Mendel's system, called Mendelism, is one of the basic principles of biology.

Mendel presented his findings to his fellow scientists in 1865, but they failed to see the revolutionary nature of his work. When he was promoted to head of the monastery in Brünn in 1868, Mendel turned his focus away from science to concentrate on his duties at the monastery. He did, however, continue work in botany, bee culture, and the weather until his death.

Mendel was widely respected and loved, but went unrecognized as the great scientific thinker that he was. Fame and due credit came to Mendel only after his death. In 1900, three other European scientists independently obtained results similar to Mendel's. The researchers realized that he had already published both the experimental data laying out his results and a general theory explaining them nearly thirty-five years earlier. SEE ALSO Biological Evolution; Genes; Genetics.

Denise Prendergast

Bibliography

The New Encyclopedia Britannica, 15th ed. Chicago: Encyclopedia Britannica, Inc., 1993.

The World Book Encyclopedia. Chicago: World Book, Inc., 1995.

The Year 2000 Grolier Multimedia Encyclopedia. Danbury, CT: Grolier Interactive Inc., 1999.

Internet Resources

MendelWeb. University of Washington, Seattle.<http://www.netspace.org/MendelWeb/>.

Mesenchyme

Mesenchyme is a tissue found in organisms during development. It consists of many loosely packed, nonspecialized, mobile cells. Mesenchyme is derived primarily from the **mesoderm**, although there are also mesenchymal cells known as the neural crest cells, which derive from ectoderm. Mesenchyme gives rise to diverse structures of the developing organism, including **connective tissue**, bone, **cartilage**, teeth, blood and plasma cells, the endothelial lining of the vessels of the circulatory and lymphatic systems, and **smooth muscle**.

Mesenchymal cells are star-shaped in appearance, with an oval-shaped nucleus and comparatively little **cytoplasm**. They are widely spaced, with considerable extracellular space between cells. This space is filled with a dense intercellular **matrix**. An important characteristic of mesenchymal cells is that they are mobile, and move with a crawling, amoeboid motion.

Mesenchymal cells are undifferentiated and are therefore **pluripotent**—that is, they have the capacity to differentiate into any number of tissue types. A group of mesenchymal cells that will differentiate into another tissue type is called a blastema.

Mesenchymal cells are contrasted with the other major embryonic cell type: **epithelial cells**. Unlike mesenchymal cells, epithelial cells are not mobile. Epithelial cells form continuous sheets, with little extracellular space between cells. All epithelial cells have two definite ends, the basal end and

mesoderm the middle layer of cells in embryonic cells

connective tissue cells that make up bones, blood, ligaments, and tendon

cartilage a flexible connective tissue

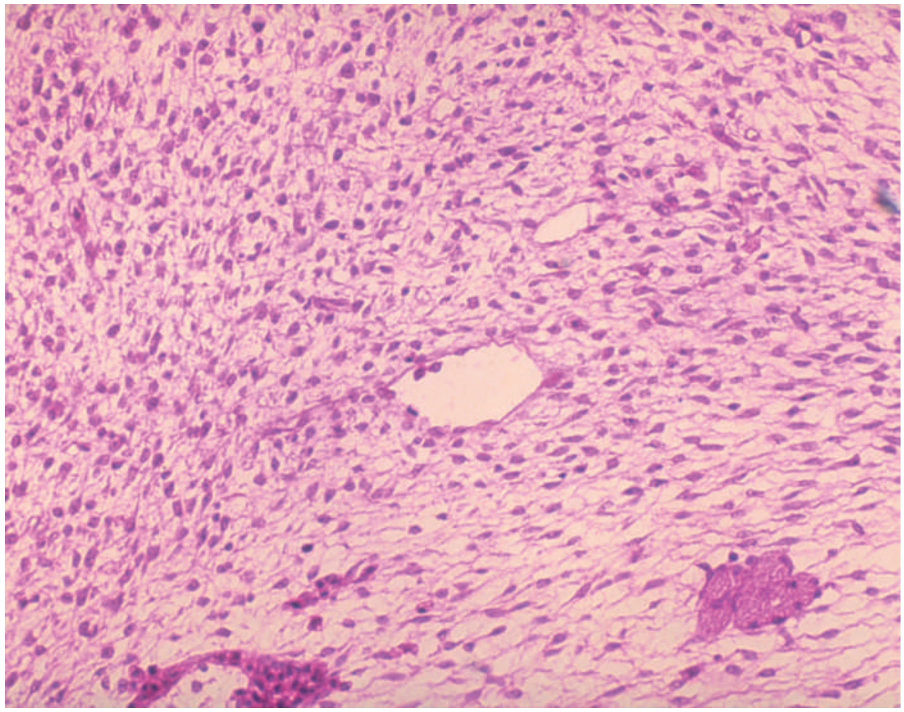
smooth muscle muscle of internal organs that is not under conscious control

cytoplasm fluid in eukaryotes that surround the nucleus and organelles

matrix the nonliving component of connective tissue

pluripotent a cell in bone marrow that gives rise to any other type of cell

epithelial cells cells that occur in tightly packed sheets that line organs and body cavities



Mesenchyme is the part of the embryonic mesoderm from which connective tissue and lymphatic and circulatory systems develop.

the apical end. Epithelial cells are attached to a structure known as basement membrane by their basal end.

Many important developmental events take place as a result of interactions between mesenchymal and epithelial cells. Often, epithelial cells are induced by adjacent mesenchymal cells, that is, they change in form or shape in response to signals from the mesenchyme. Induction occurs either via mechanical processes, in which the migrating mesenchymal cells cause changes in the arrangement of epithelial cells, or by molecular agents released by mesenchymal cells.

Epithelial-mesenchymal transitions, in which cells change from epithelial to mesenchymal morphology, are also frequent during development. These transitions take place through the loosening of the cell adhesion molecules that keep epithelial cells organized in tight sheets. The reverse transition (mesenchymal to epithelial) occurs during developmental processes as well.

Although mesenchymal cells are technically found only in embryonic tissue, some cells do remain undifferentiated in adults. These serve as stem cells, which retain the ability to differentiate into diverse types of connective tissue as they are needed by the body for regeneration or repair.

Mesenchyme initially gives rise to three types of cells—fibroblasts, which generate collagen; myoblasts, which form muscle cells; and **scleroblasts**, which form connective tissue. Scleroblasts later differentiate into **osteoblasts**, which generate bone; chondroblasts, which generate cartilage; odontoblasts, which generate dentin in teeth; and **ameloblasts**, which generate tooth enamel.

scleroblasts cells that give rise to mineralized connective tissue

osteoblasts potential bone forming cells found in cartilage

ameloblasts cells that form dental enamel

Jennifer Yeh

Bibliography

Gilbert, Scott F. *Developmental Biology*, 5th ed. Sunderland, MA: Sinauer Associates, 1997.

Gould, James L., William T. Keeton, and Carol Grant Gould. *Biological Science*, 6th ed. New York: W. W. Norton & Co., 1996.

Hildebrand, Milton, and Viola Hildebrand (ill.). *Analysis of Vertebrate Structure*. New York: John Wiley & Sons, 1994.

Metamerism

See Serial Homology.

Metamorphosis

Metamorphosis, or a change in form, in biology means the transition from a larval stage to an adult stage. In most animals, embryonic development leads to the formation of a larval stage with very different characteristics than the adult stage. Larval morphology, or form, may be specialized for some function such as growth (which requires feeding and associated structures) or dispersal. Some larval forms, called exotrophic, feed, while others, called **endotrophic**, are nonfeeding. Juvenile and adult forms often live in very different environments.

endotrophic deriving nourishment from within

Cnidarians have varying types of metamorphosis. Some species have three distinct life history stages: the planula, medusa, and polyp. The planula stage is the free-living larval stage. The medusa stage involves a single individual or a colony of individuals that act as a single free-swimming organism (examples include jellyfish and man-o-war). The polyp stage is **sessile** (adhered to the substrate) and may involve a single individual or a colony of individuals (examples include sea anemones and corals). Some species lack the free-swimming medusa stage. In others, the medusa is the dominant life history stage and the polyp stage is lacking completely.

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

sessile immobile, attached

Molting and metamorphosis in **arthropods** is controlled by environment and **hormones**. Insects experience no size increase in the egg, pupal (the thirdstage in the life of an insect that undergoes complete metamorphosis), or adult stages. All growth occurs during the intermediate larval or nymphal stages. Anametabolous (without change) metamorphosis occurs in the primitive insect groups Colembola, Diplura, Protura, and Thysanura. Juveniles change little except in size and proportion from egg to adult. After reaching adulthood, defined as sexual maturity, they continue to molt, adding antennal segments.

molting the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

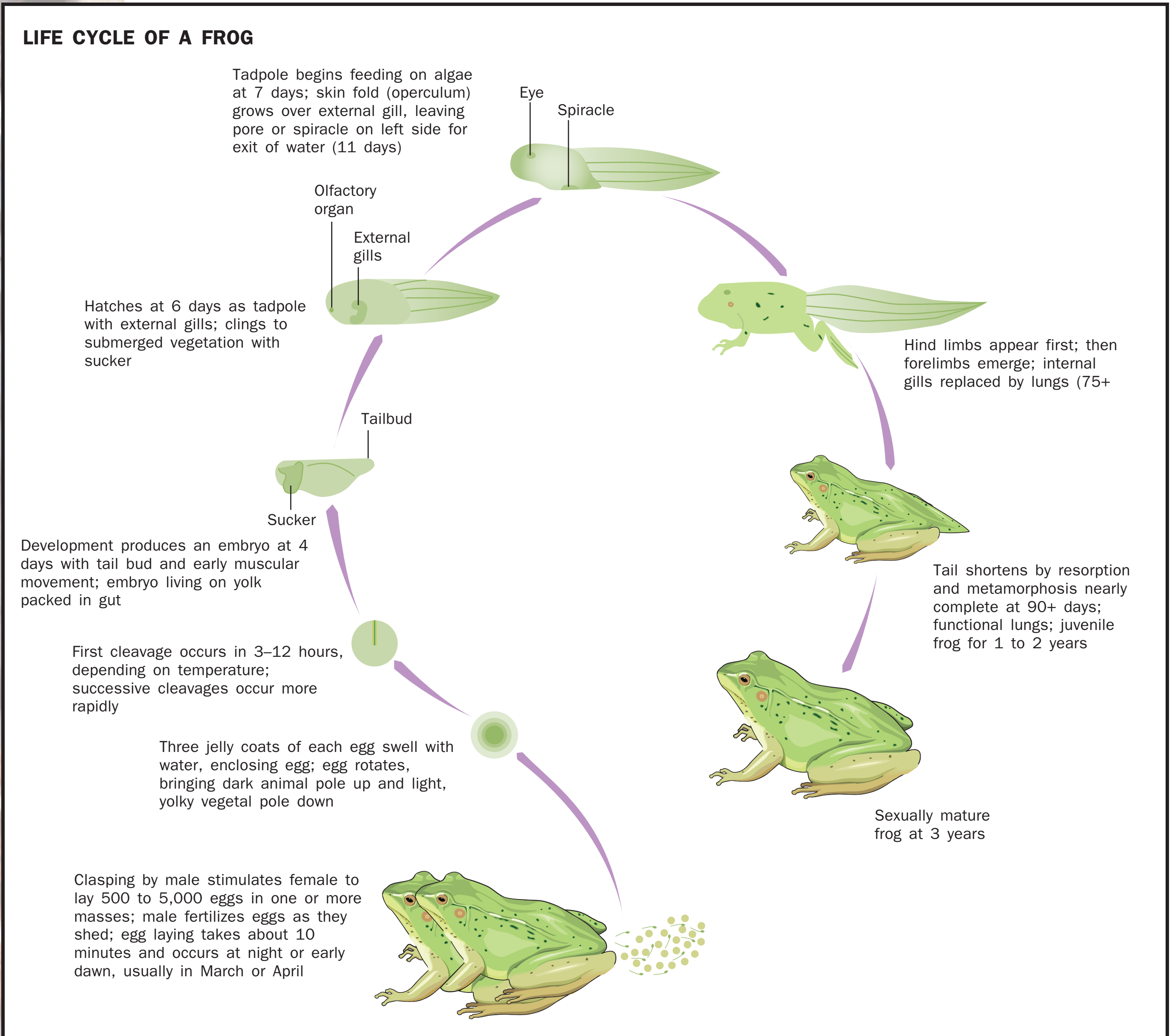
hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

Many insects (including dragonflies, grasshoppers, and cockroaches) and **crustaceans** (crawfish and crabs) develop through hemimetabolous (incomplete or gradual) metamorphosis. In hemimetabolous metamorphosis, the insect egg hatches into a nymph. The nymph is similar to the adult in general morphology, only smaller. The nymph is an actively feeding stage, and as it grows it must shed its **exoskeleton** and produce a new, larger one. This process is called molting. In insects with hemimetabolous metamorphosis, the gonads do not mature until after the final molt.

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

exoskeleton hard outer protective covering common in invertebrates such as insects

Some insects (including flies, butterflies, wasps, and bees) have holometabolous metamorphosis (they undergo a complete metamorphosis,



The life cycle of the leopard frog (*Rana pipiens*). Metamorphosis occurs when the tadpole grows legs, and ends with the resorption of the tail.

instars the particular stage in an insect or arthropod between moltings

having distinct larval and pupal stages). There are four distinct stages in the life cycle of holometabolous insects: egg, larva, pupa, and imago (adult). The larva is segmented and wormlike. The larval stage is a feeding stage and consists of several subdivisions called **instars**. Each instar ends in molting, which allows the larva to grow.

The final instar ends with pupation. Prior to pupation, the animal stops feeding and the cuticle hardens and darkens to form the puparium (pupal chamber), where metamorphosis will take place. The pupa begins to darken just prior to the emergence of the imago. In the larvae of these organisms, imaginal disks (clusters of cells carried with a larva that will develop into different adult body parts) are formed. These disks will produce adult organs, but they remain quiescent, or inactive, in the embryo until the appropriate time.

Most, but not all, amphibians have a biphasic (two-phase) life history with an **aquatic** larval stage that **metamorphoses** to become an adult, a process known as indirect development. Many frogs have a free-living, aquatic larval stage as a tadpole. Near the end of the larval stage, many larval structures are reabsorbed or remodeled and adult structures begin to form.

aquatic living in water

metamorphoses changes drastically from its larval form to its adult form

During metamorphosis bones begin to ossify, the tail is reabsorbed, limbs form, and larval respiratory and feeding structures (including gills and a beak with keratinized—covered with a tough protein like our fingernails—mouth parts) are replaced by adult structures (including **lungs** and movable jaws). The digestive system is remodeled to accommodate a transition from a largely **herbivorous** diet to one that is strictly **carnivorous**.

lungs sac-like, spongy organs where gas exchange takes place

herbivorous term describing animals that eat plants

carnivorous term describing animals that eat other animals

In salamanders, the larval stage is more similar to the adult stage than is the case with frogs. Metamorphosis usually involves the replacement of larval gills with lungs; **ossification** of the skull, vertebral column, and limbs; and the remodeling of the tail and feeding apparatus to conform to the requirements of life on land.

ossification the deposition of calcium salts to form hardened tissue such as bone

Although this familiar mode of development is common among amphibians, some salamanders, caecilians, and frogs lack a free-living larval stage. In many species with a monphasic life history, a miniature version of the adult is hatched directly from the egg (direct development) in what is called **ovoviparity**, or birthed by the female, in what is known as **viviparity**.

ovoviparity having offspring that hatch from eggs retained in the mother's uterus

viviparity having young born alive after being nourished by a placenta between the mother and offspring

The loss of a free-swimming larval stage has been hypothesized to release a major limit on morphological diversification in some groups of direct-developing frogs, because the pre-pattern established by larval structures is no longer present. Evidence of this morphological release can be seen in the great diversity of species and **morphologies** attained by some amphibian groups that have lost the free-living tadpole stage.

morphologies the forms and structures of an animal

Andrew G. Gluesenkamp

Bibliography

Brusca, Richard G., and Gary J. Brusca. *Invertebrates.* Sunderland, MA: Sinauer Associates, 1990.

Gilbert, Scott F. *Developmental Biology*, 5th ed. Sunderland, MA: Sinauer Associates, 1997.

Gould, Stephen Jay. *Ontogeny and Phylogeny*. Cambridge, MA: Harvard University Press, Belknap Press, 1977.

Kalthoff, Klaus. *Analysis of Biological Development*, 2nd ed. Boston: McGraw-Hill, Inc., 2001.

Metazoan

In the tenth edition of his book *Systema Naturae* (1758), Swedish botanist Carolus Linnaeus developed a biological classification system (now known as the Linnaean System) that placed all organisms into seven hierarchical groupings. He suggested that all organisms could be classified as belonging to two kingdoms, the Plantae (plants) and the Animalia (animals), and that members of these kingdoms could be distinguished by whether they have the ability to "sense" (both plants and animals grow and live, but only

animals sense). This two-kingdom classification system remained virtually unchallenged for over a century.

prokaryotes single-celled organisms that lack a true cell nucleus

eukaryotes organisms containing a membrane bound-nucleus and membrane-bound organelles

Today, most biologists group living things into five kingdoms: the Monera, the Protista, Fungi, Plants, and Animals. The Monera includes all **prokaryotes**. The monerans include the most ancient forms of life and were the only organisms on Earth from around 3.5 to 1.5 billion years ago. The Protista is a diverse group of single-celled **eukaryotes** that originally derived from the Monera. The protists gave rise to the other three kingdoms: the multicellular fungi, plants, and animals.

autotrophs organisms that make their own food

absorption the movement of water and nutrients

photosynthesis converting sunlight to food

heterotrophs organisms that do not make their own food

protozoa a phylum of single-celled eukaryotes

Plants are distinguished from fungi and animals because they are **autotrophs**, meaning that they gain all their nutrients and energy from inorganic materials and from the Sun. Plants take nutrients from the soil through **absorption**, the passing of molecules through pores in cells; they take energy from the Sun through **photosynthesis**. Fungi are different from plants and animals because they are **heterotrophs** (they require preformed organic material, that is, material made by other organisms), which obtain their nutrients through absorption. Animals, on the other hand, are heterotrophs that obtain their nutrients through ingestion, the active intake of other organisms or decomposing organic material. Today's Animalia, also called the Metazoa, differs from the Animalia of Linnaeus in that it does not include any of the animal-like unicellular eukaryotes, commonly termed the **Protozoa**, which are now grouped in the Protista.

flagella cellular tail that allow the cell to move

Multicellularity evolved in the Protista a number of times. The commonly held view is that multicellularity derived from colonial unicellular ancestors, which formed loose collections of interconnected cells. The benefit of being part of a colony is that individual cells may become specialized for certain tasks, such as sensation, secretion, or gamete production, and thus raise the efficiency of the colony as a whole. As these colonial organisms become more intimately associated, some members may lose their **flagella** to become completely dependent on their neighbors. At the point when a colony transports nutrients from cell to cell, eliminating the necessity of all cells to feed individually, the colony becomes a true multicellular organism.

aquatic living in water

habitats physical locations where an organism lives in an ecosystem

niche how an organism uses the biotic and abiotic resources of its environment

Multicellular eukaryotes arose approximately 700 million years ago in **aquatic habitats**. One of the first benefits that multicellularity allowed was an increase in organism size. Greater size and greater cell number allowed greater variation in organism shape and structure. Consequently, the diversity of multicellular life exploded and began occupying a variety of new **niches**. Around 400 million years ago, multicellular eukaryotes living at the edges of lakes and streams colonized land, giving rise to the enormous diversity of terrestrial multicellular life seen today.

consumers animals that do not make their own food but instead eat other organisms

The Metazoa contains more species than any other kingdom. While plants are relatively immobile and utilize simple molecules as a food source, animals have become specialized **consumers** of all types of organisms, including other animals.

Brief Survey of the Diversity of the Animal Kingdom

The sponges are a group of sedentary aquatic animals first classified as plants. Although sponges and other animals evolved from protists, sponges may have arisen independently from the other animals. Sponges obtain their nutrients by drawing water into a central cavity and filtering the water for food. They are able to move water through their bodies through the coordinated beating of flagellated cells that line their pores. Sponges differ from other animals in that they lack distinct body tissues and body symmetry.

A second group of animals that may also have independently evolved from protists contains the **cnidarians** and the ctenophorans. These animals are **radially symmetrical**, meaning that their body parts are arranged symmetrically around one main axis. Examples include jellyfish, sea anemones, and corals. Cnidarians differ from ctenophorans in that their mouth and anus form a single opening, whereas ctenophorans have separate openings for the mouth and anus so that food moves in a single direction through the gut.

The remaining metazoans are more closely related to each other than to the other animals. They may be classified into three groups: the **acoelomates**, the **pseudocoelomates**, and the coelomates. All these animals are **bilaterally symmetrical**, meaning that their bodies can be divided into mirror images through only a single plane.

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

radially symmetrical an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

acoelomates animals without a body cavity

pseudocoelomates animals with a body cavity that is not entirely surrounded by mesoderm

bilaterally symmetrical describes an animal that can be separated into two identical mirror image halves

Acoelomates are animals that lack internal body cavities. The acoelomates include the flatworms and the ribbon worms. Flatworms have distinct organs but do not have a fully formed digestive tract or a means for transporting oxygen through the body. Thus all cells must undergo respiration individually, necessitating a flat body whereby all cells have access to oxygen at the body surface. Ribbon worms are similar to flatworms but have a complete digestive tract and a simple circulatory system.

Pseudocoelomates have a simple, fluid-filled body cavity in which many of the internal organs float. The body cavity protects the internal organs from external jarring and allows them to grow somewhat independently from the rest of the body. The pseudocoelomates include the rotifers and the nematodes. Nematodes are probably the most numerous of all animal species, inhabiting virtually every corner of Earth. One of the most well-studied organisms in the world is the nematode *Caenorhabditis elegans*, a roundworm that lives in soil.

The third group of bilaterally symmetrical metazoans, the coelomates, have a relatively complex body cavity inside which the organs are suspended from the body wall. Most coelomates can be further divided into two groups, the **protostomes** and the **deuterostomes**, which are distinguished by the way in which cells of their **zygotes** divide. Protostomes include **mollusks** such as snails, **annelids** such as earthworms, and **arthropods** such as insects. The deuterostomes include **echinoderms** such as starfishes and chordates such as humans. SEE ALSO BINOMIAL (LINNAEAN SYSTEM); PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Todd A. Schlenke

protostomes animals in which the initial depression that starts during gastrulation becomes the mouth

deuterostomes animals in which the first opening does not form the mouth, but becomes the anus

zygotes fertilized eggs

mollusks large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

annelids segmented worms

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

Bibliography

Ax, Peter. *Multicellular Animals: A New Approach to the Phylogenetic Order in Nature.* New York: Springer-Verlag, 1996.

Brusca, Richard C., and Gary J. Brusca. *Invertebrates.* Sunderland, MA: Sinauer Associates, 1990.

Hanson, Earl D. *The Origin and Early Evolution of Animals.* Middletown, CT: Wesleyan University Press, 1977.

Linnaeus, Carolus. *Systema Naturae*, 10th ed. Stockholm: Laurentius Salvius, 1758.

Lipps, Jere H., and Philip W. Signor, eds. *Origin and Early Evolution of the Metazoa.* New York: Plenum Press, 1992.

Nielsen, Claus. *Animal Evolution, Interrelationships of the Living Phyla.* Oxford: Oxford University Press, 1995.

Willson, Mary F. *Vertebrate Natural History.* Philadelphia: Saunders College Publications, 1984.

Internet Resources

Maddison, David R., and Wayne P. Maddison. *The Tree of Life.* <http://phylogeny.arizona.edu/tree/phylogeny.html>.

Migration

populations groups of individuals of one species that live in the same geographic area

Migration is defined as the regular, usually seasonal, movement of all or part of a **population** of animals. Many different animals migrate, including birds, hoofed animals, bats, whales, seals, and salmon. One-way movement of animals that do not return is called emigration. Emigration is due to different causes and is not considered migration. Also, the regular daily movements that many animals undertake are not considered migration.

Most birds and mammals that migrate follow an annual or seasonal pattern related to cyclic variations in temperature, vegetation, or precipitation. Salmon and some other fishes do not migrate annually. Instead, they return to their place of birth in order to reproduce. Some ethologists do not consider these movements migration but reserve the term for cyclic movements. In some parts of the world, animals will suddenly move into a new area temporarily. These sudden and temporary movements are called irruptions. Irregular movements, such as irruptions, are generally due to population growth during periods of abundant food followed by dispersal when food supplies diminish.

aquatic living in water

Most migrations involve horizontal movement. Animals move north and south with the seasons or move in a circular pattern to take advantage of cyclic rain patterns or new forage growth. Some animals, however, migrate by changing elevation. **Aquatic** animals may move from deeper water to the surface according to the season. Many birds, mammals, and insects migrate to higher or lower elevations in mountainous areas. This kind of migration produces the same kind of change in the environment as horizontal migration but involves only small horizontal displacements.

Invertebrate Migration

Some shrimp and crabs migrate for purposes of reproduction. Pregnant females move into shallow water to lay their eggs. The shallow water environment has fewer large predators, so the chances of the baby shrimp growing to maturity is increased. After they mature the shrimp move into deeper water to feed.

Probably the best known insect migrant is the monarch butterfly (*Danaus plexippus*). In the summer, these insects move northward as far as Canada's Hudson Bay, where they breed and reproduce. Adults from the last generation of the year migrate southward in autumn through Oklahoma and

Snow geese fly away from a grain field near Delta, Utah, a resting place for many migrating birds.

Texas. Many move as far south as the mountains of central Mexico. After overwintering in the tall firs of these mountains, they follow spring northward, breeding and laying eggs on their preferred milkweed plants. Since a few of the returning butterflies are members of the first generation that developed from the overwintered insects, they can be considered true migrators. Most insects that arrive in the north, however, have been born in route. The longest distance recorded for the complete flight of an individual monarch butterfly is 3,010 kilometers (1,870 miles), truly a remarkable flight for this tiny insect.

Vertebrate Migration

The three categories of migratory fishes are oceanodromous, **anadromous**, and **catadromous**. Oceanodromous fish live and migrate entirely in the ocean. The many species of herring with different migration patterns are typical of oceanodromous fish. Anadromous fish live in the sea and migrate to freshwater to breed. Pacific salmon are typical. They hatch from eggs in mountain streams or lakes. The young feed and grow in the freshwater, then migrate to the sea after a year. Adult fish usually remain in the sea for two or three winters, where they grow to full size. Then they undergo dramatic **physiological** changes and migrate back to the stream where they were born. There the females lay eggs that are fertilized by the males. Then both sexes die. Some Atlantic salmon breed two or three times.

anadromous moving from the ocean up a river to spawn

catadromous living in freshwater but moving to saltwater to spawn

physiological the basic activities that occur in the cells and tissues of an animal

Catadromous fish reverse the behavior pattern of anadromous fish. Catadromous fish spend most of their lives in freshwater, then they migrate to the sea to breed. Eels of the genus Anguilla are the best known. Both European eels and North American eels spawn in an area of the Atlantic Ocean known as the Sargasso Sea. The larval forms of the fish are carried by the Gulf Stream to the shallow waters of the continental shelves. After about two years, when the larval eels are about 8 centimeters (3 inches) long, a **metamorphosis** occurs. The nearly transparent free-swimming larval eels are transformed into bottom-dwelling, dark-colored, cylindrical fish. Their migration upstream is spectacular, as the young fish gather by millions, forming a dense mass several miles long. In freshwater, the eels grow to full size.

metamorphosis a drastic change from a larva to an adult

They live for several years in freshwater, then undergo a final metamorphosis before they swim back to the Sargasso Sea to spawn.

Terrestrial reptiles and amphibians do not migrate regularly enough to be significant, although some species migrate vertically. Reptiles and amphibians have evolved other strategies to deal with adverse environmental conditions, such as hibernation and estivation. Sea turtles are the exception. Most sea turtles migrate to beaches to lay their eggs. They then disperse back into the ocean. Green sea turtles (*Chelonia mydas*) lay their eggs on the coast of Costa Rica in Central America and then disperse through the Gulf of Mexico and the West Indies.

The taxonomic class Aves includes most of the best known migrating species. Most species of birds require a large input of food to maintain their body temperature and other behaviors. Many birds have evolved behaviors that allow them to move to areas where food is more abundant. Birds have evolved a highly efficient means for traveling swiftly over long distances with great economy of energy.

Migratory birds do not differ greatly in gross physiological characteristics from nonmigratory birds. There is a spectrum of birds from completely nonmigratory species to species that fly thousands of kilometers every year.

Since insect populations drop dramatically during the winter, insectivorous species of birds, such as warblers, flycatchers, and wagtails, are highly migratory and typically spend the winter in the tropics. The geographical arrangement of the North American continent determines migration routes for many species of North American birds. Principal routes are known as flyways. They include the Mississippi flyway, the central flyway, the Pacific flyway, and the Pacific oceanic route. Many birds spend the winter in the states that border the Gulf of Mexico, but the principal wintering areas are in Mexico and Central America. Panama has the greatest density of winter bird residents in the world.

Tropical regions do not have the four seasons of temperate regions, but they do have cyclic rainy and dry seasons. Birds of tropical regions migrate according to these wet and dry seasons.

Arctic terns (*Sterna paradisaea*) are the world champion migrators. These birds breed in the coastal regions of northern Europe, Asia, and North America. They then fly south and spend the winter in the extreme southern Pacific and Atlantic along Antarctic pack ice 17,600 kilometers (10,940 miles) from their breeding range. American populations of the Arctic tern cross the Atlantic to Europe, then fly south along the coast of western Europe. Arctic terns thus travel farther than any other bird species.

Most terrestrial mammals do not migrate. True migration among terrestrial mammals occurs mostly among large hoofed animals living in **habitats** with wide fluctuations of climatic and **biotic** conditions. For example, before the central United States was largely fenced in, American bison (*Bison bison*) migrated regularly. Large herds containing millions of animals moved in circular routes to the southern part of their range in winter and back north when spring rains brought fresh grass to the northern part of their range.

habitats physical locations where an organism lives in an ecosystem

biotic pertaining to living organisms in an environment

In North American Arctic regions, caribou (*Rangifer tarandus*) regularly migrate between the open tundra, where they calve, and the forest, where they spend the winter months. In winter, each caribou herd moves independently of the other herds in response to local conditions. Then in the spring, the herds move back onto the tundra. These migrations follow the same routes from year to year.

In contrast to terrestrial mammals, marine and flying mammals typically do migrate because of their inherently greater mobility. The only true flying mammals are the many species of bats. Huge colonies of Mexican free-tailed bats (*Tadarida brasiliensis*) spend the summer in Texas and adjoining states. The Congress Avenue Bridge in Austin, Texas, is home to the largest urban bat colony in the world, with around 1.5 million bats. It is a huge bat nursery containing females and nursing babies, called pups. Since they are insectivorous, these bats leave around the middle of November for their winter home in Mexico. They return in mid-March when the insect population in Texas increases dramatically. Most of the females in the Congress Avenue colony give birth to a single pup in early June.

> Mexican free-tailed bats are among North America's most important animals, from both an ecological and agricultural standpoint. They consume phenomenal volumes of insects nightly, a large number of which are agricultural pests. Serious bat population decline has been observed, largely due to human activities (i.e., the destruction of old buildings or the use of pesticide) and vandalism of important roosting habitats

Among mammals, the marine mammals are the distance record holders. Antarctic whales, such as humpback whales (*Megaptera novaeangliae*), migrate regularly to the tropics. Whales migrate to areas rich in food, particularly the northwestern coast of Africa, the Gulf of Aden, and the Bay of Bengal. Northern whales, such as blue whales (*Balaenoptera musculus*), have the same migratory habits as Antarctic whales. They migrate northward along the east coast of the United States, then through Davis Strait to Baffin Bay (north of Canada) or to waters off northern Scotland or the coast of Norway.

Migration Routes

Birds tend to follow well-defined migration routes called flyways. A population of birds may be scattered over thousands of square kilometers. As they begin their migration, the birds may be spread out over a migration front hundreds of kilometers wide. These routes are determined by geographical factors, ecological conditions, and meteorological conditions. Some routes cross oceans. American golden plover fly over open ocean from the Aleutian Islands southwest of Alaska to Hawaii, a distance of 3,300 kilometers (2,050 miles).

Many birds fly at relatively low altitudes. Hawks and other passerines, however, fly at altitudes as great as 4,000 meters (13,120 feet). The highest altitude ever recorded for migrating birds is 9,000 meters (29,520 feet) for geese near Dehra Dun in northwest India.

Some birds fly nonstop. Others are **diurnal**, flying during daylight hours and resting at night. Pelicans, storks, birds of prey, swifts, swallows, and finches migrate during daylight hours. Other birds reverse the pattern. Cuckoos, flycatchers, thrushes, warblers, orioles, and buntings fly at night and rest during the daylight hours.

diurnal active in the daytime

Most birds abandon their instinctive territoriality during migration. Even unrelated birds with similar habits sometimes travel together. Some birds migrate in large flocks. Geese, ducks, pelicans, and cranes fly in well-known V-shaped formations that allow each bird to receive lift from the bird just in front.

Finding Their Way

Animals use several different techniques to navigate while migrating or to locate the place of their birth. Experiments have demonstrated the ability of animals to orient themselves geographically. Starlings have returned to their nests after being moved 800 kilometers (500 miles) away; swallows have found their way home from more than 1,800 kilometers (1,120 miles). A Manx shearwater (*Puffinus puffinus*) flew 4,900 kilometers (3,040 miles) across the Atlantic from Massachusetts to Britain in twelve days. Laysan albatrosses (*Diomedea immutabilis*) found their way back to Midway Island in the Pacific after being released at Whidbey Island, Washington. The journey covered 5,100 kilometers (3,170 miles) and took ten days. Experiments with fish and mammals have demonstrated similar homing ability.

Some homing animals use landmarks. The use of landmarks, however, cannot explain how migrants find their way along routes covering many hundreds or thousands of kilometers.

Birds apparently possess a compass sense. This sense is probably related to a sensitivity to Earth's magnetic field. When homing pigeons were released with tiny magnets attached to their necks, they were unable to navigate. Experiments have also shown that the orientation of birds is partly based on celestial bearings. In one well-known experiment, indigo buntings were placed in compartments in a planetarium and shown star patterns. Scratch marks on sensitive paper showed that the birds attempted to move "north" according to the star patterns displayed on the dome of the planetarium.

Experiments have shown that salmon and similar fish apparently use Sun orientation while at sea to find their way back to the general area of the stream in which they hatched. Once in the correct general area, salmon apparently use their sense of smell to locate their home waters.

What Triggers Migration?

Migration is part of the life cycle of animals. Metabolic patterns usually change prior to migration, and fats accumulate in the body tissues. Food consumption increases in the autumn reaching a peak at the beginning of the migration season. These fundamental physiological changes are apparently controlled indirectly by the pituitary gland. The pituitary acts as a sort of internal clock. Variations in temperature and hours of daylight are detected by the pituitary gland. The pituitary then influences the development of gonads and all other metabolic processes, including the thyroid gland. The thyroid gland excretes the chemical substances that cause the physiological changes that prepare the animal for migration. The pituitary serves only to prepare the animal for migration. Actual migration is triggered by appropriate environmental conditions, such as precipitation, availability of food, temperature, and weather conditions. A sudden period of cold weather during autumn may induce the immediate departure of many migrants.

Evolution and Ecology of Migration

Migration as a behavior among birds and mammals probably appeared gradually. Erratic dispersals were probably the precursors of true migration. Such erratic dispersal would have led to greater survival rates and reproductive success among animals that moved to the most favorable places.

These originally erratic movements gradually acquired stability through **natural selection**. In some cases, original habitats were in present-day wintering areas, and animals developed a tendency to leave in spring in order to breed in other territories. Seasonal changes of weather and food supply in these newly settled regions forced the animals to migrate in fall, and they thus retreated to their former range. Many birds now nesting in the Northern Hemisphere, such as hummingbirds, tyrant flycatchers, tanagers, orioles, and swifts, have distinct tropical characteristics. These birds may have gradually spread northward as glacial ice receded.

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

The evolution of migration must be related to the ecological significance of migration. Migration allows fast-moving animals to exploit variations in resources and to move into areas where they could not remain year-round without the ability to move rapidly. Exploitation of peaks of food production, such as the dramatic increase of insect populations in temperate regions in the springtime, would not be possible without migratory populations. SEE ALSO HABITAT.

Elliot Richmond

Bibliography

Aidley, David J., ed. *Animal Migration.* New York: Cambridge University Press, 1981.

Billington, Elizabeth T. *Understanding Ecology.* New York: F. Warne, 1971.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth, 1990.

Orr, Robert T. *Animals in Migration.* New York: Macmillan, 1970.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer, 1987.

Schmidt-Koenig, Klaus. *Migration and Homing in Animals.* New York: Springer-Verlag, 1975.

Swingland, Ian R., and Paul J. Greenwood, eds. *The Ecology of Animal Movement.* Oxfordshire, U.K.: Clarendon Press, 1983.

Terborgh, John. *Where Have All the Birds Gone? Essays on the Biology and Conservation of Birds that Migrate to the American Tropics.* Princeton, NJ: Princeton University Press, 1989.

Mimicry

Animals that are toxic, armed with spines, or are otherwise unpalatable, or disagreeable, to predators often exhibit conspicuous colors or patterns. These superficial characteristics, called **aposematic** signals, are used to warn potential predators of the animal's physical or chemical defenses. The distinct colorations are highly conspicuous against certain backgrounds. This imposes a cost on the aposematic prey because the predators can more readily spot them. However, the predators will also be quick to learn and remember which prey to avoid because of the distinctiveness of the signals. Of course, if the prey is not sufficiently unpalatable, then the costs are greater than the benefits for the attacked animal.

aposematic a feature or signal that serves to warn

To evaluate whether the benefits outweigh the costs of any predator/prey strategy, the Evolutionary Stable Strategy (ESS) should be taken into

A monarch butterfly (left) and a viceroy butterfly. The viceroy evolved to look like the monarch as a defensive mechanism.

account. The ESS is a strategy that, when common among members of a particular role—such as aposematic coloration of prey—is not invaded or displaced over evolutionary time by any rare alternative. In addition, at evolutionary stability, each role has its own ESS.

An important aspect of aposematic signaling is the evolution of another defense, mimicry. A mimic is a predator or prey that bears a superficial resemblance to another species. The mimic resembles the model, which exhibits aposematic coloration. There are two forms of mimicry: **Batesian mimicry** and Mullerian mimicry.

Batesian mimicry a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

In Batesian mimicry, a palatable species mimics an unpalatable model, thereby gaining protection through the traits of another species. For example, juveniles of the harmless lizard species *Heliobolus lugubris*, inhabitants of the Kalahari Desert of southern Africa, mimic the color and posture of the ooglister beetle, a species that sprays noxious fluids at predators. As the lizards mature and grow larger than the average beetle, they develop cryptic coloration as a line of defense.

Another example is the monarch butterfly. Monarch butterflies store **cardiac** poisons acquired from milkweed plants they eat as larvae and are therefore distasteful and potentially harmful to other species. Viceroy butterflies, by contrast, are harmless and palatable and so need a good defense to ward off predators. The viceroy is protected by having wings of the same coloration pattern as the monarch butterfly. Many innocuous snakes mimic the conspicuous red, white, and black markings of the poisonous coral snake in an attempt to protect themselves.

cardiac relating to the heart

It is important to note that for Batesian mimicry to be effective, there must be a larger **population** of models than mimics so that predators are not clued in to the fact that they are being tricked.

population a group of individuals of one species that live in the same geographic area

Mullerian mimicry involves two or more unpalatable, aposematically colored species that resemble each other in appearance. This strategy evolved so that predators will learn more quickly to avoid animals with particular warning signs.

Some predators practice a reverse mimicry in order to trap their prey. Some species of snapping turtles, for example, have tongues that resemble wriggling worms. By sticking their tongues in the water, these turtles are able to lure small fish that are looking for a meal of worms.

Although mimicry seems a rather straightforward tactic, several conditions must be met in order for it to function as an ESS. The first condition for the strategy to be successful is that very conspicuous signals of aposematic coloration should be avoided so that it is somewhat difficult for predators to learn to avoid the aposematically patterned prey. Second, increasing prey unpalatability should increase the chances that any attacked prey will survive because the predator will quickly learn species avoidance after attacking the prey. It is important to note that the degrees of unpalatability and signal conspicuousness at ESS depend on the predators' patterns of **learning**.

learning modifications to behavior from experience

Despite all the warning patterns and colors, predators do sample aposematic prey on occasion. And although Mullerian mimicry is found among quite a few species, Batesian mimicry is considered a rare defensive strategy. The balance between the employment of mimicry and its success rate supports the notion that these aposematic signals are a relevant ESS.

Danielle Schnur

Bibliography

Begon, Michael, John L. Harper, and Colin R. Townsend. *Ecology*, 2nd ed. New York: Blackwell Scientific, 1990.

Bradbury, Jack W., and Sandra L. Vehrencamp. *Principles of Animal Communication*. Sunderland, MA: Sinauer, 1998.

Campbell, Neil A. *Biology*, 3rd ed. Redwood City, CA: Benjamin/Cummings Publishing Company, Inc., 1993.

Modern Synthesis

The Modern Synthesis describes the **fusion** (merger) of Mendelian **genetics** with Darwinian evolution that resulted in a unified theory of evolution. It is sometimes referred to as the Neo-Darwinian theory. The

fusion coming together

genetics the branch of biology that studies heredity

Modern Synthesis was developed by a number of now-legendary evolutionary biologists in the 1930s and 1940s.

> Ernst Mayr, Theodosius Dobzhansky, Gaylord Simpson, and Ledyard Stebbins are considered the founders of Modern Synthesis.

The Modern Synthesis introduced several changes in how evolution and evolutionary processes were conceived. It proposed a new definition of evolution as "changes in **allele** frequencies within **populations**," thus emphasizing the genetic basis of evolution. (Alleles are alternate forms of the same gene, characterized by differences in DNA sequence that result in the construction of proteins that differ in amino acid composition.) Four forces of evolution were identified as contributing to changes in allele frequencies. These are random genetic drift, gene flow, **mutation** pressure, and **natural selection**. Of these, natural selection—by which the best-adapted organisms have the highest survival rate—is the only evolutionary force that makes organisms better adapted to their environments. Genetic drift describes random changes in allele frequencies in a population. It is particularly powerful in small populations. Gene flow describes allele frequency changes due to the immigration and emigration of individuals from a population. Mutation is a weak evolutionary force but is crucial because all genetic variation arises originally from mutation, alterations in the DNA sequences resulting from errors during replication or other factors. The Modern Synthesis recognized that the majority of mutations are deleterious (have a harmful effect), and that mutations that are advantageous usually have a small **phenotypic** effect. Advantageous mutations may be incorporated into the population through the process of natural selection. Changes in species therefore occur gradually through the accumulation of small changes. The large differences that are observed between species involve gradual change over extensive time periods. Speciation (the formation of new species) results from the evolution of reproductive isolation, often during a period of **allopatry**, in which two populations are isolated from one another.

allele one of two or more alternate forms of a gene

populations groups of individuals of one species that live in the same geographic area

mutation an abrupt change in the genes of an organism

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

phenotypic physical and physiological traits of an animal

allopatry populations separated by a barrier

There are several differences between the Modern Synthesis and the older Darwinian conception of evolution. First, mechanisms of evolution other than natural selection are recognized as playing important roles. Second, the Modern Synthesis succeeds in explaining the persistence of genetic variation, a problem that Charles Darwin struggled with. The dominant genetic theory of Darwin's time was blending inheritance, in which offspring were thought to be the genetic intermediates (in-between versions) of their two parents. As Darwin correctly recognized, blending inheritance would result in the rapid end of genetic variation within a population, giving natural selection no material to work with. Incorporating Gregor Mendel's particulate theory of inheritance, in which the alleles of a gene remain separate instead of merging, solves this problem.

There were several key players involved in the Modern Synthesis. The theory relied on the population genetics work of R. A. Fisher and Sewall Wright. Theodosius Dobzhansky made extensive studies of natural populations of the fruitfly *Drosophila* that supported many aspects of the theory. Ernst Mayr developed the biological species concept and created models concerning how speciation occurs. George Gaylord Simpson helped integrate paleontological observations into the theory behind the Modern Synthesis. G. Ledyard Stebbins contributed tenets (principles) based on his botanical work.

Since the 1990s it has been recognized that the Modern Synthesis omits some biological disciplines that are also relevant to evolution. In particular, much attention has focused on patterns of **ontogeny** and development. SEE ALSO BIOLOGICAL EVOLUTION; DARWIN, CHARLES; MAYR, ERNST; GENES; GENETICS; MENDEL, GREGOR; SIMPSON, GEORGE GAYLORD.

ontogeny the embryonic development of an organism

Jennifer Yeh

Bibliography

Futuyma, Douglas J. *Evolutionary Biology*, 3rd ed. Sunderland, MA: Sinauer Associates, 1998.

Huxley, Julian. *Evolution: The Modern Synthesis*. New York: Harper and Brothers, 1942.

Mayr, Ernst. *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. New York: Columbia University Press, 1942.

Simpson, George Gaylord. *Tempo and Mode in Evolution*. New York: Columbia University Press, 1944.

Molecular Biologist

Molecular biology is a branch of biology that has been growing in importance since the 1940s. It developed out of the sciences of **genetics** and biochemistry. Genetics is the study of **heredity**, the process by which certain characteristics of an organism are handed down from parent to offspring. Biochemistry is the study of chemical compounds and processes in organisms. Molecular biologists seek to explain biological events by studying the molecules within cells. They are especially interested in the molecular basis of genetics and inheritance and the production of proteins. Proteins are large, complex molecules that are an essential part of all living cells.

genetics the branch of biology that studies heredity

heredity the passing on of characteristics from parents to offspring

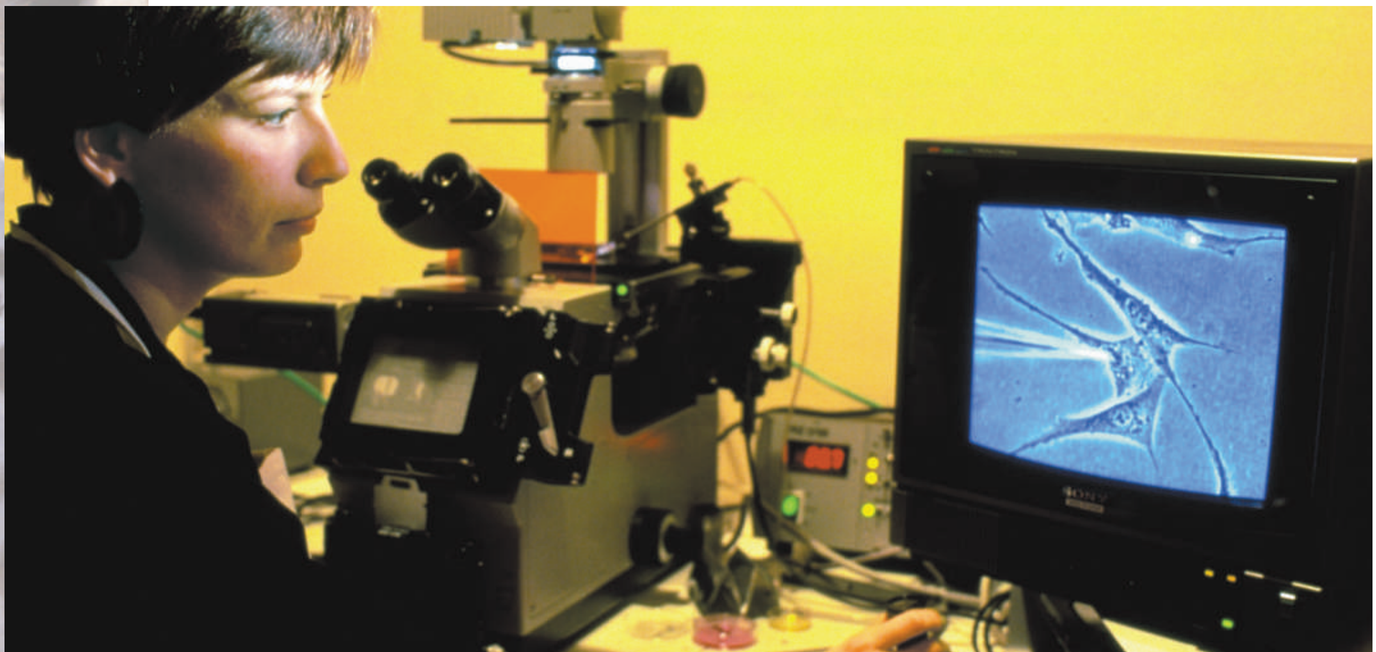
Most molecular biologists are involved in research and development. Some conduct basic research to expand knowledge without the direct aim of benefiting humans. Others may conduct applied research, which is used to benefit humans directly. Applied research generally focuses on issues important to the health, agricultural, and environmental sciences.

At the turn of the twenty-first century, some molecular biologists are involved in a very important study, the **Human Genome Project**. This international research program aims to identify all of the approximately 30,000 **genes** of humans. Molecular biologists are also involved in related investigations of the genetic makeup of several nonhuman organisms. These include *Escherichia coli* (a microscopic organism found in the human gut), the fruit fly, and the laboratory mouse.

Human Genome Project a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

genes segments of DNA located on chromosomes that direct protein production

Many molecular biologists are employed by county, state, and federal agencies. Also, they may be employed by private industries such as a pharmaceutical corporation, an animal vaccine supply company, or a laboratory doing tests for doctors and health departments. At the beginning of the twenty-first century, emerging job opportunities for molecular biologists include environmental and pollution control companies and the biotechnology industry. The biotechnology industry uses molecular biology research to improve agricultural crops, develop new tests for disease screening, and develop new drugs. Also, some molecular biologists work at universities and colleges. They teach classes, train students in how to perform research, and



A molecular biologist executes a DNA microinjection technique.

conduct their own research in their particular area of interest. An important part of the research is writing up the results for publication. Publication of research allows new information to be shared with the scientific community. Also, publication is important in obtaining grant funding for future research projects.

At the high school level, persons interested in becoming a molecular biologist should study math, chemistry, physics, biology, English, writing, and computer studies. Although there are career opportunities for molecular biologists with bachelor's degrees, most professionals have either a master's or doctoral (Ph.D.) degree. College-level course work generally includes biology (microbiology, genetics, **ecology**, and so on), chemistry, physics, and computer science. SEE ALSO Genes; Genetics.

ecology the study of how organisms interact with their environment

Denise Prendergast

Bibliography

Cosgrove, Holli R., ed. *Encyclopedia of Careers and Vocational Guidance*, 11th ed. Chicago: Ferguson Publishing Company, 2000.

Morange, Michel. *A History of Molecular Biology.* Cambridge, MA: Harvard University Press, 1998.

The Year 2000 Grolier Multimedia Encyclopedia. Danbury, CT: Grolier Interactive Inc., 1999.

Internet Resources

Experiences in Molecular and Cellular Biology. Emporia State University. <http://www.emporia.edu/biosci/exmolcel.htm>.

Molecular Biology

Molecular biology is the study of life processes on a small scale. As a whole organism is composed of cells, so are these cells composed of tightly regu-

lated molecular machinery that keep them alive and functioning. Molecular biologists use chemical and biological tools to study DNA, RNA, proteins, and the interactions between them.

These tools have allowed scientists to have a far more detailed understanding of cellular processes than was imagined possible a century ago. One of the most groundbreaking developments in this field has been the **polymerase** chain reaction (PCR), first conceived by Kary B. Mullis in the 1970s. This technique, which uses DNA-copying polymerases derived from bacteria found in hot springs, can be used to isolate a tiny needle of DNA from a nucleic haystack and copy it many times over. Today, PCR is used in nearly every molecular biology lab to reproduce **genes** and obtain enough copies of them to study the genes efficiently. This allows scientists to put the genes in other cells, to activate them, or to match them to their protein products.

polymerase an enzyme that links together nucleotides to form nucleic acid

genes segments of DNA located on chromosomes that direct protein production

Molecular biologists also study proteins. They frequently do this through electrophoresis, in which proteins are separated by size as they drift through a thickened gel, propelled by electric current. Once the proteins are separated out by size, a scientist may "probe" the proteins with **antibodies** specific for only one protein shape and determine if that particular protein is present. The antibody will be radioactive or have some visual marker for easy detection. This technique is called a Western blot. One can also run DNA and RNA through electrophoretic gels and probe with complementary nucleic acids. The double-stranded DNA or RNA is split, and an exact negative copy of the gene is introduced to the gel. The negative copy will stick fast to the positive copy, so if the gene is on the gel, its presence is quickly identified.

antibodies proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

With these techniques, and others, such as growing cells in culture and the purification and harvesting of **bioactive proteins**, molecular biologists are among the best researchers to examine health, disease, and development in animals and humans. While **ecology** and behavior are useful for large-scale understanding of long-ranging processes in biology, molecular biologists are able to study and manipulate organisms on an individual level and study the mechanisms by which they operate. As molecular biology improves, more and more life processes are seen as the product of biochemical interactions, and scientists are more and more able to paint a complete picture of the physical interactions that make life work. SEE ALSO Cells; PCR.

Ian Quigley

bioactive proteins proteins that take part in biological processes

ecology study of how organisms interact with their environment

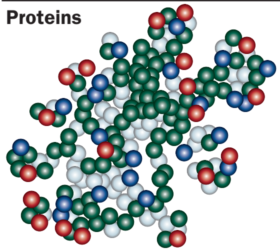
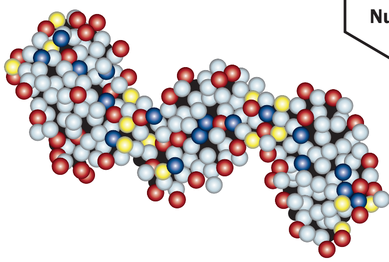
Molecular Systematics

Molecular systematics is the use of molecular **genetics** to study the evolution of relationships among individuals and species. The goal of systematic studies is to provide insight into the history of groups of organisms and the evolutionary processes that create diversity among species.

For thousands of years, **naturalists** have looked at the world and attempted to describe and explain biological diversity. This attempt to examine

genetics the branch of biology that studies heredity

naturalists scientists who study nature and the relationships among the organisms

Class	Typical subunit	Roles	Examples
Proteins 	Amino acid	Serve as enzymes	Lactase
		Structural components	Hair, cartilage
		Peptide hormones	insulin
Nucleic Acids 	Nucleotide	Store genetic information	DNA
		Direct production of proteins	RNA

Classes of macromolecules. Redrawn from Johnson, 1998.

and classify is called systematics—a system for imposing order on the seeming chaos of nature. In 1758 Swedish naturalist Carolus Linnaeus devised a hierarchical classification system using two-part Latin names to categorize plants and animals. This system is still used today. Linnaeus was opposed to the theory of evolution, and his system was originally based on morphological features of structure and form. However, evolutionists rapidly adopted the Linnaean system and developed it into a classification based on phylogenetics, the evolutionary development of species. By 1866, German zoologist Ernst Haeckel had published a collection of detailed phylogenetic "trees" depicting what was then known about the evolutionary history of life.

physiology study of the normal function of living things or their parts

Interest in phylogeny waned over much of the nineteenth century, replaced by an emphasis on genetics, **physiology**, and geographic variances. That began to change with the work of botanist Walter Zimmerman in the 1940s, and German zoologist Willi Hennig, in the 1950s and 1960s. These scientists pioneered the definition of objective criteria for determining the shared genetic attributes of living and fossil organisms. A revolution in molecular biology took place in the 1960s. Methods for determining the molecular structure of proteins and amino acids allowed biologists to begin to estimate **phylogenetic** relationships. The exponential growth of molecular systematics in the late twentieth century is due to a combination of increased sophistication in molecular biology techniques, and computer advances in hardware and software that allow scientists to model large and complex data sets.

phylogenetic relating to the evolutionary history of species or group of related species

molecular clocks using the rate of mutation in DNA to determine when two genetic groups spilt off

genes segments of DNA located on chromosomes that direct protein production

Molecular systematists use a variety of techniques to derive phylogenetic trees. Polymerase chain reaction (PCR) is used to investigate variations of DNA on a large scale. Gene amplification is also fundamental to new approaches to DNA fingerprinting. Scientists can use "**molecular clocks**" to predict both past and future molecular divergences in **genes**.

This theory claims that molecular change is sufficiently constant to determine how current genetic lineages branch off from a common ancestor and to determine when the branching occurred. Genetic markers are used to make inferences about relationships between environment and morphology, as well as physiology and behavior.

The importance of phylogenetic trees, or estimates of evolutionary history, are that they allow biology to be predictive. Much as a chemist can use the periodic table of elements to predict chemical reactions, biologists can use phylogenetic trees to analyze biological variation and make predictions about behavior, morphology, and physiology, as well as biomolecular structure and other biological attributes.

The applications of molecular systematics in medicine are particularly important. The ability to predict the course of evolution allows scientists to track epidemic **pathogens**, research zootonic viruses (animal viruses that are transmissible to humans), understand the evolution of pharmaceuticals and drug resistance, and make predictions about emerging diseases. For example, phylogenetic studies of a form of influenza called influenza A have revealed reliable evolutionary behavior that can be used to predict how the viruses that cause influenza will evolve. This allows scientists to prepare vaccines for future strains in advance. Research into when simian immunodeficiency virus began to be transmitted to humans is vital to understanding how the transmission occurred and perhaps to prevent future zootonic transmissions.

pathogens disease-causing agents such as bacteria, fungi, and viruses

Phylogeny is also an integral part of interpreting any coevolutionary relationships such as host and parasite. In the example of the **coevolution** of insects and their host plants, the plants evolve chemical defenses against the insects, who then evolve resistances to the chemicals. Because there are a limited number of chemical defenses available to the plants, researchers looked at whether insects are more likely to stay with the same plant as it evolves, or to switch to plants that contain chemicals to which they are already adapted. Studies of beetle phylogeny shows a closer match to plant chemistry than to plant phylogeny, indicating that the beetles have learned to switch plants as the host evolves new defenses.

coevolution a situation in which two or more species evolve in response to each other

Behavioral ecologists use phylogeny to reconstruct the evolution of behaviors. Molecular data can clarify the connections between animals previously thought to be unrelated. For example, flying foxes (*Pteropus*, also known as fruit bats), in contrast to other bats, have been shown to share significant features of brain organization with primates. These shared features lead scientists to believe that wings and flying evolved independently in these two lineages.

Evolution is not something that just happened in the past. It can be observed in the present and used to predict the future, by employing molecular systematics to compare data across genes, individuals, populations, and species.

Nancy Weaver

Bibliography

Hillis, David M. *Molecular Systematics.* Sunderland, MA: Sinauer Associates, Inc., 1996.

Johnson, George B. *Biology: Visualizing Life*. New York: Holt, Rinehart and Winston, Inc. 1998.

Molluska

fossil record a collection of all known fossils

phyla the broad, principal divisions of a kingdom

herbivores animals who eat plants only

invertebrates animals without a backbone

exoskeleton a hard outer protective covering common in invertebrates such as insects

mantle the tissue in mollusks that drapes over the internal organs and may secrete the shell

epidermis the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

calcium a soft, silvery white metal with a chemical symbol of Ca

The phylum Molluska is one of the largest of all animal groups. Not only does it contain about 110,000 living species, the **fossil record** indicates a long and extensive history.

The major mollusk groups, called classes by most taxonomists (scientists who study the relationships of plants and animals), are the Gastropoda (snails and slugs), the Bivalvia (clams, mussels, and shipworms), the Cephalopoda (squid, octopuses, cuttlefish, and nautilus), the Polyplacophora (chitons), the Scaphopoda (tooth shells), the Monoplacophora (a single-shelled animal), and the little-known Aplacophora (a questionable mollusk).

Of all animal **phyla**, the mollusks are perhaps the most difficult to describe in terms of a "typical" mollusk. In fact, no one characteristic is unique to the mollusks and shared by all species. Their body shapes are immensely different. In terms of feeding and behavior, mollusks range from docile, grazing **herbivores** to stealthy and aggressive predators. Most mollusks are marine, except for a few snails and clams that are found in damp terrestrial or freshwater environments.

Some characteristics of mollusks are unique to the group, but many are characteristic of **invertebrates** in general. However, researchers have identified a suite of characteristics that are combined in some generalized way within the mollusks. Mollusks do not have a central rod or backbone-type support. They do not have an **exoskeleton**.

Perhaps the most important characteristic of mollusks is the presence of a specialized tissue called the **mantle**. The mantle is part of the **epidermis**, or skin, of the mollusk. It is filled with mucous glands and is very slippery to the touch. The mantle contacts the shell only at the outer edges. The inner epidermis where the shell is no longer in contact with the mantle is filled with fluid and acts as a sort of protective cushioning for the mollusk's soft body.

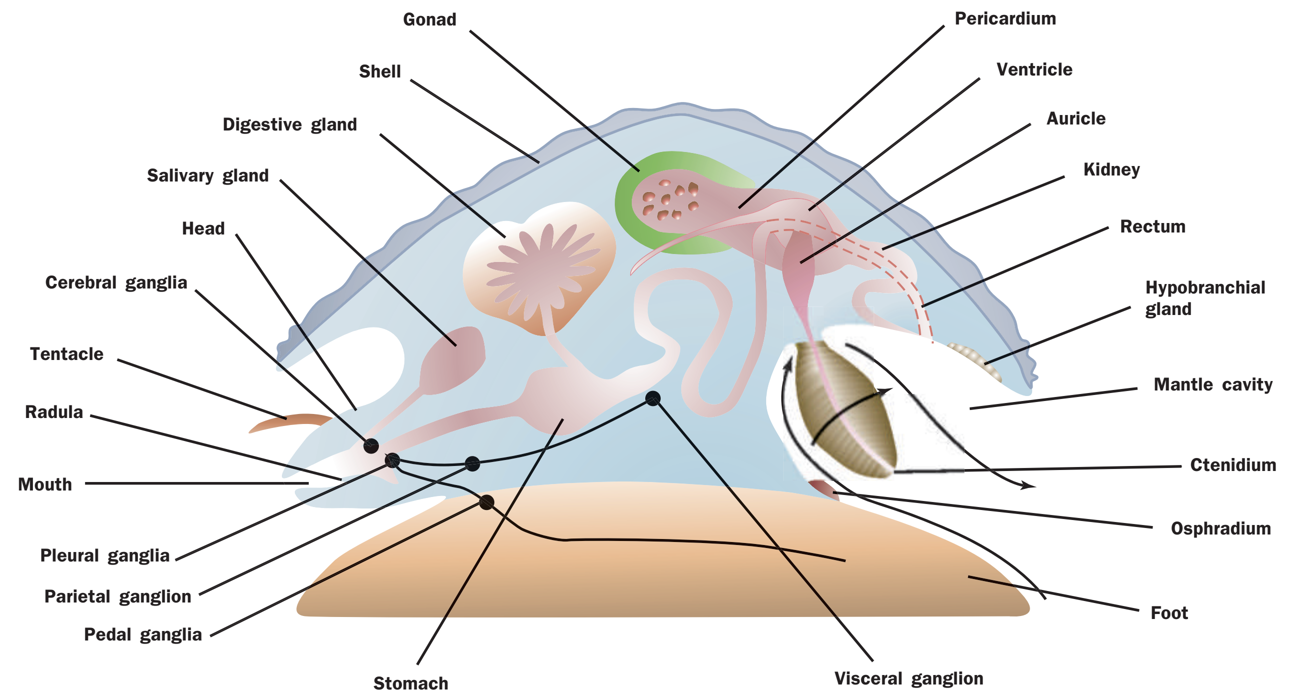
The major function of the mantle is to secrete a substance that hardens into a three-layered shell. The outermost layer of the shell is a tough, solid deposit of **calcium** carbonate and is called the periostracum. The middle layer is a strengthening sheet of more calcium carbonate crystals. The innermost layer is made of organic chemicals that, when seen alone, capture light and appear to be multicolored. This layer is called the nacreous or prismatic layer. The beautiful appearance of this layer as seen in the inner shell of an abalone. The nacreous layer is also responsible for pearls. When a foreign particle penetrates the mantle, the shell-secreting cells in the mantle attach to the particle and build up layers of pearl around it.

The influence of the mantle and the resulting shell development is one of the most distinctive characteristics of the mollusks. Most living mollusk species have shells, although many have adapted to life without it. Remnants of the primitive shell can be found in the bodies of mollusks like the slugs and squids.

Gastropods

gastropods mollusks that are commonly known as snails

The **gastropods**, the snails and slugs, are one of the most familiar groups of mollusks. The name comes from a misunderstanding. Early biologists be-



Cross-section of a mollusk. Redrawn from Grove and Newell, 1969.

lieved that the stomach of the gastropod was located in the muscular single "foot" on which the animals move, and that the animals ate with this foot. As a result, they named them "stomach-foot" (gastro-pod). Today we know gastropods do not eat with their "foot," but the name remains.

The body of a gastropod body rests on this single muscular "foot." The foot looks somewhat like a pedestal, and is the organ responsible for locomotion, or movement from place to place. Many species can withdraw their foot into their shell for protection, as gastropods are considered a tasty food item for many predators, including humans. Often, a gastropod will simply pull its shell over the foot for protection from predators.

The head end of the foot contains the sensory organs and often a set of retractable antennae. In most snails the mouth is lined with a sharp, zipperlike structure called a radula. The radula is used for scraping algae off rocks. However, there are many predatory species in which the mouth is located on the end of a proboscis, or long snout. This proboscis is used to bore into the shells of other animals. Some species also inject poison into the soft bodies of their prey before using the mouth to consume it.

The shells of gastropods are the most spectacular part of the gastropod body. Over millions of years, gastropods evolved elaborately coiled and brightly colored shells as protection for their soft internal organs. The diversity of coiling shapes, from plain spirals to intricate towers, makes these animals valuable for shell collectors. Unfortunately, this has led to severe **population** reductions in many species. The beautiful shell of the sea conch, which is often depicted in pictures and movies as a type of musical instrument, is a prized collector's item, and the conch is rapidly becoming hard to find.

population a group of individuals of one species that live in the same geographic area

lungs sac-like, spongy organs where gas exchange takes place

hermaphroditic having both male and female sex organs

The gastropods are one of the successful groups of mollusks, so much so that they are considered to be pests in many areas. Pulmonates, a group that includes slugs and snails who have evolved **lungs**, can survive in almost any temperate climatic region. They have been so successful, in part, because of their reproductive strategies. Most mollusks are either male or female. One onate, the familiar garden snail, is **hermaphroditic**, with both male and female reproductive organs. Being hermaphroditic allows the snail to reproduce anywhere at any convenient time.

Many snails live in freshwater ponds and lakes. The rest of the mollusks, with the exception of some clams, are all marine. The fact that snails live on land is important for many researchers who study climatic fluctuations, as many species are intolerant of even slight climatic changes. Snail fossils are often studied to interpret temperature and humidity in the past.

operculum a flap covering an opening

Slugs—gastropods that do not have shells—are also pulmonates. The pulmonates are considered to be the most derived of the mollusks. The most primitive mollusks are the Prosobranchia. These gastropods are the largest and oldest group of gastropods. They have an **operculum**, which is a small shell flap used to cover the foot when withdrawn into the shell cavity. They usually have a pair of gills and the sexes are mostly separate. The Opisthobranchia are a small group of gastropods who are very diverse in body form and function. In the opisthobranchs the body shell is greatly reduced. Some are small and round giving rise to the name bubble shell. All are marine. Many of the members of this group are burrowers who cause a lot of damage to rocks and the wood of many sailboats.

Many opisthobranchs have lost their shell entirely. Some of these animals are called the nudibranchs, who are probably the most beautifully colored animals on Earth. They have colorful projections on their backs that can be used for respiration, digestion, or protection if they contain stinging cells.

Bivalvia

The bivalves, or clams, are another highly successful mollusk group. Bivalves have two shells, or valves, that are compressed on either side of the body. The shells are made from the excretions of the mantle as in gastropods, but are very different in shape and some functions.

The two shells enclose most of the body, and strong muscles inside the shell keep the two valves tightly closed. The shells open only to take in and release water or to allow the foot to extend into the sand.

Like gastropods, bivalves have a strong muscular foot that protrudes from the valves. However, bivalves do not use their foot as much for moving from place to place. Many bivalves do use the foot for moving through the sand, but it is more often used to anchor the animal in the fine sediments where it lives.

body plan the overall organization of an animal's body

The **body plan** of bivalves is similar to that of gastropods but has many basic differences. The gills are paired and very large, and gas exchange occurs on the surface of these structures. The gills actually evolved primarily for the purpose of food gathering and their gas exchange function is secondary. The circulatory system is open, which means that blood is

pumped by the heart through arteries into openings or sinuses. It is recaptured by veins and pumped back to the heart. The blood simply diffuses over the organs at the sinuses. Bivalve blood is poor in **hemoglobin**, the oxygen-carrying chemical in blood, but this deficiency is compensated for by the large surface area of the gills. Fortunately, the sedentary lifestyle of the bivalve does not require great amounts of oxygen.

hemoglobin an iron containing protein found in red blood cells that binds with oxygen

Bivalves are **filter feeders** who take in water through a front opening, called an in-current siphon, and release it through an ex-current siphon. The digestive system includes an esophagus, stomach, long intestine, and an anus. Once the water is taken in, it passes over the gills, and mucus that coats the gills captures organic debris in the water. This organic material is transported to the esophagus by **cilia**.

filter feeders animals that strain small food particles out of water

cilia hair-like projections used for moving

Bivalves do not have a very evolved sensory system, but are limited to a few ganglia that respond to environmental stimuli. They have no antennae. Pectens, or scallops, are the only bivalves that have eyes complete with lenses, corneas, and **retinas**.

retinas layers of rods and cones that line the inner surface of the eye

Bivalves have separate sexes. Reproduction occurs by releasing sperm and eggs in the water. In some species, the **gametes** (sperm and egg) are taken into the body and **fertilization** occurs within. In others, fertilization takes place in the external environment of the water.

gametes reproductive cells that only have one set of chromosomes

fertilization the fusion of male and female gametes

All bivalves are **aquatic**. Some forms live in freshwater, but it is more common to find them in marine environments. Their diversity is largely based on the way they feed, the structure of their gills, and where they live.

aquatic living in water

Cephalopoda

Cephalopods include the squid, octopus, cuttlefish, and the survivor of an ancient lineage—the nautilus. Their variety of forms and functions is so varied that entire books have been written about specialized groups of cephalopods.

Shells, which are so typical of mollusks, appear to be absent in the cephalopods. In both squid and cuttlefish, an internal vestige of the shell remains inside the soft body. Anyone who has ever seen the “cuttlebone” used in parakeet and parrot cages may not realize that this is the remnant of the ancient mollusk shell. The squid have an even more reduced shell that exists as a simple clear plasticlike film that runs the length of the body. The octopus has the vestige of a shell that has been put to use as mouthparts that are quite effective for biting prey.

The sensory systems of the nautilus, octopus, and squid are highly developed. These animals are extremely intelligent and have shown that they have memory and can solve problems of a simple nature. They are acutely aware of their environments and can respond to threats with a wide array of defense tactics. The octopus and squid are well-known for squirting dark colored “ink” into the water to confuse a predator, then darting away in the flash of an instant.

Cephalopods are the swiftest mollusks. While most mollusks are sedentary or sluggish, cephalopods can swim quite fast at times and are masters of deep-ocean living. Locomotion is accomplished by means of jet propulsion in which a strong ex-current siphon spurts out water to propel the animal away from danger. Cephalopods sneak up on their prey, using their

tentacles to stealthily reach out towards the victim or to delicately slide along the ocean bottom.

Squid, octopus, and cuttlefish are very unlike the nautilus. The relationship between an octopus and a nautilus is hard to see unless the animals are closely examined, but both animals have similar tentacles, which they use for grasping prey. The tentacles can wrap around a prey item such as a shrimp and pull it to the mouth.

ammonites an extinct group of cephalopods with a curled shell

Scientists know little about the soft body evolution of the cephalopods, but the fossil record of coiled shell species is well documented. The ancestors of the nautiloids are the **ammonites**, animals with spirally coiled shells that, unlike gastropod shells, have separate chambers. These chambers functioned in gas regulation and allowed the animal to move up and down in the water column. Some ammonites are believed to have dived so deeply down into the water searching for prey that, as a result of increasing water pressure, they developed very intricate infoldings of the shell. The infoldings increased the surface area of the fragile shell, which in turn increased its strength. These shells could have withstood enormous underwater pressures. The graceful and highly intricate shells of the ammonites are valued by people all over the world.

Other Mollusk Groups

It is easy to find general mollusk characteristics in other mollusk groups. The polyplacophorans, or chitons, are shelled grazing animals found on rocks in the intertidal zone. The scaphopods have shells that look like long pointed teeth. They live in the sand and filter food from the water. A rare, recently discovered monoplacophoran called neopilina is a single-shelled animal that is considered to be a "living fossil" as scientists had thought they were extinct. Scientists believe the monoplacophorans represent the primitive form of the mollusks.

Brook Ellen Hall

Bibliography

Barth, Robert, and Robert Broshears. *The Invertebrate World.* Philadelphia: Saunders College Publishing, 1982.

General Biology. New York: Grove and Newell, University Tutorial Press, 1969.

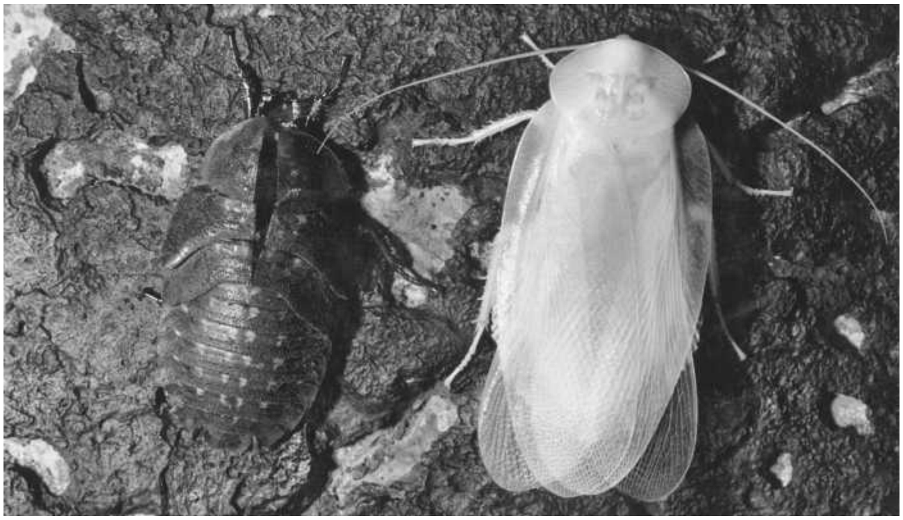
Pechenik, Jan. *Biology of the Invertebrates.* Boston: Prindle, Weber & Schmidt, 1985.

Molting

exoskeleton hard outer protective covering common in invertebrates such as insects

One of the general characteristics that defines the phylum Arthropoda (which includes insects, spiders, and crustaceans) is an external skeleton, also called an **exoskeleton**. The arthropod exoskeleton completely covers the outside of the body and the muscles inside adhere to it. Exoskeletons are hard and protect the body. Because the exoskeleton is hard and rigid, an arthropod cannot grow unless it sheds its old exoskeleton and secretes a new one. This process is called molting.

Arthropod growth is limited to molting, so growth happens in steps rather than continuously. The stages between moltings are called instars.



A cockroach shown after molting, next to the skin it shed.

The extent of an individual's growth between molts and the length of time between molts are related to the temperature as well as to the amount of food and water an individual gets.

Warmer temperatures and more food and water can shorten the instar length and make the individual bigger. Other cues, such as the length of the day, are used to determine the timing of molting. Most insects have a specific end point to their growth, and after their final molt they are sexually mature adults. Most insects with wings acquire wings only in their adult stage. For example, except for the absence of wings, baby crickets are born looking exactly like adult crickets but are tiny in size. Crickets undergo several molts and live through several instars as they grow bigger. In their final molt, they become sexually mature and gain wings for flight.

Beneath the exoskeleton is an underlying cell layer called the epidermis, which secretes the exoskeleton, also called the cuticle. The exoskeleton is noncellular and made of **chitin** and proteins, which give the exoskeleton its rigid and protective properties. The exoskeleton and the epidermis together form the **integument** of an arthropod.

chitin a complex carbohydrate found in the exoskeleton of some animals

integument a natural outer covering

The molting process is a series of steps. It is controlled by the hormone **ecdysone**. Ecdysone is secreted from glands behind the brain. Once it is released the molting process begins. The arthropod builds a new exoskeleton underneath the old one. The epidermis pulls away from the existing exoskeleton. This creates a space between the epidermis and the exoskeleton. This space is filled with a gel that promotes shedding of the old exoskeleton.

ecdysone a hormone that triggers molting in arthropods

Under this gel, the epidermis secretes a new cuticle. This requires a lot of energy. The new cuticle is secreted in various layers, and many biochemical processes change the newly excreted cuticle from cellular secretions into the insoluble form of the new exoskeleton. At this point, the new exoskeleton is still soft and pliable.

The gel that is between the new and old cuticles contains digestive **enzymes**. These enzymes start to break down the old exoskeleton once the new cuticle has been made insoluble and can resist being damaged by these

enzymes proteins that act as catalysts to start biochemical reactions

enzymes. These digestive enzymes dissolve the inside of the old exoskeleton and the products are reabsorbed by the individual and used in making the new cuticle. This recycling of material reduces the amount of energy needed for molting. Only the inside of the old exoskeleton can be reused. The outside of the exoskeleton is shed in a process called **ecdysis**.

ecdysis shedding the outer layer of skin or exoskeleton

Ecdysis consists of splitting the exoskeleton, usually along the back of the arthropod, and crawling out of the old exoskeleton. Old exoskeletons of insects can be found in nature. They look just like the insect did but are hollow inside.

When an individual first emerges from the old exoskeleton following ecdysis, it is very vulnerable because the new exoskeleton is quite soft. Newly emerged individuals are wrinkly and whitish. The swallowing of air by the individual expands the cuticle. This pulls out the wrinkles and makes the individual become larger during molting. After expansion of the cuticle, another biochemical process takes place that hardens and darkens the exoskeleton. This biochemical process is a reaction to oxygen in the air. It can take several hours for an individual to undergo expansion and hardening.

Even though molting happens only occasionally, most arthropods continue to add layers to the inside of the exoskeleton all the time. Some insects do this every twenty-four hours and form growth rings similar to those of trees. SEE ALSO Skeletons.

Laura A. Higgins

Bibliography

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, 1999.

Evans, Howard E. *Insect Biology*. Menlo Park, CA: Addison Wesley Longman, 1984.

aquatic living in water

habitat physical location where an organism lives in an ecosystem

estuaries areas of brackish water where a river meets the ocean

baleen fringed filter plates that hang from the roof of a whale's mouth

extant still living

homodont teeth with a uniform size and shape

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

plankton microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

Morphological Evolution in Whales

Whales are the only group of mammals to have adopted an exclusively **aquatic** lifestyle. Their entire life cycle, from birth until death, is carried out in an aquatic **habitat**. The terms "whale" and "cetacean" are usually used interchangeably, cetaceans being the scientific term for whales, dolphins, and porpoises. However, "whale" is also sometimes used to distinguish some of the larger species of the order Cetacea from the other two major groups, the dolphins and porpoises.

Cetaceans are found in almost all oceans and their connecting seas, as well as in **estuaries** (wide tidal river mouths) and rivers. Whales range in size from the 1-meter-long (3 feet) dolphins and porpoises to the 30-meter-long (100 feet) blue whale. The seventy-seven **extant** species of whales each belong to one of two suborders, the Odontoceti (toothed whales) and the Mysticeti (**baleen** whales). The toothed whales—porpoises, dolphins, and most of the smaller whales—have **homodont** (uniform in size and shape) teeth or are toothless. The odontocetes use their teeth to feed on fish and **crustaceans**. The mysticetes are toothless, but strain **plankton**

This humpback whale emerges from underneath the water's surface in Glacier Bay National Park, Alaska. The anatomical structures of the whale's front flippers is very similar to that of the human hand.

and small crustaceans using a dense fringe of bristled plates called baleen (whalebone) that hangs from the roof of their cavernous mouth.

The extinct Archaeoceti appeared in the early part of the Eocene epoch (about 50 million years ago). Although they do not show all the specialized body characteristics of the odontocetes and mysticetes, their spindle-shaped body and horizontal tail show that they were well adapted to an aquatic lifestyle. Unlike the extant whales, archaeocetes have **heterodont** (different in size and shape) teeth and their nostrils are located midway along the snout. Based on the fossil evidence, archaeocetes went extinct slowly, disappearing sometime during the Pliocene epoch (2.5 to 7 million years ago).

heterodont teeth differentiated for various uses

Morphological Specializations of Extant Whales

Whale form and structure departed dramatically from that of terrestrial mammals, adopting a fishlike appearance. The whale body is streamlined, with a large head and nondifferentiated neck, and has a **dorsal** fin made up of **connective tissue** and skin on the back. The tail is a T-shaped, horizontally flattened, boneless fluke, which serves as the major propulsive force during locomotion. Whales swim using an up-and-down wavelike motion rather than the side-to-side bending motion used by most fish.

Like other mammals, whales have **lungs** and breathe air. They inhale and exhale through a single nostril or a pair of nostrils on top of their head, toward the back. The waterspout that emerges from this "blowhole" is simply water vapor expelled from the lungs during exhalation along with a small amount of water collected near the edges of the blowhole.

The whale skull has undergone other changes in addition to the relocation of the nostril(s) and the development of homodont teeth and baleen.

dorsal the back surface of an animal with bilateral symmetry

connective tissue cells that make up bones, blood, ligaments, and tendon

lungs sac-like, spongy organs where gas exchange takes place

The upper jaw is thicker at the back end, while the lower jaw is a horizontal bar rather than an L-shape, such as in humans. The cranium and brain have become wider so that their widths are greater than their lengths, a very unusual situation in mammals. This elongation of the cranium and the brain is referred to as a "telescoping of the skull." The relative sizes and shape of the various skull bones have changed as a result of this telescoping.

Whale skin is hairless except for a few tactile hairs. In addition, the skin lacks sweat or oil glands and feels like smooth rubber. A thick layer of blubber lies underneath the skin, aiding in buoyancy, insulating the body, and storing energy in the form of fat.

When compared to the limbs of terrestrial mammals, whale forelimbs have been transformed into flippers, while the hind limbs have been lost. The bones of their upper forelimbs have been reduced in size and the number of **phalanges** in each digit has increased, resulting in elongated "hands." Although whales do not have hind limbs, all species have a pelvic bone, and a few species have thighbones.

phalanges bones of the fingers and toes

Fossil Evidence for the Origin of Whales

Certain details concerning the evolution of whales remain unknown. Scientists agree that whales evolved from some kind of primitive **ungulate** (hoofed mammal), but because we do not have a fossil of the animal that was intermediate between the terrestrial and aquatic whale ancestors, it is difficult to classify whales relative to their closest mammalian relatives, the artiodactyls (camels, pigs, **ruminants**, and hippopotamuses). Fossil data suggests that whales and artiodactyls share a recent ancestor, but whales differ from other ungulates in a number of significant skeletal characteristics.

ungulate animal with hooves

ruminants plant eating animals with a multi-compartment stomach such as cows and sheep

The important morphological differences between the two orders of extant whales, the odontocetes and the mysticetes, also lead scientists to believe that the branch that eventually gave rise to modern whales split off from the rest of the mammalian tree long ago. The first fossil representatives of both orders appeared during the Oligocene epoch (about 38 to 25 million years ago). Some paleontologists look for clues about whale origins in the Cenozoic era, particularly in the Paleocene and early Eocene epochs (50 to 65 million years ago). Other paleontologists who believe that a Paleocene or Eocene origin would not have allowed sufficient time for the extreme morphological changes look for answers within the Cretaceous period of the Mesozoic era (65 to 130 million years ago).

Molecular Evidence for the Origin of Whales

Molecular DNA studies performed during the 1990s provide a more precise placement of whales on the mammalian **phylogenetic** tree (diagram representing the evolutionary relationships between mammal groups). Several different scientific teams working on different parts of the cetacean **genome** have all concluded that whales should be classified as artiodactyls, not as a sister group as suggested by the fossil evidence. The molecular evidence indicates that whales are most closely related to hippopotamuses. The affinity to water exhibited by hippopotamuses has led some scientists to wonder about the aquatic tendencies of the most common ancestor of whales and hippos.

phlogenetic relating to the evolutionary history

genome an organism's genetic material

Despite the agreement of the results drawn of molecular studies performed on cetacean DNA, certain aspects of the origin of whales remain under dispute. Paleontologists maintain that whales should not be classified as artiodactyls and warn against drawing conclusions about the nature of whale ancestors based on a hypothesized relationship between whales and hippos. SEE ALSO Fossil Record; Geological Time Scale; Morphology.

Judy P. Sheen

Bibliography

Monastersky, Richard. "The Whale's Tale." *Science News* 156, no. 19 (1999):296–298.

New Encyclopedia Britannica. Chicago: Encyclopedia Britannica, 1994.

Pearl, Mary Corliss. "Whale." *The Illustrated Encyclopedia of Wildlife.* Lakeville, CT: Grey Castle Press, 1991.

"Whale." *Grzimek's Animal Life Encyclopedia. Whale.* New York: Van Nostrand Reinhold Company, 1975.

Morphology

Morphology, broadly defined as the study of animal form, is a field that helps us understand animal diversity and animal history. For centuries, scientists have been interested in how animals are put together and how the parts work together to make functioning organisms that can run, fly, swim, eat, and survive. Early scientific efforts focused on descriptive methods in which scientists dissected specimens and described the musculoskeletal and other body systems with words and detailed drawings.

As new techniques were developed, scientists began to specialize along the lines of various subdisciplines, including **functional morphology** and ecological morphology. Morphologists moved beyond what had started as a purely descriptive science and began to ask and answer more complex questions.

functional morphology study of form and function

Functional morphology emphasizes the mechanics of a particular structure—how it works. For example, a functional morphologist might examine the pattern of musculoskeletal activity involved in an activity such as running. Using techniques such as high-speed video, X-ray video, force-platform measurements, and EMGs (electromyographs, or recordings of electrical activity in muscles), the scientist can determine a joint's range of motion, the duration and intensity of muscle activity, and the order in which the muscles activate to produce a pattern of movement.

Functional morphologists are often interested in the performance limits of a particular system. They ask questions such as: How much force can the human jaw produce? How fast can a lizard sprint on an inclined surface? How much weight can a thigh bone stand before it breaks?

Ecological morphology (also called "ecomorphology") considers the structure of an organism in the context of its **habitat** and ecological role. Ecological morphologists are more interested in how structures are actually used in nature than in the limits to which structures can be pushed in an artificial laboratory setting. Ecological morphologists distinguish between a structure's biological role and its function. Therefore, they usually

habitat physical location where an organism lives in an ecosystem spend some time familiarizing themselves with the habits and natural surroundings.

Ecological morphologists ask questions such as: How does the shape of a hawk's beak help it tear through the flesh of its prey? How does the shape of fish larvae help them disperse along wave-swept shores? How does the shape of a bat's wing help it maneuver while catching insects at night?

Although these specific research areas are worthy of pursuit in and of themselves, many scientists promote an integrative approach to the study of morphology that brings together these and other aspects of morphological research. Evolutionary morphology draws lessons from functional and ecological morphology to determine how structures evolved. Using a comparative method, morphologists put structures into a historical context and draw conclusions about how a structure came to exist based on structural and/or functional similarities and differences between related animals.

climate long-term weather patterns for a particular region

When variations in environmental pressures and biological roles are taken into account, morphological differences can lend insight into the origin of animal diversity. As animals evolve over time, their morphology adapts to specific selective pressures such as prey type and abundance, predator type and abundance, **climate**, and habitat characteristics. The diversity of animal form reflects the complex interactions between animals and their environment. SEE ALSO Adaptation; Morphological Evolution in Whales.

Judy P. Sheen

Bibliography

Kardong, Karl V. *Vertebrates: Comparative Anatomy, Function, Evolution.* Boston: McGraw Hill, 1998.

Wainwright, Peter C., and Steve M. Reilly, eds. *Ecological Morphology: Integrative Organismal Biology.* Chicago: University of Chicago Press, 1994.

Mouth, Pharynx, and Teeth

enzymes proteins that act as catalysts to start biochemical reactions

The digestive system functions to receive, store, and break down food to absorb nutrients. Both physical and chemical digestion processes begin in the mouth. The presence of food in the mouth causes the salivary glands to deliver saliva into the mouth. Often even the smell or anticipation of food will cause activation of the salivary glands. Digestive **enzymes** in saliva begin to moisten, soften, and dissolve the food before passing it to the next stage of the digestive system. Saliva also contains mucin, which protects the mouth from abrasion, and buffers, which prevent dental cavities by neutralizing acid in the mouth. The tongue is used to taste and manipulate food during chewing.

Fish, amphibians, and reptiles principally use teeth to grip prey and prevent it from escaping until it can be swallowed whole. Birds have no teeth, but many have bills with serrated edges for shredding. Often the upper bill is hooked for seizing and tearing apart prey. Other bill shapes are designed for seed eating and fishing. Because snakes have no limbs, their mechanism of feeding has been modified. Rapid strikes, venom, and constriction are used to immobilize prey. Backward-curving fangs also help snakes to seize and hold prey. Snakes tend to eat large prey items, and they are able to unhinge their jaws to swallow them. For some animals, the physical reduction of food is necessary to release nutrients from indigestible components and to increase the surface contact between food and digestive juices. Physical reduction of food in the mouth is accomplished by the chewing, rasping, and grinding of teeth. The function and type of teeth depend upon the specialized food habits of the animal.

Mammals exhibit true mastication, meaning that their teeth are involved in chewing as opposed to just tearing or crushing. Mammals typically have four types of teeth. The incisors at the front of the mouth are used for biting, cutting, and stripping; the canines are used for seizing, piercing, and tearing. Further back in the mouth, premolars and molars are used for grinding and crushing. Carnivores have well-developed canines for seizing prey and tearing meat. **Herbivores** have reduced canines, but well-developed molars for grinding. Their teeth help them break apart the tough cellulose walls of plants to access nutrients. Rodents have self-sharpening incisors that grow throughout life and must be worn away by gnawing to keep them from growing too long.

The teeth of some **vertebrates** have evolved to serve functions other than feeding. For example, elephant tusks are modified upper incisors used for defense, attack, and rooting for food. Male wild boars have modified canines that are used as weapons in male-to-male combat. Elk use specialized teeth to make mating and territorial calls.

After food is physically and chemically reduced in the mouth, it passes to the next stage of digestion. Food is swallowed when the tongue pushes the food to the back of the mouth and into the pharynx. The pharynx acts as an intersection between the esophagus and the **trachea**. The esophagus leads to the stomach, whereas the trachea leads to the **lungs**. The epiglottis, a **cartilaginous** flap, covers the trachea during swallowing to prevent food and fluid from entering the lungs. Food then enters the esophagus and **involuntary muscles** contract to push food into the stomach.

Invertebrates have comparable feeding and digestive mechanisms to those of vertebrates. Invertebrates do not possess true teeth. However, they often have beaks or toothlike structures for biting and holding. Insects have three pairs of appendages on the head that serve multiple functions. The first pair, the mandibles, are primarily for crushing. The second pair, the maxillae, serve as grasping jaws, and the third, the labia, as probing and tasting tongues. Food that has been broken down into smaller pieces enters the mouth, often with the help of extended maxillae. As with vertebrates, salivary glands produce enzymes to help break down food. The reduced food then enters the crop, an organ similar to the vertebrate stomach, for further digestion.

In insects, the form and structure of mouthparts varies dramatically depending upon the type of feeding. Locusts eat leaves and have grinding and cutting mandibles. Mosquitoes and butterflies have sucking or siphoning mouthparts. The common housefly has spongelike mouthparts with which they lap up food they have liquefied with salivary secretions.

This yawning lion in Botswana displays sharp and dangerous teeth. Since the lion is carnivorous, it's long canines are predominant features of its mouth.

herbivores animals who eat plants only

vertebrates animals with a backbone

trachea the tube in air-breathing vertebrates that extends from the larynx to the bronchi

lungs sac-like, spongy organs where gas exchange takes place

cartilaginous made of cartilage

involuntary muscles muscles that are not controlled by will

invertebrates animals without a backbone

Other invertebrates have interesting structures used for procuring and reducing food. For example, *Nereis*, a **carnivorous** polychaete (marine worm), have a muscular pharynx with **chitinous** jaws that they turn inside out quickly to seize prey. The pharynx then retracts and the prey is swallowed. **Crustaceans** often reduce the size of food using shredding devices like the tearing, beaklike jaws in cephalopod **mollusks** (i.e., squid). Snails have a radula, a rasping structure in the mouth, for scraping algae off rocks. SEE ALSO Digestive System.

carnivorous term describing animals that eat other animals

chitinous made of a complex carbohydrate called chitin

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

Alisha K. Holloway

Bibliography

Campbell, N. A. *Biology*, 3rd ed. Redwood City, CA: Benjamin/Cummings Publishing Company, Inc., 1993.

Hickman, Cleveland P., Jr., Larry S. Roberts, and Allan Larson. *Integrated Principles of Zoology*, 9th ed. Dubuque, IA: Wm. C. Brown Publishers, 1995.

Hildebrand, M. *Analysis of Vertebrate Structure*, 3rd ed. New York: John Wiley & Sons, Inc., 1988.

Muscular System

Independent movement is a unique characteristic of animals. Most animal movement depends on the use of muscles. Together, muscles and bones make up what is known as the musculoskeletal system. This combination provides protection for the body's internal organs and allows for many kinds of movement. Whether the movement is as simple as opening the eyes or as complex as flying, each is the result of a series of electrical, chemical, and physical interactions involving the brain, the central nervous system, and the muscles themselves.

Muscle is the flesh, minus the fat, that covers the skeleton of **vertebrate** animals. Muscles vary in size and shape and serve many different purposes. Large leg muscles such as hamstrings and quadriceps control limb motion. Other muscles, like the heart and the muscles of the inner ear, perform specialized involuntary functions. Despite the variety in size and function, however, all muscles share similar characteristics.

At the highest level, the entire muscle is composed of many strands of tissue called **fascicles**. These are the strands of muscle that can be seen in red meat or chicken. These strands are made up of very small fibers. These fibers are composed of tens of thousands of threadlike myofibrils, which can contract, relax, and lengthen.

The myofibrils are composed of up to ten million bands laid end-to-end called **sarcomeres**. Each sarcomere is made of overlapping thick and thin filaments called **myofilaments**. The thick and thin myofilaments are made up of contractile proteins, primarily **actin** and **myosin**.

vertebrate an animal with a backbone

fascicles close clusters

sarcomeres segments of striated muscle fibrils which are divided by thin dark bands

myofilaments any of the ultramicroscopic filaments, made up of actin and myosin, that are the structural units of a myofibril

actin a protein in muscle cells that works with myosin in muscle contractions

myosin the most common protein in muscle cells, responsible for the elastic and contractile properties of muscle; it combines with actin to form actomyosin

voluntary muscles muscles with fibers of cross bands usually contracted by voluntary action

Types of Muscle Tissue

Muscles are categorized as either voluntary or involuntary. The muscles that animals can deliberately control are known as **voluntary muscles**. Those that cannot be controlled by the animal, such as the heart, are called **in-**

voluntary muscles. Vertebrates also possess several different types of muscle tissue: cardiac, smooth, and striated or skeletal.

The electrograph displays the interaction of actin-myosin filaments.

The muscle types are classified on the basis of their appearance when viewed through a light microscope. **Striated muscle** appears striped (striated) with alternating light and dark bands. Smooth muscle lacks the alternating light and dark bands.

Cardiac muscle. Cardiac muscle makes up the wall of the heart, which is called the myocardium. In humans the heart contracts approximately seventy times per minute and can pump nearly 5 liters (4.5 quarts) of blood each minute. The fibers of the heart muscle are branched and arranged in a netlike pattern. The involuntary heart contraction is stimulated by an electrical impulse within the heart itself at the sinoatrial node.

Smooth muscle. Smooth muscle cells are organized into sheets of muscle lining the walls of the stomach, intestines, blood vessels, and diaphragm, and parts of the urinary and reproductive systems. The smooth muscle contractions push food through the digestive system, regulate blood pressure by adjusting the diameter of blood vessels, regulate the flow of air in the **lungs** and expel urine from the urinary bladder. These body functions are involuntary and controlled by the **autonomic nervous system**.

involuntary muscles muscles that are not controlled by will

striated muscle a type of muscle with fibers of cross bands usually contracted by voluntary action

lungs sac-like, spongy organs where gas exchange takes place

autonomic nervous system division of the nervous system that carries nerve impulses to muscles and glands

Skeletal or striated muscle. Skeletal muscle, which is muscle tissue attached to bones, makes up a large portion of an animal's body weight—sometimes between 40 and 60 percent. Skeletal muscles move parts of the skeleton in relation to each other. They contain abundant blood vessels that transport oxygen and nutrients, nerve endings that carry electrical impulses from the central nervous system, and nerve sensors that relay messages back to the brain. Skeletal muscles are responsible for the conscious or voluntary movements of the trunk, arms and legs, respiratory organs, eyes, and mouthparts of the animal. They are used for such actions as running, swimming, jumping, and lifting.

These distinctive muscle types can be observed throughout the evolution of vertebrates, however the arrangement of muscles varies according to differing environmental and survival needs. In fish, for example, most of the skeletal muscles fan out from either side of the backbone. Muscle makes up nearly 60 percent of the fish's body and nearly all of it is involved in moving the tail and spine.

As vertebrates evolved and adapted to life on land, the down-the-spine muscle arrangement began to change. More muscle power was needed for moving the limbs. Limb muscles became both bigger and longer. Some muscle fibers in a frog's hind legs can be nearly a quarter as long as the frog's body, which is proportionately much longer than the muscles in many fish. More muscles developed in the chest to be used for breathing, as vertebrates began spending more time on land. In mammals, this led to the development of the diaphragm, an involuntary muscle that helps to bring air into the lungs.

How Muscles Contract

Nerves connect the spinal column to the muscle. The place where the nerve and muscle meet is called the **neuromuscular junction**. Inside the muscle fibers, a signal from the nervous system stimulates the flow of calcium, which

neuromuscular junction the point where a nerve and muscle connect causes the thick and thin fibers (myofibrils) to slide across one another. When this occurs, the sarcomere shortens, which generates a force. The contraction of an entire muscle fiber results when billions of sarcomeres in the muscle shorten all at once.

The "sliding-filament theory" suggests that these thin and thick filaments become linked together by molecular cross bridges, which act as levers to pull the filaments past each other during the contraction of the muscle fiber. Myosin molecules have little pegs, called cross bridges, that protrude from the thick filament. During contraction, another molecule, called actin, appears to "climb" across these bridges.

Movement in invertebrates. Movement occurs in all animals, including those without highly developed musculoskeletal systems. Nearly all groups of animals, including relatively simple organisms such as jellyfish and flatworms, have rudimentary muscle fibers that are specialized to move parts of the body. The number of muscles is not necessarily related to the size of the organism or the presence of a skeletal system. For example, a caterpillar may have 2,000 separate muscles compared with some 600 muscles in the human body.

Movement in **invertebrates** is caused by the same contractile proteins, actin and myosin, that function in the muscles of vertebrates. This primitive muscle tissue is triggered into action by nerves, **hormones**, or the built-in rhythm of the organism.

Simple protozoans such as the *Ameoba*, can either contract or extend their one-celled body in any direction. Other protozoans move by means of contractile fibers contained in **cilia** and **flagella**. Cilia are minute, hairlike, projections that stick out from the cells of some animals. Cilia allow protozoa to move freely through their **aquatic** environment. Another adaptation is the **flagellum** (pl., flagella), a whiplike structure found in sponges. A flagellum moves by a beating pattern that mimics a snakelike undulation.

Both smooth and striated muscle are present in invertebrate animals ranging from **cnidarians** to **arthropods**. Flatworms have muscle fibers in three directions, the contraction of which will move the body in multiple planes much like a human tongue. The body wall of earthworms contains both an outer and an inner layer. Contraction of the outer layer causes the body to lengthen and the action of the inner layer shortens it, producing the wiggling motion of the worm.

The only invertebrates without this layered arrangement of muscle tissue are the **mollusks**, **crustaceans**, and insects. They do, however, have many separate muscles, varied in size, arrangement, and attachments, that move the body segments and the parts of the jointed legs and other appendages. These muscles are fastened to the internal surfaces of the **exoskeleton**. Clams and other **bivalve mollusks** use strong muscle contractions to keep their shells tightly shut at high tide. Once the shell-closing muscles have contracted, they can remain tightly shut for hours without tiring. SEE ALSO Locomotion; Skeletons.

Leslie Hutchinson

invertebrates animals without a backbone

hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

cilia hair-like projections used for moving

flagella cellular tail that allow the cell to move

aquatic living in water

flagellum cellular tail that allows cells to move

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

mollusks large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

exoskeleton hard outer protective covering common in invertebrates such as insects

bivalve mollusks mollusks with two shells such as clams

Bibliography

Hickman, Cleveland, Larry Roberts, and Frances Hickman. *Integrated Principles of Zoology*, 8th ed. St. Louis, MO: Times Mirror/Mosby College Publishing, 1990.

Huxley, H. E. "The Mechanism of Muscular Contraction." *Science* 164 (1969):1356–1365.

Randall, David, Warren Burggren, and Kathleen French. *Eckert Animal Physiology: Mechanisms and Adaptations*, 4th ed. New York: W. H. Freeman & Company, 1997.

Rome, L. C., and R. P. Funk. "Why Animals Have Different Muscle Fiber Types." *Nature* 355 (1988):824–827.

Internet Resources

"Muscle." *Encyclopedia Britannica Online*. 1994-2001. <http://members.eb.com/>.

Museum Curator

Museum curators care for, manage, organize, and develop the objects in a museum. Museum curators may do some or all of the following tasks:

- acquire new items for the museum's collection;
- examine items for the collection to determine their condition and whether they are authentic;
- identify and classify items;
- keep and maintain inventory records about all items in the collection;
- arrange and oversee conservation and restoration work for the items;
- make sure that climate and pest control issues are seen to at all times to protect the items in the collection;
- organize and prepare displays, which can include traveling and arranging for loan exhibitions;
- conduct research or oversee research on collection pieces;
- educate the public about the collections, which generally involves lecturing and writing;
- raise funds for the museum, which can include applying for grants and attending social events with private museum donors;
- supervise a staff, which can consist of volunteers, interns, students, collection managers, technicians, junior curators, and secretarial staff.

This museum curator prepares the bones of an Allosaurus for public display.

As this list shows, museum curators must not only be experts in their field but also have very good people skills and writing skills. A museum curator must be very dedicated, often spending long hours traveling and weekends and evenings at social events raising money for the museum.

To become a museum curator, one must follow a long period of training in a discipline. Generally, at a museum, a person starts as an assistant and works her or his way up to associate, then to full (or senior) curator. Museum curators may specialize in a specific discipline such as art, natural history, science, or technology.

Museum curators need a well-rounded education. In high school, one should take courses in English, literature, creative writing, history, art, the sciences, business, and foreign language. Math and computer skills are also essential. Museum curators must have a bachelor's degree, and most museums require their chief curators to have a doctoral (Ph.D.) degree. Museums generally hire curators who have degrees in fields related to the museum's specialty. While some persons attend college and obtain degrees in museum studies (museology), most get degrees in their particular areas of interest, such as biology or paleontology. Earning two graduate degrees, in museum studies and a specialized subject, can make a person a more valuable curator. In order to get hands-on experience, college students can apply for internship programs at a museum. These internships generally last a year or less and involve work on a project identified by the museum. Also, volunteering at a museum is a good way to get experience.

Denise Prendergast

Bibliography

Cosgrove, Holli R., ed. *Encyclopedia of Careers and Vocational Guidance*, 11th ed. Chicago: Ferguson Publishing Company, 2000.

Internet Resources

American Association of Museums. <http://www.aam-us.org/>.

Occupational Outlook Handbook, 2000–01 Edition. <http://stats.bls.gov/ocohome.htm>.

Natural Resources

Natural resources are those elements of the environment that are considered valuable to humans. These can be raw materials, such as trees for lumber and ore for manufacturing, or things that are directly consumed, such as groundwater to drink and animals to eat. The word "natural" means that there has been no modification by humans. A "resource" is something that is necessary for growth and reproduction. Natural resources can be divided into three categories: perpetual resources, like the Sun; potentially renewable resources, like forests; and nonrenewable resources, like fossil fuels.

While a resource can be something that is necessary for an animal as well as a human, the term "natural resource" is always used in the human context. The use of this term has increased with the growing awareness of the need to manage the use of these resources to ensure their existence in the future. Many of these resources grow or form at a much slower rate than the rate at which humans are using them, and so their future is in peril. Methods to protect natural resources are complex, involving education, reduction in demand, and large-scale recycling. Global cooperation will be vital to the success of all of these tactics.

Perpetual Resources

In the context of human usage, natural resources can be divided into three categories based on the possibility of resource renewal. The first category is perpetual resources. Phenomena such as solar rays, wind, tides, and flowing water will always exist within the scope of human existence. The Sun, which drives many of these phenomena, is not likely to burn out for billions of years. Harnessing solar energy or the motion of the wind or water will not decrease the quantity of these resources, which is the obvious advantage of perpetual resources.

Solar cells take the energy from the Sun's rays and turn them into electricity that can charge batteries and drive household equipment and even

some specially designed automobiles. Windmills produce energy generated by the turning of their blades. But neither solar nor wind energy is commonly used because other energy sources, such as coal and gas, are less expensive in proportion to the amount of energy produced. Until a worldwide financial demand for alternative energy sources develops, technologies for exploiting these sources will lag behind common energy sources in their relative efficiency.

Solar panels on top of houses are becoming a more common instance and source of natural power in the United States.

There are difficulties in harnessing some perpetual energy sources. One example is hydroelectric power, which is generated from flowing water that spins turbines which in turn generate electricity. The problem here is that to create enough energy for a large-scale hydroelectric plant, it is necessary to build huge dams. These dams must increase the potential energy of the water. They must also ensure that energy delivery does not stop during seasonal decreases in water flow on the rivers upon which the dams are built.

These huge dams allow sediments in the water to settle out so that ultimately, in anywhere from 40 to 300 years, the system becomes clogged. Also, the lake that is formed inundates the upstream shallow **habitat** on

habitat physical location where an organism lives in an ecosystem

which many fishes rely, changes the downstream flow patterns, and does not allow species to travel the full length of the river, which some species need to do for breeding purposes.

Renewable Resources

With the growing realization that some resources are being used up, there has been a focus on renewable resources, the second category of natural resources. This category includes plants, animals, fertile soils, and clean air and water. These may be more accurately described as potentially renewable, because in many places they are not being actively renewed. That is because in the short term it is more economical to exhaust one area and then go to a new one instead of renewing the resource.

Harvesting trees, for example, is most economical when the entire forest is harvested, which is known as clear-cutting. That way, machines have easier access to do the cutting and transport of the logs. Unfortunately, the cleared landscape does not support the same species that were there previously. In addition, this landscape is subject to extensive soil erosion. To maintain the forest in its prior state, some trees must remain standing to conserve the soil, and efforts must be made to replant the same species that were harvested. Both cost more money and take more time than simply moving to a new area to harvest.

Another example involves drinking water. In many areas, drinking water supplies are contaminated because of poor sewage systems and runoff from human activities like farming and industry. It is proving less expensive to haul water in from other areas than to correct the cause of the problem. Therefore, this approach is becoming more common. Until an increase in consumer demand for resources that are truly being renewed alters political action and financial motivation, many potentially renewable resources will continue to be threatened.

Nonrenewable Resources

The third and final category of natural resources is nonrenewable resources, which includes fossil fuels and minerals. These resources take extensive geological time to form, and are therefore essentially finite. Oil and natural gas are fossil fuels, which constitute an essential energy source of developed countries. They are burned to generate electricity and to power combustion engines, as in automobiles and airplanes. Minerals like iron and gold are mined from the earth as low-quality ore and then processed into pure forms that are used as building materials.

Nearly all the steps for obtaining and using nonrenewable resources are harmful to the environment. Drilling and mining to get the raw materials almost always drastically disturbs or destroys the area being explored. Processing the raw materials involves a great deal of energy and chemicals that produce toxic by-products. Finally, the use of fossil-fuel-based products like gasoline causes air and water pollution.

The conservation of natural resources involves many steps, the first of which is a global change of attitude toward conservation that places a priority on reducing consumption. The number of people and the amount of resources each person consumes must be reduced in order to lower the usage of natural resources. This will be no easy matter. Reducing the number of people having an impact would be a difficult step for areas where large families are of religious or economic importance. Also, reducing the amount each person consumes is contrary to the notion of progress in the most developed countries. Hopefully, education will help reduce the demand for nonrenewable resources and increase the use of perpetual and renewable resources before shortages dictate these changes. SEE ALSO Habitat; Habitat Loss.

Jean K. Krejca

Bibliography:

Dunell, Lee. *State of the Ark: An Atlas of Conservation in Action.* London: Gaia Books, 1986.

Jeffries, Michael J. *Biodiversity and Conservation.* London: Routledge, 1997.

Mackenzie, Susan H. *Integrated Resource Planning and Management.* Washington, D.C.: Island Press, 1996.

Miller, G. Tyler, Jr. *Environmental Science*, 3rd ed. Belmont, CA: Wadsworth Publishing, 1991.

Warren, Andrew, and Frank Barrie Goldsmith, eds. *Conservation in Practice.* London: Wiley, 1974.

Natural Selection

Natural selection is the differential survival and reproduction of individuals with particular **phenotypes**, the physical manifestation of **genotypes**. Natural selection works only on the phenotypes of individuals. Natural selection produces adaptation when the phenotype is heritable. Natural selection is the most important cause of biological evolution.

phenotypes the physical and physiological traits of an animal

genotypes the genetic makeup of different organisms

Charles Darwin was the creator of the concept of evolution by natural selection. In his 1859 book, *On the Origin of Species*, the most important book on evolution, Darwin put forth his argument and supported it with multiple examples. Darwin's idea of natural selection was heavily influenced by an essay on human population growth written in 1798 by English economist Thomas Malthus. Malthus pointed out that every organism has the ability to produce more individuals than the environment can support, and that many individuals die without reproducing. Darwin recognized that variation among individuals is always present, and that some individuals with particular combinations of traits are more likely to survive than other individuals with different combinations of traits. With so much variation, and more individuals being produced than can survive, the individuals with the combination of traits that are best suited to their environment will survive better and reproduce more than other individuals. This is natural selection as Darwin described it.

Darwin also identified artificial selection, which works in the same way as natural selection except that humans are the selective force rather than the environment. Artificial selection, for example, has produced domesticated animals. One of the best illustrations of artificial selection is the breeding of dogs, as humans selectively bred dogs to have specific characteristics. Beagles were bred to bark as they chased after foxes. Labrador retrievers were bred to swim and to carry game birds that had been shot down over water back to shore. Other characteristics selected for included body size,

color, hair length, and personality. Dogs are all the same species, but there are clearly huge amounts of variation among breeds.

sexual selection selection based on secondary sex characteristics that leads to greater sexual dimorphorphism or differences between the sexes

Darwin also identified a third type of selection, **sexual selection**. Sexual selection is the differential ability of individuals to win mates and reproduce. Most animal species have sexual dimorphism, that is, the different sexes have different traits. Sexual dimorphism results from sexual selection. Bird songs, elaborate coloration, and the other characteristics that help males attract mates are sexually selected traits. For example, male guppies have bright spots of pigmentation that attract females. Males that are more brightly colored mate with more females.

populations groups of individuals of one species that live in the same geographic area

There are three forms of selection: directional, stabilizing, and diversifying. Directional selection changes the average value of a trait in some **populations**. For example, female guppies that prefer to mate with male guppies that have more orange spots will increase the average number of orange spots on males in the next generation. Stabilizing selection reduces variation in a population by selecting against the extreme individuals. In a similar example, females liked males that had only five spots of orange, but disliked males with more or less than five spots. Diversifying selection increases the variation in a population by favoring the extreme individuals, for example males with lots of orange spots or with no orange spots, and disfavoring males with average amounts of orange spots. SEE ALSO ADAPTATION; BIOLOGICAL EVOLUTION; DARWIN, CHARLES.

Laura A. Higgins

Bibliography

Andersson, Malte. *Sexual Selection.* Princeton, NJ: Princeton University Press, 1994.

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Endler, John A. *Natural Selection in the Wild.* Princeton, NJ: Princeton University Press, 1986.

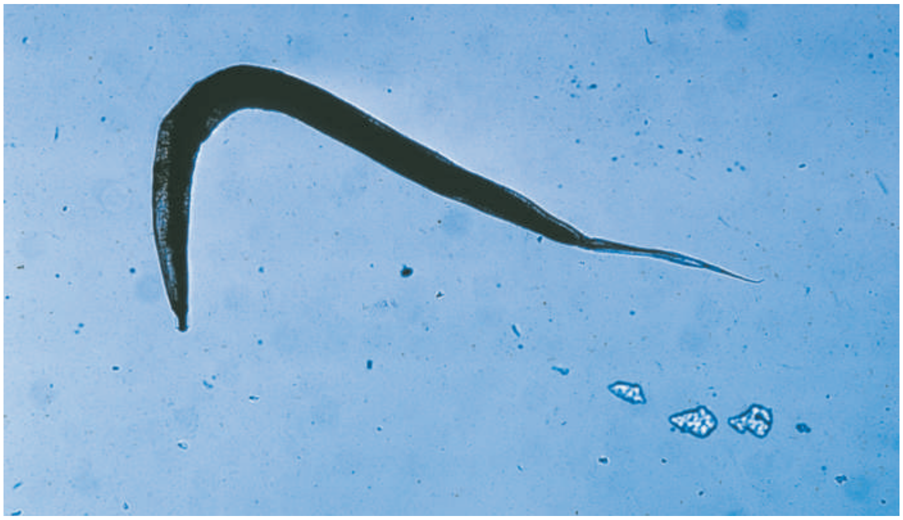
Futuyma, Douglas J. *Evolutionary Biology*, 3rd ed. Sunderland, MA: Sinauer Associates, Inc., 1998.

Nematoda

habitat physical location where an organism lives in an ecosystem

ecosystems self-sustaining collections of organisms and their environments

The Phylum Nematoda consists of the species commonly known as roundworms. There are approximately 12,000 described species, but the actual number could be many times higher. Nematode worms are extremely abundant; often, several hundred species, and as many as a million individuals, inhabit a square yard of soil. Nematodes are also extremely varied ecologically. They are found in almost every imaginable **habitat**, including terrestrial (land-based), freshwater, and saltwater **ecosystems**, as well as within other organisms as parasites. Nematodes can be herbivorous, carnivorous, or parasitic, and include both generalists (who make use of a wide variety of resources) and specialists (who make use of only particular resources). They play a particularly critical role in decomposition and nutrient cycling, where they are often the intermediate decomposers that partly break down organic materials so that they can then be dealt with by bacterial decomposers.



A pinworm. Adult pinworms live in the large intestine of humans.

Characteristics of Nematodes

Roundworms are small, slender, unsegmented worms which are tapered at both ends. They have a circular cross section. Different species of nematodes are often difficult to distinguish because of their fairly uniform external morphology, or outer appearance.

Nematodes are characterized by an external (outer) layer of cuticle that is secreted by the hypodermis underneath it. The cuticle is somewhat rigid. However, it is flexible enough to permit bending and stretching, and can be penetrated by gases and water. The cuticle is **molted**, or shed, several times during the worm's growth. The hypodermis underlying the cuticle is a syncitium—that is, it consists of large cells with more than one nucleus. A layer of muscle cells is found beneath the hypodermis. All nematode muscle fibers run lengthwise along the animal's body. This single, unvaried orientation limits nematodes to their characteristic, and somewhat awkward, pattern of movement, a flailing whiplike motion that is produced by alternate contractions (shortenings and thickenings) of muscle cells on either side of the animal's body. The rigidity of the cuticle layer also limits the motion of nematodes.

molted the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

Nematodes lack a true **coelom** (body cavity) since their internal cavity is not lined by cells originating from the embryonic mesoderm. Instead, they possess a fluid-filled pseudocoel (incomplete coelum) that contains the intestine and reproductive organs.

coelom a body cavity

The nematode nervous system is characterized by an rear nerve ring around the area of the pharynx (area deep inside the mouth cavity) and two pairs of lengthwise nerve cords that run down the body. There are also **dorsal** (back) and **ventral** (belly) nerve cords as well as a set of lateral nerve cords across the body. These nerve cords transmit sensory information and coordinate movement. Nematodes have a variety of sensory receptors, including tactile (touch) receptors at the front and back ends of the body, and chemosensory (chemical-sensitive) cells at the front end. They also have light-sensitive organs organized either in ocelli (simple eyes) or distributed along the surface of the body.

dorsal the back surface of an animal with bilateral symmetry

ventral the belly surface of an animal with bilateral symmetry

Nematodes have a complete gut with a mouth and an anus. Teeth, which are used to pierce animal or plant matter, aid in obtaining food. The pharynx is muscular and pumps food through the gut, and nutrients are absorbed in the intestine. There is no internal system of circulation, so the transport of nutrients and wastes is achieved by **diffusion** (scattering). Specialized cells for excretion, which are known as rennette cells and are unique to the phylum, remove nitrogen-laden wastes. These are expelled from the nematode directly through the body wall, in the form of ammonia.

diffusion the movement of molecules from a region of higher concentration to a region of lower concentrations

Nematodes breathe across their entire body surface. This gas exchange strategy is adequate because of the small size of the worms, which means they have a high ratio of surface area to volume.

dioecious having members of the species that are either male or female

sexual reproduction a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

The majority of nematodes are **dioecious**; that is, the sexes are separate. Some species, however, are hermaphroditic, having both male and female reproductive organs. In dioecious species, males have a specialized spine for **sexual reproduction** that is used to open the female's reproductive tract and to inject sperm. Nematode sperm is unusual in that the sperm cells do not have flagella, and move using an amoeboid motion (crawling). While some species are live-bearing, most lay eggs. Eggs escape through a midbody hole called the gonopore in the female. There is no distinct larval stage. Eggs develop directly into juveniles that generally resemble the adults except that they lack mature reproductive organs. Nematodes are also characterized by an unusual feature called "eutely," in which every individual of a given species has exactly the same number of cells. This cell number is achieved by the end of the developmental period, so that subsequent growth of the animal involves increases in cell size rather than in cell number.

Nematodes of Particular Interest

Some well-known nematode parasites include hookworms, pinworms, and heartworms. Also included are *Trichinella spiralis*, which is responsible for trichinosis and uses both pigs and humans as hosts, and filarial worms, which are the primarily tropical parasites responsible for the diseases elephantiasis and river blindness.

The nematode *Caenorhabditis elegans* is one of the most well-studied living species and has served as a biological model organism for genetic and developmental studies. It was the first multicellular organism for which a complete DNA sequence was obtained.

Jennifer Yeh

Bibliography

Brusca, Richard C., and Gary J. Brusca. *Invertebrates.* Sunderland, MA: Sinauer Associates, 1990.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton and Co., 1996.

Hickman, Cleveland P., Larry S. Roberts, and Allan Larson. *Animal Diversity.* Dubuque, IA: Wm. C. Brown, 1994.

Nervous System

The nervous system is a highly precise and complex system of cells that allows animals to sense, process, and react to cues from the physical environment. The fundamental duty of the nervous system is to transfer information at relatively high speed from one part of the animal to another. Every animal has at least a rudimentary nervous system. Although plants and fungi are able to sense and respond to aspects of their environment, they do this based solely on chemical **physiological** responses and not because of the combined activity of specialized cells. The means by which a nervous system transfers information is through electrochemical signal transmission. Single nerve cells, neurons, can receive information in the form of a chemical and electrical signal, and transfer this information to other **neurons**, as well as to **somatic** cells, non-neurons.

physiological the basic activities that occur in the cells and tissues of an animal

neurons nerve cells

somatic having to do with the body

The reason and the means by which animals originally developed a nervous system are very difficult to ascertain. Certainly, ancestral animals gained an advantage by being able to sense their environment, and as multicellular organisms became very large, a fast efficient system of communication was needed. However, the function and identity of the first neuron remains a mystery.

Components of the Nervous System

The nervous system of **vertebrates** is functionally divided between the central nervous system, consisting of the brain and **spinal cord**, and the **peripheral nervous system**, including all neurons that do not have their cell bodies within the brain or spinal cord. Primarily, the nervous system is composed of four cell types: neurons, Schwann cells, oligodendrocytes, and astrocytes.

vertebrates animals with a backbone

spinal cord thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

peripheral nervous system the sensory and motor nerves that connect to the central nervous system

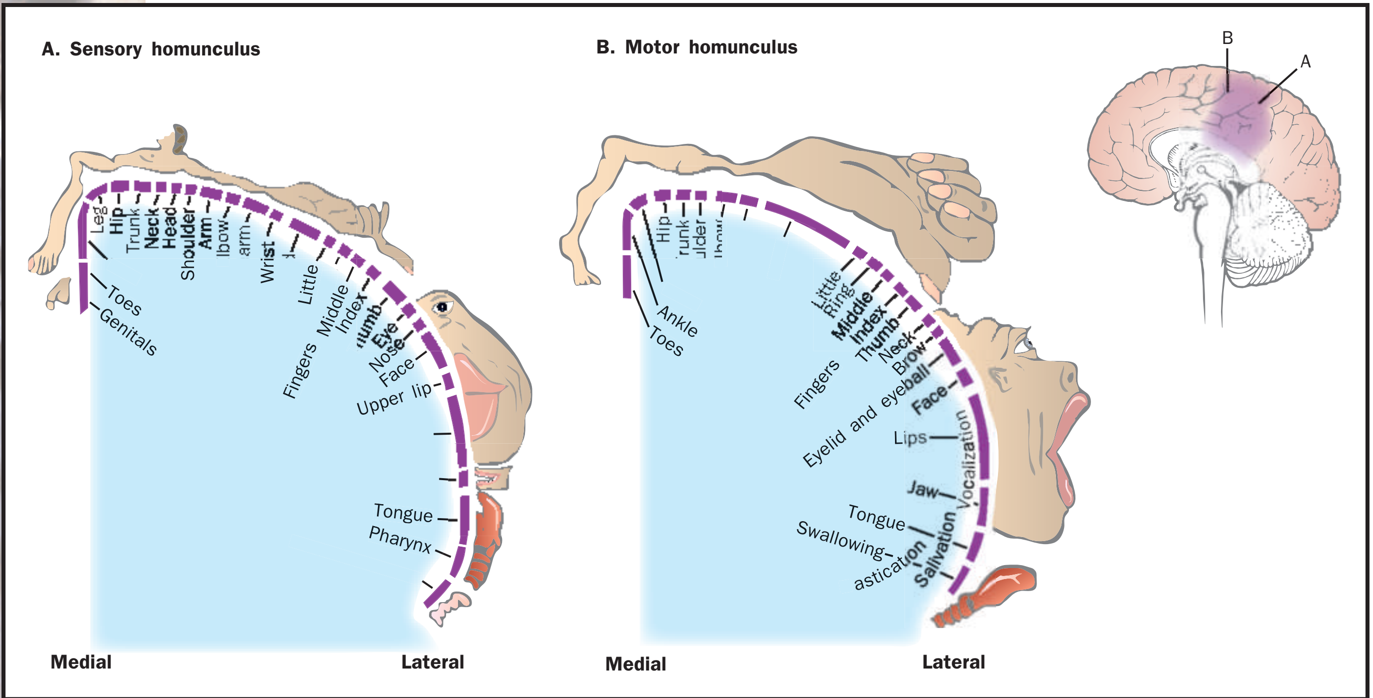
Neurons are the information transfer cells that perform the primary activity of the nervous system. Schwann cells, oligodendrocytes, and astrocytes are support cells for neurons. Schwann cells are located only in the peripheral nervous system, but they have the same function as oligodendrocytes, which are located solely within the central nervous system. Both cell types wrap a fatty myelin sheath around the axon, the electrical signal, to insulate it and thereby increase the speed of conduction. This axonal covering is white, whereas the neuron is gray, so that nerves composed primarily of **axons** look white because of the myelin, and regions formed mostly by cell bodies look gray.

axons cytoplasmic extensions of a neuron that transmit impulses away from the cell body

Support cells can also absorb excess neurotransmitter and provide certain precursor molecules that the neurons will use to construct essential proteins and metabolites. Astrocytes appear only in the central nervous system, and their function is to absorb nutrients from the bloodstream and conduct them to the neurons. Data suggests that support cells are also instrumental in directing immature neurons into their correct location during development, as well as ensuring the integrity of **synapses** and guiding regrowth of axons after injury.

synapses spaces between nerve cells across which impulses are chemically transmitted

The brain and nervous system are composed of grouped functional systems. This means that neurons can be categorized based on what kind of information they convey. These like-neurons are organized into pathways of conduction punctuated by processing nodes. The conduction pathways



Homunculus. Redrawn from Kandel, et. al, 2000.

dendrites branched extensions of a nerve cell that transmits impulses to the cell body

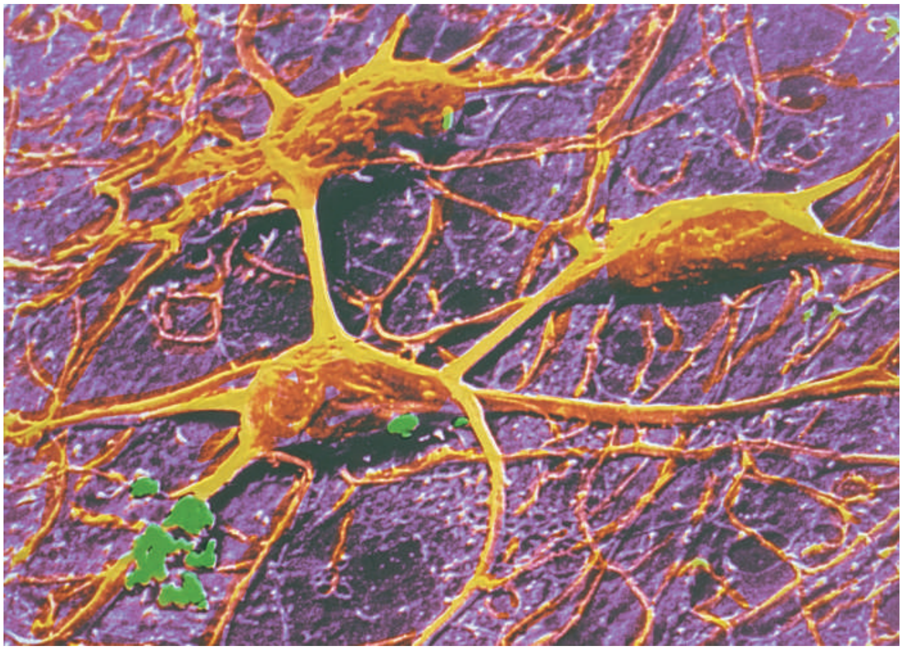
are formed of nerves or fibers containing primarily neuronal axons. The nodes, called ganglia or brain nuclei, are mostly composed of neuronal cell bodies and **dendrites**. Because information is transferred along pathways, and each node processes the information in a characteristic manner, the nervous system is referred to as a labeled-line system.

The nervous system is also called a parallel pathway system, because sensations such as sounds and visual inputs are transferred to the brain in an organized manner within separate nerves. For instance, sounds are divided up into their respective frequencies, and each frequency travels in its own fiber, parallel to the other frequency fibers grouped together within the auditory nervous system. The different sounds thus remain segregated until they are processed in the cortex. Finally, although distinct regions of the brain perform unique tasks, many overall concepts that are important psychologically to humans are not located in any one region of the brain. Memory, emotion, intelligence, and personality are all examples of emergent properties, meaning that they result from the coordinated activities of many brain regions.

action potential a rapid change in the electric charge of the cell membrane

Neurons carry information in the form of an **action potential**, which is a rapid (several milliseconds long) change in the electrical conduction of the cell membrane. When a neuron produces an action potential, it is described as firing, and a single action potential is called a spike. Action potentials are the primary form of communication between neurons, and the entire nervous system is mediated by this signal.

One may then wonder how perception can be so complex. This is because many factors contribute to the information encoded by the action potentials, including the frequency of action potentials, the probability of an action potential in any particular cell, the morphology (shape) of the neuron, the number and location of neurons that contribute the information,



This micrograph depicts three human nerve cells of the cerebral cortex and their branching fibers.

the number and location of neurons that receive the information, the type of neurotransmitter it uses, and the contributions of support cells. Furthermore, although each individual neuron can only produce an action potential for communication, this signal can have a different shape and character for different neurons.

The opposite of an action potential is a **hyperpolarizing potential**. This is instigated by inhibitory neurons, which release a neurotransmitter that decreases the probability that the neuron will fire. There may be thousands of inputs to a single neuron, or just one, and the contributions of all the factors listed above allow the combinatory activity of all the neurons in the ordered nervous system to produce consciousness, cognition (knowing), behavior, sensation, and **homeostasis** (maintenance of an organism's general health) in animals.

hyperpolarizing potential any change in membrane potential that makes the inside of the membrane more negatively charged

homeostasis a state of equilibrium in an animals internal environment that maintains optimum conditions for life

Peripheral nervous system. In vertebrates the peripheral nervous system is composed of both motor neurons, which instigate muscle movement and activity, and sensory neurons, which convey information about the external and internal state of the organism. Furthermore, interneurons are important intermediates in both sensory and motor pathways, because they connect different circuits and can modify a signal as it follows a particular course. All subdivisions of the peripheral nervous system are comprised of these three neuronal types. The peripheral nervous system can be further divided into the autonomic nervous system and the **somatic nervous system**. Because it mediates the activity of heart muscle, smooth muscle, and exocrine glands, the autonomic nervous system is also referred to as the involuntary nervous system. The somatic nervous system is called voluntary because it controls the skeletal muscles.

somatic nervous system a part of the nervous system that controls the voluntary movement of skeletal muscles

Autonomic nervous system. The autonomic nervous system is made up of the sympathetic, parasympathetic, and enteric divisions. The enteric system is a subsection of the peripheral nervous system located in the gastrointestinal tract of the gut and is responsible for mediating digestive reflexes. The high number and dense compaction of neurons in this system, and its autonomy with respect to the brain, cause some scientists to qualify it as a primitive "second brain."

parasympathetic divisions part of the nervous system that generally enhances body activities that gain and conserve energy such as digestion and heart rate

The sympathetic and **parasympathetic divisions** of the peripheral nervous system are functional opposites. Whereas the parasympathetic division is responsible for homeostatic activities, such as maintaining a basal respiratory pattern, heartbeat, and normal metabolism, the sympathetic division governs the body's reaction to extreme situations. It instigates emergency measures in response to stress from strong emotions, athletic exertions, battle, severe temperature change, and blood loss. The sympathetic division thus increases activity in the heart and other organs, the sweat glands, the vascular system, and certain smooth muscle groups. Because the autonomic division controls day-to-day bodily functions, it has been characterized as controlling "rest and digest" activities, whereas the sympathetic division is responsible for "fight or flight" reactions.

somatosensory information sensory information from different parts of the body except for the eyesm tongue, ears, and other primary sense organs

dorsal root ganglia nervous tissue located near the backbone

Somatic nervous system. The somatic nervous system allows vertebrates to monitor and control skeletal muscle output and to consciously sense aspects of the environment. Sensations originating at the skin or muscles of the trunk and limbs of an animal are called **somatosensory information**. Neurons located in the skin, muscle, joints, and ligaments of the body are specialized for transmitting somatosensory information to the central nervous system. Conveying the position of the limbs, muscle exertion, joint stress, temperature, tickle, pain, and tactile information, these sensory neurons enter the spinal cord via the **dorsal root ganglia**. The term "dorsal" means "toward the back of the body," whereas "ventral" means "toward the front of the body." Ganglia are congregations of neuronal cell bodies located outside of the brain. All sensory information enters the spinal cord from the dorsal side and then travels up to the brain.

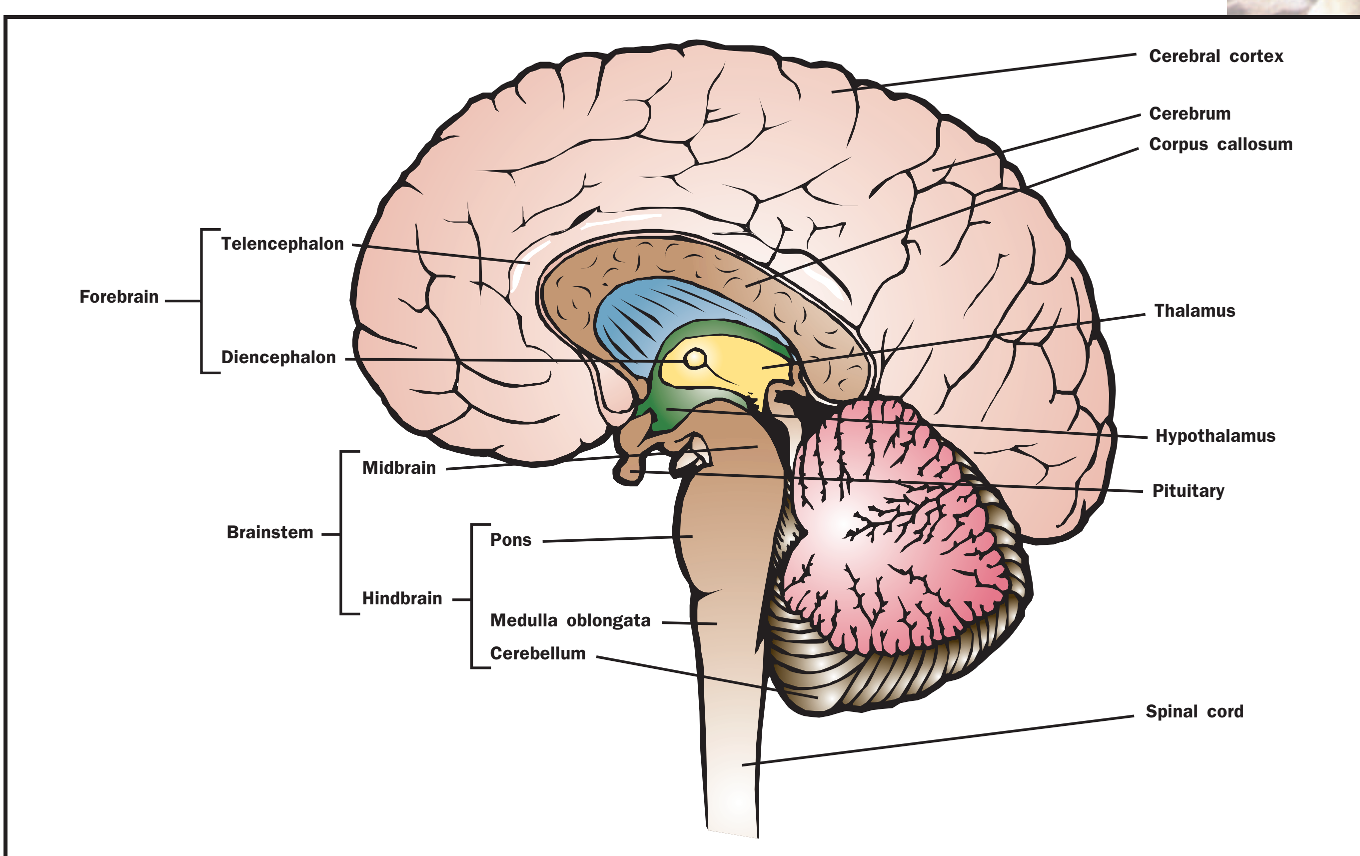
innervate supplied with nerves

Motor nerves controlling muscle movement descend from the brain and send axons out of the ventral side of the spinal cord. There are ventral roots that contain motor axons, but, unlike the somatosensory nerves, there are no motor ganglia. Motor neurons in the somatic nervous system **innervate** (connect with) skeletal muscles and can be controlled by a mix of voluntary and involuntary impulses.

Sensation and motor control of the face, head, and neck do not enter the brain through the spinal cord, but instead are transmitted through cranial nerves that pass through holes in the skull. When animals plan to make a movement, the cerebral cortex sends a message down through the brain to the spinal cord and out to that muscle. Sensory neurons located within the muscle sense its movement and send that information back up to the brain through the somatosensory pathway.

The Brain

The vertebrate brain is housed in the skull, at the rostral end of the organism, whereas the tail end of the animal is the caudal end. Quadrupedal, four-legged, animals have distinct rostral (head), caudal (tail), dorsal (back), and ventral (stomach) poles. At a point in human development, the brain bends 90° so that humans may stand vertically with face pointing forward, whereas



Anatomy of the human brain.

the quadruped's head and brain remain in the straight axis of the spinal cord. Thus, below this bend, dorsal refers to the back and ventral to the chest sides of the body; but, above the bend, dorsal refers to the upward direction and ventral points downward.

All vertebrates have a **bilaterally symmetrical** brain, meaning that specialized regions on one side of the brain are mirrored on the other side. Although animals with more complex brains contain several specialized structures and pathways that differ from one hemisphere to the other, for the most part this mirror image organization is conserved.

bilateral symmetry characteristic of an animal that can be separated into two identical mirror image halves

The brain is divided into three basic regions, the hindbrain, midbrain, and forebrain. The hindbrain contains the pons, cerebellum, and medulla oblongata. At the top of the spinal cord is the medulla oblongata, a thickened region of neural tissue responsible for basic life processes such as breathing, digestion, and control of heart rate. Directly above (rostral to) the medulla is the pons, which conducts information relating to movement, gustation (taste), respiration, and sleep. The cerebellum, a large, highly folded structure composed of six tissue layers, lies dorsal to the pons and medulla. The cerebellum smoothens and coordinates muscle movements and is responsible for learned motor patterns, such as riding a bicycle.

The midbrain lies rostral to the hindbrain, and between these regions is the cephalic flexure, the bend that disrupts the longitudinal axis of the human central nervous system. The midbrain, primarily a relay site for motor and sensory neurons, is the focus of clinical research for its involvement in motor dysfunction diseases such as Parkinson's. Additionally, it is becoming increasingly clear that complex signal properties for sensory systems are established in the midbrain, rather than higher up, in the cortex.

The forebrain can be subdivided into the diencephalon and the telencephalon. The diencephalon is situated directly rostral to the midbrain. It contains the thalamus, which is a nexus for all information destined for the cerebral cortex, and the hypothalamus. The hypothalamus serves to integrate autonomic signals and endocrine activity with the organism's behavior. It regulates body temperature, eating and digestion rates, hormonal control of mating and pregnancy, and the sympathetic division of the autonomic nervous system.

The telencephalon houses the basal ganglia, hippocampus, amygdaloid nuclei, and cerebral cortex. The first three of these structures are buried in the center of the brain, surrounded by the cerebral cortex, cerebellum, and midbrain. The basal ganglia are essential for regulating motor performance. The hippocampus is implicated in short-term memory, and with aspects of long-term memory storage. The amygdala and its associated nuclei coordinate emotion and the effect of emotional state on autonomic and endocrine functions.

The cerebral cortex is involved with higher functioning, association formation, conscious perception, thought, memory, and emotion. The two hemispheres are divided but are interconnected by a bridge called the corpus callosum. Each hemisphere is divided anatomically into four lobes that are separated by prominent folds in the tissue: the occipital, parietal, temporal, and frontal lobes. The occipital lobe is the most dorso-caudal, located at the back of the skull. It contains primary processing centers for vision. The parietal lobe, centrally located on the dorsal cortex, processes sensory and motor information from the body. A distinct fold in the cortex called the central sulcus separates the primary motor cortex (just rostral of the sulcus) from the primary sensory cortex (just caudal of the sulcus). These thin strips of cortex extending from the top of the brain around the lateral sides encode sensation and motor input to every body region in a highly predictable manner. The amount of cortex dedicated to a particular body region is in direct proportion to the amount of motor control or sensory input from that region. The temporal lobe angles down ventrally on the lateral sides of the brain. It contains higher processing centers for audition, vision, and memory. The frontal lobe is the most rostral, and it contains association areas that may be a site for the storage of long-term memories.

Specialized Systems in Animals

The nervous systems of particular animals are specialized to the life habits of those animals. For example, some migratory animals may rely on detection of electromagnetic cues from Earth's crust to guide them over great distances. Weakly electric fish sense their environment and communicate with each other through emission of electrical impulses. These specialized senses require a specialized nervous system to collect and interpret information from the environment. Marine **invertebrates**, such as the giant squid, have very different neurons from those of vertebrates. The nerve cells are unmyelinated (not myelin-containing support cells), and thus the diameter of the axon must be very large sufficiently to increase conduction speed of the neuron.

invertebrates animals without a backbone

Most invertebrates, including insects, have a centralized brain, but the most primitive animals instead have a diffuse distribution of distinct ganglia within each of their segments. These ganglia interact to control organismal activities, but there is no central processing center, as in vertebrates. Studying the simpler nervous systems of invertebrates aids in the understanding of their biological processes. SEE ALSO Growth and Differentiation of the Nervous System; Neuron; Sense Organs.

Rebecca M. Steinberg

Bibliography

Allman, John. *Evolving Brains.* New York: Scientific American Library, distributed by W. H. Freeman & Co., 2000.

Cooper, Leon N., ed. *How We Learn, How We Remember: Toward an Understanding of Brain and Neural Systems. Selected Papers of Leon N. Cooper.* River Edge, NJ: World Scientific, 1995.

Kandel, Eric R., James H. Schwartz, et al. *Principles of Neural Science.* New York: McGraw-Hill, 2000.

Kotulask, Ronald. *Inside the Brain: Revolutionary Discoveries of How the Mind Works.* Kansas City, MO: Andrews McMeel, 1996.

LeDoux, Joseph E. *The Emotional Brain: The Mysterious Underpinnings of Emotional Life.* London: Phoenix, 1999.

Purves, Dale, William S. Mark, et al. *Neuroscience.* Sunderland, MA: Sinauer Associates, 2001.

Neuron

Neurons are highly specialized cells in both form and function. They contain the same suite of **organelles** as other cells, including the nucleus, endoplasmic reticulum, **mitochondria**, and **bilipid membrane**. Unlike many cells, however, neurons are polar cells, meaning that one side of the cell has a different form and function than the other side of the cell. The **dendrites** are located at one extremity, and the **axon** is at the other end. Dendrites are an extension of the neuronal membrane. This extension stretches out from the cell body like a tree with many branches. Each "twig" of the dendritic tree is in contact with another neuron, and the function of the dendrites is to receive information from these other neurons. It is not uncommon for thousands of neurons to contact a single dendritic arbor. The axon, at the opposite pole of the cell, is generally long and unbranched until its tip, where it may have several small branches. After the dendrites pass information through the cell body to the axon, the axon passes this information to the dendrites of other neurons.

Neurons must maintain a particular internal environment. They actively pump positively charged sodium molecules from their **cytoplasm** to their extracellular space, at the same time bringing positively charged potassium ions in. This is accomplished by the sodium/potassium pump, a molecular exchange protein in the membrane that creates different concentrations of ions outside and inside the neuron. The result is that the inside of the cell is negatively charged with respect to the outside of the cell. The difference in charge between the inside and outside of the cell membrane is known as the membrane potential. If the cell is depolarized,

organelles membrane-bound structures found within a cell

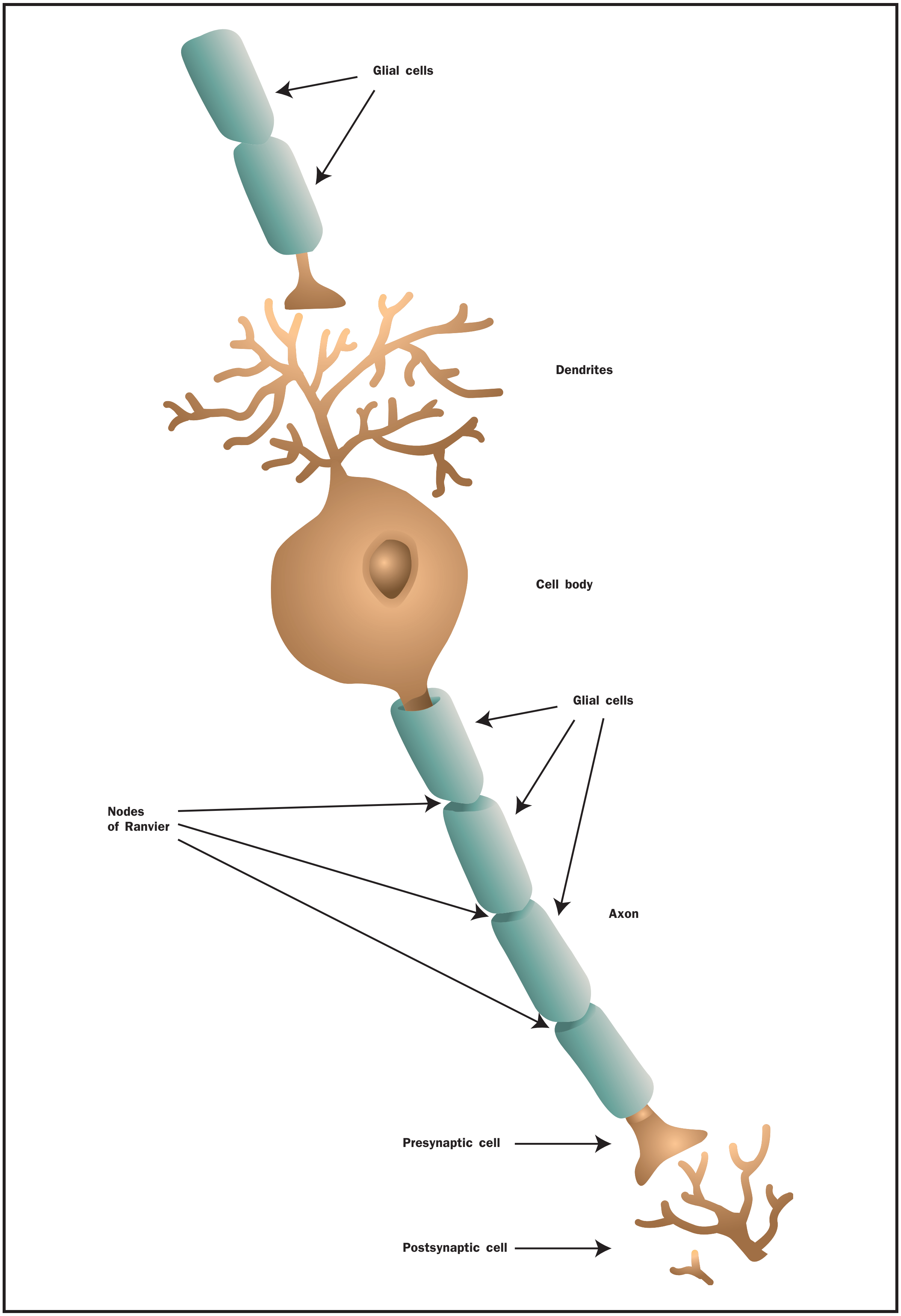
mitochondria organelles in eukaryotic cells that are the site of energy production for the cell

bilipid membrane a cell membrane that is made up of two layers of lipid or fat molecules

dendrites branched extensions of a nerve cell that transmits impulses to the cell body

axon cytoplasmic extension of a neuron that transmits impulses away from the cell body

cytoplasm fluid in eukaryotes that surrounds the nucleus and organelles



Anatomy of the neuron.

the inside of the cell contains more positive charge than normal. If the cell is hyperpolarized, the inside contains more negative charge than normal. If a neuron were disconnected from all other neurons, its membrane potential would remain constant, but when a neuron is in contact with other neurons, it receives many depolarizing signals at its dendrites. The depolarization is caused by allowing more sodium molecules to enter the cell, thereby making the inside more positively charged than normal. The depolarization begins at the tip of the dendrites and travels toward the cell body. If the depolarization is strong enough, it will not die off before reaching the cell body. If the depolarization is very strong, it will reach the axon at the other side of the cell body.

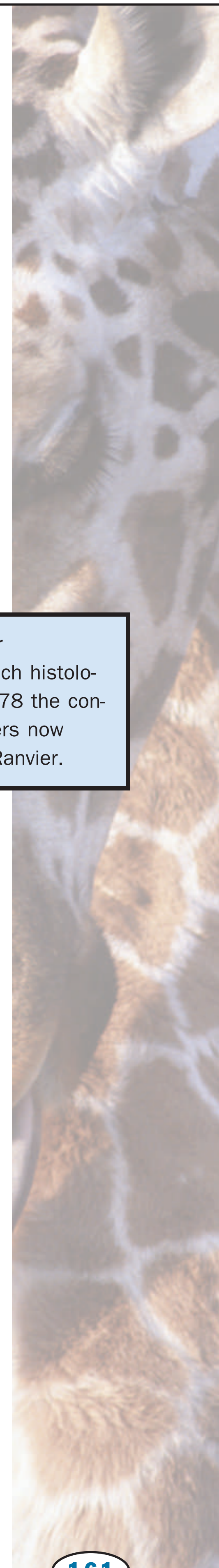
When depolarization reaches the axon, it causes an electrical chain reaction that reaches to the tip of the axon. This **action potential**, or spike, occurs as an active process by which specific ion channels open, allowing positively charged molecules into or out of the cell. First, the base of the axon becomes slightly depolarized from the dendritic signal. This causes specific sodium channels to open. Sodium then enters the axon, increasing the amount of depolarization. Soon the sodium channels fatigue and close, as potassium channels open, allowing positively charged potassium ions to leave the cell. The potassium ion flow cancels the depolarization and even hyperpolarizes the cell a little before potassium channels close and the membrane returns to its normal potential. This electrical event passes along the axon like a wave. The axon is covered by a number of specialized cells called glial cells. These cells wrap around the neuron and insulate it from ion exchange, except at small gaps called the nodes of Ranvier. Because ions can enter or leave the cell only at the nodes of Ranvier, the action potential jumps from node to node, thereby increasing its speed. Because the electrochemical signal moves so quickly through the neuron, the transmission of a signal along the axon is called firing.

action potential a rapid change in the electric charge of the cell membrane

Louis-Antoine Ranvier (1835–1922), a French histologist, described in 1878 the constriction in nerve fibers now known as nodes of Ranvier.

The manner by which one neuron's axon stimulates another neuron's dendrite is through a signal molecule called a neurotransmitter. This occurs at the synapse, a specialized region that includes the tip of one neuron's axon and the conjoining region of another neuron's dendrite. **Neurotransmitters** are stored within the axon tip in pouches of membrane called vesicles. When an action potential travels down the axon and reaches the synapse, it triggers the release of neurotransmitter-containing vesicles into the synaptic clef, the region of space between the axon of one neuron and the dendrite of another. The neuron that releases the neurotransmitter from its axon is called the presynaptic cell and the neuron that receives the neurotransmitter at its dendrites is called the postsynaptic cell. The neurotransmitter diffuses across the synaptic clef, the space between the pre- and postsynaptic cells, and binds to special neurotransmitter receptors in the dendrite of the postsynaptic neuron. These receptors open, allowing sodium ions to flow into the cell. This event is the origin of the dendritic depolarization. Neurotransmitters can be excitatory, meaning that they cause depolarization in the postsynaptic cell, or inhibitory, which means that they prevent depolarization in the postsynaptic cell. Inhibitory neurotransmitters cause a different set of receptors to open, allowing the entry of negatively charged ions such as chlorine. In this inhibition event, the negative charge hyperpolarizes the cell and decreases the probability that the postsynaptic

neurotransmitters chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell



neuron will be depolarized by excitatory presynaptic neurons. SEE ALSO GROWTH AND DIFFERENTIATION OF THE NERVOUS SYSTEM; NERVOUS SYSTEM; SENSE ORGANS.

Rebecca M. Steinberg

Bibliography

Levitan, Irwin B., and Leonard K. Kaczmarek. *The Neuron: Cell and Molecular Biology.* New York: Oxford University Press, 1997.

Nicholls, John G. *From Neuron to Brain*, 4th ed. Sunderland, MA: Sinauer Associates, 2001.

Nocturnal

Nocturnal organisms are those that are active mainly at night and sleep during the day. Their activity pattern occurs in twenty-four hour cycles, known as a circadian rhythm. Nocturnal animals include bats, cats, owls, mice, scorpions, opossums, raccoons, coyotes, cockroaches, and moths.

niche how an organism uses the biotic and abiotic resources of its environment

diurnal active in the daytime

Nocturnal animals occupy a **niche** that is complementary to that of **diurnal** animals. For example, owls have a nighttime role similar to that of hawks during the day. Moths fill the same niche at night as butterflies do during the day.

Many nocturnal animals have specialized adaptations for their nighttime activities. The eyes of most nocturnal animals are larger than those of diurnal animals, helping them to function well in low light. Many nocturnal animals have large ears that are exceptionally sensitive. An acute sense of hearing is helpful when sight cannot be relied on in the darkness. Similarly acute senses of smell, taste, and touch also aid in overcoming the disadvantages of low light conditions.

sonar the bouncing of sound off distant objects as a method of navigation or finding food

Most bats have developed a special **sonar** system called echolocation. They make high frequency calls either out of their mouths or noses and then listen for echoes to bounce from the objects in front of them. This is an effective means of finding their way around in low light and catch their food (generally insects). Fruit bats, one of the few diurnal bats, lack the ability to echolocate. This demonstrates the evolution of characteristics favoring their particular niche, in this case daylight activity versus nighttime activity.

Cats' eyes are well adapted to nocturnal activity. The eyes are relatively large, with pupils that can open wide in the dark and narrow down to slits in the sunlight. The size and position of the eyes on the head allow as much light as possible to enter them and ensure a wide field of vision. These are important factors in hunting and nocturnal prowling. A cat cannot see in total darkness, but it can see better in dim light than can most other animals. Also, cats have large, erect ears that help in the detection of prey in the darkness. SEE ALSO DIURNAL.

Denise Prendergast

Bibliography

Towle, Albert. *Modern Biology.* Austin, TX: Holt, Rinehart and Winston, 1993.

Internet Resources

Forest Preserve District of Du Page County. <http://www.dupageforest.com/CONSERVATIONIST/FALL98/night.html>.

Oligocene

O

The Oligocene epoch (39 to 22 million years ago) is the transition period between the earlier and later Tertiary period (65 to 2 million years ago).

A key feature of evolution is the ripple effect created by geographical changes that influence **climate** and therefore vegetation and ultimately the ways in which animals develop. The most important geographical event separating the Oligocene from the preceding tropical and fairly stable Eocene was the splitting off of the Australasian landmass from Antarctica. As the oceans encircled the growing polar ice cap, the waters cooled. This cooling effect was spread around the globe by circulating currents that produced a dramatic drop in temperatures and, equally important, a new climate marked by seasonal fluctuations. Many animals of the Eocene that depended on a warm climate became extinct in the Oligocene, which is sometimes called "the great divide." Changing seasons favored the rise of homeothermic (warm-blooded) animals, such as mammals, over those who could not control their metabolic temperatures, such as reptiles. Thus the lizards, turtles, and crocodiles who survived did not flourish in the way that mammals like rodents and all modern-hoofed animals did.

climate long-term weather patterns for a particular region

The climatic changes produced changes in vegetation as well. Most forests in northern latitudes (45°) became cooler, mixed coniferous-deciduous, in which the most successful mammals tended to be short-legged, stumpy-bodied browsers and **scavengers**. Fortunately for humans, tropical zones, though greatly diminished, still existed in parts of South America and Africa, where a few primates survived on the year-round fruit supply. Plentiful food sources and tropical climate allowed for the survival of the early primates.

scavengers animals that feed on the remains of animals that they did not kill

Insect groups expanded to include the social ants and termites, followed rapidly by the appearance of **insectivores**. Now that whole colonies of foods were available in a single place, the previously scarce mouse-size mammals who fed on this food also grew in size and number.

insectivores animals who eats insects

The growth of the polar ice cap locked up more and more of the ocean water, causing sea levels to drop and connecting parts of Europe and Asia that had been separate. This allowed a mingling of species throughout Eurasia from which a number of **herbivores** did not recover. Archaic predators such as the condylarths and creodonts, which were hoofed flesh eaters, began to decline and were replaced by giant, flightless, **carnivorous** birds. At over 2 meters (7 feet) tall, with deadly claws and ferocious, hatchet-like beaks, *Diatryma* and *Phorusrhacus* were the fearsome top predators of the Oligocene. They too disappeared, possibly because they were unable to protect their ground-dwelling young from the small, fast mammals that came along in the Miocene.

herbivores animals who eat plants only

carnivorous animals that eat other animals

Just as the linking of landmasses tended to produce uniformity, so isolation produced spectacular diversity. Australia had sailed off with a few ancestral marsupials, mammals whose infants crawl into a pouch, or

Oligocene epoch and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Cenozoic	Quartenary	Holocene	0.01
		Pleistocene	1.6
	Tertiary	Pliocene	5.3
		Miocene	24
		Oligocene	37
		Eocene	58
		Paleocene	66

marsupium, where they are suckled and grow to independence. Given an entire continent in which to experiment, the marsupials exploded in a riot of shapes and sizes, filling every conceivable evolutionary **niche** from herbivores and carnivores to scavengers and insectivores. Only a few of these species survive to the present.

niche how an organism uses the biotic and abiotic resources of its environment

South America also separated from the other land masses and developed its own unique mammals. The **edentates** (toothless mammals), which included anteaters, sloths, and armadillos, were enormous, slow-paced vegetarians and insectivores. For example, glyptopons (armadillos) were 3 meters (10 feet) long and baluchitheriums (rhinoceroses) were 5.5 meters (18 feet) tall and 8.2 meters (27 feet) long. A bizarre assembly of hoofed animals also flourished in this region until the Isthmus of Panama formed at the end of the Cenozoic (2 million years ago) and linked North and South America. This two-way land bridge allowed a few herbivores from the south to move north, but on the whole, the invasion of ruthless carnivores and more efficient **ungulates** (hoofed mammals) signaled the end of most of the uniquely southern mammals.

edentates lacking teeth

ungulates animals with hooves

In the Atlantic and Pacific Oceans, separated by the Isthmus of Panama, whales continued to thrive, spreading from Europe to New Zealand where they were joined by sea cows and the first seals. SEE ALSO Geological Time Scale.

Nancy Weaver

Bibliography

Asimov, Isaac. *Life and Time.* Garden City, NY: Doubleday & Company, 1978.

Fortey, Richard. *Fossils: The Key to the Past.* Cambridge, MA: Harvard University Press, 1991.

———. *Life: A Natural History of the First Four Billion Years of Life on Earth.* New York: Viking Press, 1998.

Friday, Adrian, and David S. Ingram, eds. *The Cambridge Encyclopedia of Life Sciences.* London: Cambridge University Press, 1985.

Gould, Stephen Jay, ed. *The Book of Life.* New York: W. W. Norton & Company, 1993.

Lambert, David. *The Field Guide to Prehistoric Life.* New York: Facts on File, 1985.

McLoughlan, John C. *Synapsida: A New Look into the Origin of Mammals.* New York: Viking Press, 1980.

Steele, Rodney, and Anthony Harvey, eds. *The Encyclopedia of Prehistoric Life.* New York: McGraw Hill, 1979.

Wade, Nicholas, ed. *The Science Times Book of Fossils and Evolution.* New York: The Lyons Press, 1998.

Ontogeny

Ontogeny describes the entire life history of an organism from **fertilization** to death. It includes not only embryonic and prenatal development but also postnatal growth and development.

fertilization the fusion of male and female gametes

That patterns of ontogeny can provide fascinating insights into evolutionary history has long been recognized. Possibly the most famous concept linking the two areas is the "biogenetic law" of German biologist Ernst Haeckel (1834–1919), which states that "ontogeny recapitulates phylogeny." Haeckel suggested that, in the course of its development, each organism recapitulates (repeats the stages of) its entire **phylogenetic** history by taking on the morphologies of all of its ancestors sequentially, from the most primitive ancestor to the most advanced. Haeckel favored a fairly stringent interpretation of the biogenetic law, and spent considerable time identifying the ancestors represented by different developmental stages. For example, he viewed the gastrula stage (an early embryonic stage during which the three embryonic tissue layers are formed) of **vertebrate** embryos as representing the morphology of their **invertebrate** ancestors. Later developmental stages were interpreted as representing "higher" ancestors. For example, all avian and mammalian embryos go through a developmental stage in which gill slits are highly prominent. Haeckel interpreted this stage as a recapitulation of the "fish stage."

phlogenetic relating to the evolutionary history

vertebrate animal with a backbone

invertebrate animal without a backbone

Haeckel's biogenetic theory fell into disfavor in the early twentieth century, when increasing evidence on the ontogenetic patterns and phylogenetic histories of different species indicated that there was not, in fact, a direct correspondence between the two. However, Haeckel's ideas are important because they stimulated considerable interest in embryological studies and because they emphasized the importance of links between ontogeny and evolution, an area that is still being actively studied today.

Current ideas regarding ontogeny and phylogeny rely on the concepts of another nineteenth-century scientist, Prussian-Estonian embryologist Karl Ernst von Baer. Von Baer noted that earlier developmental stages are simpler, with complexity increasing over time. He also emphasized development as a process in which related species diverge over time. That is, all species resemble each other fairly closely during the earliest stages of development, and gradually diverge in form over the course of ontogeny. The fertilized egg, the earliest stage of ontogeny, represents the time when different species are most similar.

Karl Ernst von Baer (1792–1876) was a pioneer of descriptive and comparative embryology.

Von Baer also stated that the "general" characteristics of a species appear before the "specific" ones, so that traits that characterize more inclusive groups, such as the phylum to which an individual belongs, appear earlier than those that characterize more restricted groups, such as the genus or species. This is apparent in human development in multiple ways. For example, the development of the neural tube, a trait possessed by all chordates, is a fairly early ontogenetic event, whereas the development of such species-specific features as the characteristic human facial or limb morphology appear much later.

There was a resurgence of interest in ontogeny as it relates to evolution in the late twentieth century. Stephen Jay Gould, an American paleontologist and evolutionary biologist, brought considerable attention to the

field with the publication of his 1977 book, *Ontogeny and Phylogeny*. Of particular interest to evolutionary biologists and those who study morphology is the idea that the patterns and processes of development can channel or constrain the way in which evolution occurs. Several evolutionary biologists have attempted to explain morphological evolution as the product not only of **natural selection** but also of developmental constraints. SEE ALSO DARWIN, CHARLES; GOULD, STEPHEN JAY; HAECKEL'S LAW OF RECAPITULATION; PHYLOGENETICS SYSTEMATICS; VON BAER'S LAW.

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

Jennifer Yeh

Bibliography

Futuyma, Douglas J. *Evolutionary Biology*, 3rd ed. Sunderland, MA: Sinauer Associates, 1998.

Gould, James L., and William T. Keeton, with Carol Grant Gould. *Biological Science*, 6th ed. New York: W. W. Norton & Co., 1996.

Gould, Stephen Jay. *Ontogeny and Phylogeny*. Cambridge, MA: Harvard University Press, Belknap Press, 1977.

Hildebrand, Milton, and Viola Hildebrand (ill.). *Analysis of Vertebrate Structure*. New York: John Wiley & Sons, 1994.

Ordovician

The Ordovician period (500 to 440 million years ago) comes after the Cambrian in the early Paleozoic era. The period is named for a Celtic tribe named the Ordovices who once lived in the area of Wales (in Britain) where the rocks were first studied. Ordovician limestones are over 6.4 kilometers (4 miles) thick in places and are found on all continents except Antarctica. The uniformity and thickness of the bed indicates a long period of warm and stable **climate** that allows them to develop.

climate long-term weather patterns for a particular region

phyla the broad, principle divisions of a kingdom

niche how an organism uses the biotic and abiotic resources of its environment

In fact, the Ordovician period was as remarkable for the diversity of its species as the Cambrian period was for the appearance of most major **phyla**. A burst of evolutionary creativity in shape, size, and function tripled the number of marine species that appeared. Specialization became the dominant theme of life, with new forms filling every possible **niche**.

The appearance of highly efficient predators such as the nautiloids and the lobster-size sea scorpions forced the marine community to evolve protective strategies or disappear. Various species responded by developing larger size, thicker shells, or more elaborate defenses. A proliferation in the shapes of the shells of **bivalve mollusks** allowed them to burrow deeply into sand or mud. Other mollusks learned to swim freely by rapidly clapping their valves together. And still others developed intricate teeth-and-socket arrangements that allowed them to close so tightly that they were almost impossible to open.

bivalve mollusks mollusks with two shells such as clams

Exploring the oceans of the Ordovician world would have been quite similar to exploring the oceans of today. Sea urchins, starfish, and sea lilies lived in profusion among the rocks. The first great coral reefs appeared and gave shelter to **crustaceans** of all kinds. Sea mats, sea snails, and sea cucumbers abounded in the tide pools. A huge diversity of bivalve mollusks made their slow way across the muddy ocean floor, leaving their tracks and burrows in the **fossil record**.

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

fossil record collection of all known fossils

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

Ordovician period and surrounding time periods.

The very first primitive fishes appeared, slow and heavily armored, without fins or heads with brains. These agnathans (jawless fishes) were the first animals to have a **notochord** (flexible rod spine), a precursor of a true spinal chord. These chordates were the ancestor of all animals with backbones.

notochord a rod of cartilage that runs down the back of chordates

While almost all animals of the Ordovician were marine, another remarkable occurrence is recorded in the rocks of northwest England. There, arthropods (animals with jointed legs) that lived in shallow, freshwater pools left the first tracks in fossilized mud. Scientists speculate that evaporation of their pools forced these centipede-like creatures to adapt to terrestrial conditions. From this point on, the arthropods, a group that includes insects, spiders, and crabs, ruled the land for 40 million years.

The massive Ordivician limestone ends abruptly with a jumble of glacial till, indicating an ice age that so disrupted Earth's climate that more than half of all species became extinct. This first great extinction wiped out huge numbers of **trilobites**, with their precise and sensitive eyes, **brachiopods**, **crinoids**, and other marine **invertebrates**. The life-forms that survived the cataclysmic end of the Ordovician contributed to the genetic makeup of the animal kingdom to the present. SEE ALSO GEOLOGICAL TIME SCALE.

trilobites an extinct class of arthropods

brachiopods a phylum of marine bivalve mollusks

crinoids an echinoderm with radial symmetry that resembles a flower

invertebrates animals without a backbone

Nancy Weaver

Bibliography

Fortey, Richard. *Life: A Natural History of the First Four Billion Years of Life on Earth.* New York: Viking Press, 1998.

Gould, Stephen Jay, ed. *The Book of Life.* New York: W. W. Norton & Company, 1993.

Lambert, David. *The Field Guide to Prehistoric Life.* New York: Facts on File, 1985.

Osmosis

See Transport.

Osteichthyes

Osteichthyes, or bony fishes, includes two major groups: Sarcopterygii, or lobe-finned fishes, and Actinopterygii, or ray-finned fishes. The characteristics that unite this diverse group include **lungs** or a gas-filled swim bladder derived from lungs, segmented fin rays, bone, and bony scales. Although the tetrapods (including birds, reptiles, mammals, and amphibians)

lungs sac-like, spongy organs where gas exchange takes place

are formally within the Sarcopterygii, they are discussed within their own entries; only animals commonly thought of as "fishes" are discussed here.

Sarcopterygii (Lobe-Finned Fishes)

vertebrates animals with a backbone

pectoral of, in, or on the chest

Although only eight sarcopterygian fish species exist today, they are interesting because scientists believe they are the likely descendants of the fishes that gave rise to the terrestrial **vertebrates**, or tetrapods. The defining feature supporting this notion is a limblike fin with supporting bones that attach to the pelvic and **pectoral** girdles. There are six species of lungfish (Dipnoi or Dipneusti) found in Africa, South America, and Australia. Lungfish have true lungs, which allow them to live in stagnant water. African lungfish can survive for many months in a dry lake bed, protected by a mucus cocoon.

Coelacanths (Crossopterygii) were thought to have gone extinct 70 million years ago along with the dinosaurs until they were rediscovered near South Africa in 1938. There are two species, both large, up to 2 meters (7 feet) long, which prey on fish and squid in the deep waters of the Indian Ocean. Coelacanths are thought to rest on their lobed fins on the ocean floor. They have apparently evolved from a shallow-water, air-breathing ancestor, but their lunglike swim bladders are now filled with fat.

Actinopterygii (Ray-Finned Fishes)

With over 21,000 species distributed over the fresh and salt waters of the world, actinopterygians match the diversity of birds, mammals, reptiles, and amphibians put together. The fins of ray-finned fishes are attached to their body by fin rays, rather than lobes.

cartilaginous made of cartilage

asymmetrical lacking symmetry, having an irregular shape

brackish a mix of salt water and freshwater

About thirty-five species are "primitive" actinopterygians. The Chondrostei have a **cartilaginous** skeleton and lack true scales, and they have an **asymmetrical** tail like a shark's. They include the sturgeons, noted for their caviar and among the largest fishes found in freshwater, and the filter-feeding paddlefish of the Mississippi River. Gars (Semionotiformes, family Lepisosteidae) are sit-and-wait predators restricted to the fresh and **brackish** waters of North America. Gars have a cylindrical body covered with armorlike scales and a long snout lined with sharp teeth. Their large swim bladder functions as a lung, allowing them to live in stagnant water. The alligator gar, found in the southern United States and Mexico, reaches 3 meters (10 feet) in length. The single existing species in the last major group of "primitive" actinopterygians, the bowfin (Amiiformes), is also a sit-and-wait predator restricted to North American freshwaters.

The remaining actinopterygians are teleosts, characterized by a symmetrical tail, highly maneuverable fins, and jaws adapted for sucking.

Bony-Tongues, Eels, and Herring

Most bony-tongues (Osteoglossomorpha) are African electric fishes (Mormyridae), which forage and communicate by producing electrical fields. The group also includes the large arapaima of South America and the mooneye and goldeneye of the upper Mississippi drainage. Tarpon and eels are familiar representatives of the Elopomorpha, characterized by larvae called

A moray eel in Wreck Bay, Australia.

leptocephali, which are transparent, very slender-bodied, and leaflike. Eels are long, small-headed fishes with sharp teeth, adapted for living in tight crevices or burrows.

Freshwater eels (family Anguillidae) spend most of their lives preying on fishes and **invertebrates** in freshwater. They then migrate to specific breeding grounds in the ocean, usually a distance of thousands of kilometers, and can even travel on land if conditions are damp enough. European and North American eels from the Atlantic slope all migrate to the deep waters of the Sargasso Sea area of the North Atlantic Ocean to spawn. The clupeomorphs include some of the most abundant vertebrates, shad, herring (Clupeidae), and anchovies (Engraulidae). Most species in this group school (live in groups) in open water. They filter-feed on **plankton** that they catch on modified gill rakers, specialized structures associated with the gills.

invertebrates animals without a backbone

plankton microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

Pikes and Salmon

Pikes (family Esocidae) are sit-and-wait predators restricted to northern Eurasia and North America. The largest of the pikes, the muskellunge of the North America Great Lakes region, can be as much as 1.8 meters (6 feet) long and weigh as much as 36 kilograms (80 pounds). These long, sharp-toothed fishes grab their prey sideways, turn it around, and swallow it headfirst.

There are only about 150 species of salmonids (Salmoniformes), but they are the dominant fishes of cold-water streams and lakes in northern regions and are of substantial economic importance for food and sport fishing. Familiar salmonids include trout, largely restricted to freshwater lakes and streams, and salmon, most of which spend most of their lives at sea. They use a sophisticated sense of smell to detect the stream they were born in and return there to spawn a single time and die.

Ostariophysi

pharyngeal having to do with the tube that connects the stomach and the esophagus

About one-quarter of all known fishes belong to this diverse group, which dominates Earth's freshwaters. Three main features characterize the Ostariophysi: (1) **Pharyngeal** teeth, located in the throat behind the gills, are used for processing food once swallowed and allow for specialization on different food types. (2) Weberian ossicles, a series of bones connecting the swim bladder (which acts like an eardrum) to the inner ear, allow for sensitive hearing. (3) *Schreckstoff*, or "fright substance," is a chemical they give off when injured that causes other fish of the same species to dive for cover or swim closer together. These three features may account for the success of Ostariophysi, particularly in murky lakes and streams where visibility is limited.

nocturnal active at night

The 1,600 species in Cyprinidae (minnows and carps) are the dominant freshwater fishes in Eurasia, Africa, and North America but are absent from South America and Australia. They are mostly small, tapered, silvery fishes, although some, like the Colorado squawfish, can attain lengths of 2 meters (7 feet). Male North American shiners (genus *Notropis*) turn bright red or orange and defend nests. Suckers (Catostomidae), found in North America and Asia, have extendable, fleshy lips specialized for sucking algae and other food from the bottom. The order Characiformes, which includes tetras, piranhas, and pencilfishes, is a diverse group of 1,200 species restricted to South America, southern North America, and Africa. The order Siluriformes (2,000 species) is made up of the catfish, most of which are **nocturnal** and characterized by sensitive barbels on the snout that look like cat whiskers.

Cod, Anglerfishes, Killifishes, and Livebearers

dorsal the back surface of an animal with bilateral symmetry

habitats physical locations where an organism lives in an ecosystem

The diverse group Paracanthopterygii includes the abundant and economically important codfishes (Gadiformes, 700 species), elongated fishes with three **dorsal** fins and a chin barbel, which are mostly found in open oceanic waters. Anglerfishes and frogfishes (Lophiiformes) are cryptic, bottom-dwelling fishes. They have a structure that looks like a fishing pole growing out of the head. The top of the "fishing pole" looks like a fish or invertebrate, and the fish uses the pole and "fish" to entice prey. The Atheriniformes include many small, colorful freshwater fishes popular in the aquarium trade. The Atherinidae include the silversides of North American brackish waters and the Australian rainbowfishes. Killifishes (Cyprinodontidae and related families) are often found in very confined **habitats** such as

desert springs. Some species live in tiny puddles in the rain forest and jump from puddle to puddle during rains.

The African and South American species restricted to temporary pools have the shortest life spans of any vertebrate. Eggs can remain dormant in dry mud for most of the year, but the fish hatch and grow rapidly to maturity during the rainy season, sometimes living only three months before ponds dry up again. Livebearers (Poeciliidae and Goodeidae), restricted to the New World, include the mosquitofish, introduced worldwide and a threat to native wildlife, and the colorful guppies and swordtails.

Acanthopterygii

With about 9,000 species, this group of "spiny-rayed fishes" is composed of the dominant fishes of the oceans as well as numerous inhabitants of freshwater. The Gasterosteiformes are mostly long, covered in armored plates, and characterized by males that share parental duties. They include the sticklebacks (Gasterosteidae), whose males build and defend nests, as well as the seahorses and pipefishes (Syngnathidae), whose males carry the eggs and hatchlings in specialized pouches on their belly. The Scorpaeniformes include 1,000 species of mostly bottom-dwelling fishes such as sculpins and rockfish. The group is characterized by very spiny dorsal and anal fins, often associated with venom glands, which in some tropical scorpionfishes can cause death to humans. The 500 species of flatfishes (Pleuronectiformes) such as sole, halibut, and flounders, are uniquely adapted to life on the ocean bottom. When they are larvae they look like most other fish larvae, but as they develop they undergo a **metamorphosis** in which one eye migrates to the other side of the head. As a result, the adult flatfish has a bottom side with no eyes and a top side with two eyes. The top side can sometimes change color to match the background of the ocean bottom. The Tetraodontiformes include the pufferfishes and triggerfishes, which are slow-swimming, heavily armored fishes with "beaks" that they use to feed on coral and invertebrates. Some, like the balloonfish, can inflate rapidly with water when confronted with a predator.

metamorphosis a drastic change from a larva to an adult

The ruling perches, or Perciformes, are 7,000 species characterized by spiny fins and a two-part dorsal fin. They include the North American basses and sunfishes (Centrarchidae) and the family Percidae, which includes the perches of Eurasia and the walleyes and brightly colored darters of North America. Drums (Sciaenidae) are mostly coastal fishes that use low-frequency sounds during courtship. Cichlids (Cichlidae) have greatly diversified throughout the New World and African tropics; the Rift Lakes of Africa contain hundreds of species of cichlids restricted to each lake, many of which are highly specialized to a particular feeding task. For example, some fishes eat only the scales on the left sides of other fishes, while others have mouths specialized for sucking out the eyes of other fishes. Closely related marine fishes include the colorful wrasses (Labridae) and parrotfishes (Scaridae), in which some individuals can change sex from female to male. The cleaner wrasse specializes in removing parasites from other fishes. The colorful damselfishes (Pomacentridae) are unusual among marine fish in that they care for their young; males in some species build and defend nests. The group includes the anemonefish, which have developed an immunity to the sting of the anemone and can live and reproduce within its tentacles. The more than 800 species of gobies (Gobiidae) are small fishes found in fresh and salt water; their pelvic fins are fused to form a sucking disk. These fishes have colonized habitats such as small crevices among rocks, tide pools, and streams above waterfalls, and some, like the mudskipper, can travel on land. Tuna and mackerel (Scombridae) are "warm-blooded" for efficient muscle activity and rapid swimming.

Other Actinopterygians

filter feeders animals that strain small food particles out of water

The Stenopterygii include the bristlemouths, small, luminescent **filter feeders** that live in the deep oceans and may be the world's most abundant vertebrate. Lanternfishes (Scopelomorpha) use luminous lures to catch prey. Lizardfishes (Cyclosquamata) are well-camouflaged sit-and-wait predators who live on coral reefs. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Gil G. Rosenthal

Bibliography

Moyle, Peter B. *Fish: An Enthusiast's Guide.* Berkeley: University of California Press, 1993.

Moyle, Peter B., and Joseph J. Cech, Jr. *Fishes: An Introduction to Ichthyology*, 3rd ed. Upper Saddle River, NJ: Prentice-Hall, 1996.

Nelson, Joseph S. *Fishes of the World*, 3rd ed. New York: John Wiley & Sons, 1994.

P

Paleontologist

fossil record a collection of all known fossils

Paleontologists study the history of life on Earth as shown in the **fossil record**. Fossils are the traces of organisms that lived in the past and are preserved in Earth's crust. Paleontology involves the identification and naming of fossil species and organisms and the determination of the environment in which they lived. Paleontology is considered a subcategory of geology. It is a very broad science that uses biology, geology, chemistry, and physics. There are many subdivisions in the field of paleontology, including:

vertebrate an animal with a backbone

invertebrate an animal without a backbone

- **vertebrate** paleontology, the study of fossils of animals with backbones;
- **invertebrate** paleontology, the study of fossils of animals without backbones;
- micropaleontology, the study of fossils of single-celled organisms;
- paleobotany, the study of plant fossils;
- paleoecology, the study of ancient environments;
- biostratigraphy, the study of the fossils in rock layers from different areas to determine their relative ages.

As can be seen by this list, paleontology is more than just the study of dinosaurs. Modern paleontology attempts to understand life-forms as they are related to extended family trees, some of very ancient origins. Thus, paleontologists are frequently involved in studies of evolutionary biology and can be considered systematists, which means that they study the evolutionary relationships among organisms.

A paleontologist cleans the remains of the jawbone of a *Tyrannosaurus rex*.

Most paleontologists work in geology programs of colleges or universities. They do research and teach classes. Smaller numbers of paleontologists work in museums. There, they carry out their own research and sometimes teach and assist with exhibits. A much smaller number of paleontologists work for government geological surveys. Until recently, paleontologists found work with oil companies, helping to search for oil. However, this field has declined as a source of employment for paleontologists.

Research in paleontology generally involves doing fieldwork, analyzing the fossils, and writing up one's findings for publication and presentation. Analysis of fossils begins with carefully measuring and describing them. Next, the fossils are dated by various methods. Then the fossils and the rocks in which they were found are used to learn information about the history of Earth. Finally, the fossils are used to fill in missing information about the fossil record and are related to present-day organisms.

A paleontologist must have a doctoral (Ph.D.) degree. A bachelor's degree can be obtained in either geology or biology. Graduate schools generally require a full year of chemistry, physics, and mathematics (through calculus) at the undergraduate level. It is also important to have strong writing and computer skills. After getting a bachelor's, one can get a master's and then a doctoral degree or, alternatively, enter a doctoral program directly. If an individual has not had much experience with research in college (such as writing a senior thesis), then it might be best to get a master's degree first. It generally takes from two to three years to complete the master's program. A Ph.D. program usually takes from four to six years if the candidate already has a master's, and from six to eight years if he or she does not. The courses most important to paleontology include mineralogy, stratigraphy and sedimentation, sedimentary petrology, invertebrate paleontology, **ecology**, invertebrate and vertebrate zoology, evolutionary biology, and genetics. SEE ALSO PALEONTOLOGY.

ecology study of how organisms interact with their environment

Denise Prendergast

Bibliography

Cosgrove, Holli R., ed. *Encyclopedia of Careers and Vocational Guidance*, 11th ed. Chicago: Ferguson Publishing Company, 2000.

The Year 2000 Grolier Multimedia Encyclopedia. Danbury, CT: Grolier Interactive Inc., 1999.

Internet Resources

Paleontological Research Institution. Cornell University.<http://www.priweb.org>.

Paleontology

fossil record a collection of all known fossils

Paleontology is the study of the history of life as revealed in the **fossil record**. Fossils are remnants or traces of living organisms from past geologic ages that have become preserved in Earth's crust. They include not only the skeletons or shells of deceased creatures, but also burrows, footprints, eggs, and fossilized feces (excrement), known as coprolites.

vertebrate an animal with a backbone

invertebrate an animal without a backbone

ecosystems self-sustaining collections of organisms and their environments

taxonomy the science of classifying living organisms

phylogenetic relating to the evolutionary history of species or group of related species

extant still living

flora plants

fauna animals

Paleontology draws extensively from both biology and geology. Some subdisciplines of paleontology are defined by the types of organisms that are studied. Examples are **vertebrate** paleontology, **invertebrate** paleontology, paleobotany, and micropaleontology (study of single-celled fossils). Paleoecologists study extinct **ecosystems**. Related areas include biostratigraphy, the study of fossil distributions in different strata (rock layers), and taphonomy, which examines the process of fossil formation. Biological disciplines in which contributions of paleontology are particularly critical include systematics and **taxonomy**. They focus on determining **phylogenetic** relationships (the sequence of branching events in evolutionary history which have resulted in the production of divergent species) between extinct as well as **extant** organisms. Another such discipline is comparative anatomy, which examines the morphology (form) and structure of organisms. Still another is evolutionary biology, which examines how biological organisms change over time.

The study of the fossil record also permits the identification of periods of major change in biological diversity. Sudden shifts in **flora** and **fauna** result from major events involving the extinction of organisms, such as the one that eliminated the dinosaurs at the end of the Cretaceous period. In fact, geological eras are bounded by these sudden changes.

Taphonomy examines the processes by which fossils are formed. Any event that occurs between the death of an organism and its fossilization is of interest to taphonomists. The first step to fossilization is burial. Burial can occur in a number of ways; corpses may be buried by sediments in rivers, by sand, or in the bottoms of lakes or oceans. After burial, corpses may be compressed and distorted by the surrounding sediment. There is also a lengthy period of remineralization following burial. During this time, bone is replaced by minerals carried through the rock by water. Remineralization does not necessarily obscure fine detail because the replacement occurs on a minute scale.

scavengers animals that feed on the remains of animals they did not kill

During the process of fossilization, much information about the biology of organisms is lost. Damage to the corpse, either by **scavengers** or from weather or erosion, may occur prior to burial, and distortion from a

number of sources can occur afterwards. Soft parts of organisms are fossilized much less frequently than hard parts, and information on color, **physiology**, or behavior is particularly likely to be lost. It is because of the incompleteness of most fossils that paleontologists have developed a well-deserved reputation for inferring (deducing) huge amounts of information on the biology of organisms from fragmentary, or partial, remains.

physiology study of the normal function of living things or their parts

The proper dating of fossil material is often critical to paleontological studies. Relative dating considers the relative placement of different rock strata; younger rock layers are formed on top of older layers. Also, similar sequences of strata that are found in different locations are likely to date from the same period. Absolute dates for fossil material are usually estimated using radioisotopes. This method makes use of the fact that radioactive atoms decay into more stable atoms at a known rate. SEE ALSO FOSSIL RECORD; GEOLOGICAL TIME SCALE; PALEONTOLOGIST.

Jennifer Yeh

Bibliography

Futuyma, Douglas J. *Evolutionary Biology*, 3rd ed. Sunderland, MA: Sinauer Associates, 1998.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton and Co., 1996.

Parasitism

Parasitism describes a relationship between two species, a parasite and its host, in which the parasite benefits, while the host is harmed. Parasitism is one form of **symbiosis**, which more generally describes any situation involving a close relationship between organisms of different species.

symbiosis any prolonged association or living together of two or more organisms of different species

Parasites are different from predators and parasitoids (which also derive benefits from certain interspecific interactions while harming the other participant) in that the host of a parasite is not necessarily killed. Instead, parasites derive benefits from their hosts, most often nutritional resources and shelter, over a longer period of time. It is in fact advantageous to parasites if they do not harm their hosts too badly, because that prolongs the period during which parasites can obtain benefits from hosts. However, in some cases, the impact of parasites on a host is great enough to cause disease, and in extreme cases, the death of the host may also occur.

Parasitism is a common survival strategy among biological organisms, and many species are characterized by parasitic lifestyles for all or part of their lives. All the major kingdoms of life include some parasitic species. In addition, there are very few biological species that are free of parasites altogether.

ectoparasites organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

endoparasites organisms that live inside other organisms and derive their nutrients directly from those organisms

Categories of Parasites

Parasites may be grouped by any of several traits. **Ectoparasites** live outside the body of the host, usually on the body surface. Well-known ectoparasites include fleas, ticks, and leeches. **Endoparasites** live within the host's body. Endoparasites can further be divided into those that live within

host cells (bacteria and viruses), and those that live in spaces in the host's body (all other, generally larger, endoparasites).

obligatory parasites animals that can exist only as parasites

facultative parasites organisms that can survive either as parasites or free-living

Parasites may also be grouped depending on whether they are **obligatory parasites**, which must have a host in order to survive, or **facultative parasites**, species for which a parasitic lifestyle is optional. Facultative parasites adopt parasitic lifestyles if the opportunity arises, but they are also able to live free of a host organism.

microparasites very small parasites

macroparasites parasites that are large in size

vertebrates animals with a backbone

Parasites are also grouped based on their size. **Microparasites** include viruses, bacteria, and fungi. These reproduce within the host and are characterized by comparatively small size and short life cycles. Microparasites also induce an immune response in the host, so that the ability to exploit a certain individual may be temporary. **Macroparasites**, on the other hand, typically describe larger parasites such as insects, worms, or **vertebrates**. They are larger in size (usually visible to the eye) and do not reproduce in the body of the host. Instead they release offspring which then find and infect new hosts.

Parasites may derive any of a number of benefits from their interactions with host species. Some obtain only nutrients, while others also gain shelter and a site for reproduction. They also vary in the closeness of their relationship to their host. Mosquitoes, for example, visit vertebrate hosts only to feed. Certain mites, on the other hand, remain intimately associated with their hosts throughout their lives.

Parasitic Life Cycles

monoxenous a life cycle in which only a single host is used

progeny offspring

Life cycles of parasites may be simple or complex. Parasites that are characterized by a simple or direct life cycle have only one host and are described as **monoxenous**. The parasite generally spends most of its life in or on the host, and may reproduce within the host. Because offspring must be transmitted to other hosts, however, the parasite or its **progeny** must have some way of leaving the host, surviving in the external environment for some period, and locating and infecting a new host. Parasites with simple life cycles have both parasitic and free-living life stages. The proportion of the total life cycle spent in each stage varies according to the parasite.

heteroxenous a life cycle in which more than one host individual is parasitized

Parasites with more complex life cycles involving multiple hosts are described as having indirect or **heteroxenous** life cycles. The primary host of a heteroxenous species is the one in which adult parasites live and reproduce. The secondary or intermediate host is used by immature life stages of the parasite and is also essential. In many cases, the parasite passes through critical developmental stages in the intermediate host. The intermediate host may also aid in transmitting parasites to their final host. Fleas, for example, are sometimes intermediate hosts for mammalian parasites such as tapeworms.

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

A well-studied parasite with a complex life cycle is the liver fluke. Parasitic flukes reach adulthood in the bile duct of a primary host species such as a sheep or a cow. Flukes can cause extensive damage to the liver. During reproduction, eggs are released by flukes into the host's digestive system, ultimately passing out of the host in fecal material. Once the eggs hatch, immature juveniles infect a snail as an intermediate host. In the intermediate host, development and **asexual reproduction** occurs. At a further developmental stage, the parasite leaves the intermediate host and encysts on local vegetation. When the parasites are ingested, along with the vegetation, by a sheep or cow, they enter the intestine and then migrate to the liver and bile duct, ready to begin a new generation.

Some parasites are transmitted directly from one host to another by species, often insects, described as vectors. One particularly effective vector for vertebrate parasites is the mosquito, which plays a role in the transmission of numerous parasites including heartworm, the viruses that cause yellow fever and encephalitis, and *Plasmodium*, the **protozoan** that causes malaria.

protozoan a member of the phylum of single-celled organisms

Examples of Parasites

Species in countless taxonomic groups have parasitic lifestyles. The protozoans include several well-known parasite groups, such as amoebas and the organisms responsible for malaria. Malaria is a serious disease that occurs in large portions of the world, particularly in tropical areas. The malaria protozoan has a complex life cycle that involves **asexual reproduction** in humans and other vertebrate species, and **sexual reproduction** in mosquitoes. Mosquitoes also act as vectors for malaria, transmitting the parasites from one vertebrate host to another.

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

sexual reproduction reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

There are several groups of parasitic worms. The flat, ribbonlike parasitic worms of the class Cestoda are known as tapeworms. Tapeworms reside in the small intestines of their hosts, where they live in a constant bath of well-processed nutrients. For this reason, tapeworms do not need and have lost several **physiological** systems such as the circulatory and digestive systems. Food **absorption** occurs directly across the entire body surface of tapeworms.

physiological the basic activities that occur in the cells and tissues of an animal

absorption the movement of water and nutrients

Nematodes, or roundworms, include many important parasitic species. Well-known nematode parasites include pinworm, the large human roundworm, hookworm, and heartworm, which affects dogs and cats. In addition, parasitic nematodes cause diseases such as river blindness and elephantiasis, which results in blocked lymph flow and causes swellings in the body. *Trichinella spiralis*, which causes the disease trichonosis following the ingestion of uncooked, infected pork, is also a nematode worm.

A third group of parasitic worms are the trematodes, or flukes. Aside from the liver flukes mentioned above, trematode species are responsible for schistosomiasis and other significant diseases in humans.

There are also vertebrate parasites. One example is the lamprey, a primitive fish species that feeds by attaching to other fishes with a circular tooth-filled mouth and sucks blood and other bodily fluids. Lampreys are often ultimately fatal to their hosts.

Many plant species are parasitic. The most famous of these is probably mistletoe, which infests various species of trees. Its "roots" tap into the tree's phloem network in order to intercept resources. Mistletoe is spread by birds, which transport the sticky white seed-berries from tree to tree.

Brood Parasitism

One special form of parasitism is brood parasitism. Brood parasites are species, most commonly birds, that lay their eggs in nests of another species.

The host species devotes the considerable energy required to brood eggs till hatching and to feed the chicks.

Brood parasites include species such as wydahs, cuckoos, and the brown cowbird of North America. Often, brood parasites increase their chance of success by laying eggs that resemble those of the host. Some brood parasites raise their own nest in addition to leaving eggs in the nests of other individuals, while others are exclusively parasitic. Some brood parasites are very specific about the hosts they exploit, while others use a wide variety of hosts. The brown cowbird, for example, is known to leave eggs in the nests of more than 200 different songbird species. Brood parasites will sometimes eject an egg from the host nest as they deposit their own egg. In addition, newly hatched brood parasite nestlings may eject eggs or step-siblings as well.

Parasitic nestlings elicit automated feeding behaviors from their adoptive parents by calling and opening their beaks wide. Classic photos of brood parasitism often show smallish parents feeding chicks that are significantly larger than they are. In some instances of brood parasitism, the energy devoted to raising a parasite prevents parents from raising chicks of their own. In others, brood parasites manage to coexist with the host offspring.

Certain potential host species can detect the addition of a foreign egg by a brood parasite and will abandon the nest and begin again elsewhere. In some cases, seeing adult brood parasites near their nest is enough to trigger abandonment.

Social Parasitism

Social parasitism is a special form of parasitism unique to certain social insects, particularly ants. Socially parasitic ants derive some or all of their resources from other ant species. In some cases, this involves no more than the stealing of food resources from other ant colonies, either of the same species or of a different species. However, in more extreme cases, socially parasitic ant species do not build their own nests or raise their own offspring. Instead, their strategies involve killing the queen of another colony and then making use of the workers, or stealing and enslaving workers from other colonies. In the most extreme case, the socially parasitic species actually lives within the nest of a host species, using host workers to raise young and obtain resources.

The Importance of Parasitism in the Evolution of Species

Parasitism is hypothesized to affect the evolution of many biological species. For example, parasitism may play a role in group size—larger groups of conspecific organisms are known to be more vulnerable to infestation by parasites. The naked mole rat, a highly social rodent species in which individuals live in large colonies, is probably "naked" (that is, practically hairless) because hairlessness reduces opportunities for parasite invasion. On the other hand, parasitism may promote the evolution of sociality by encouraging such social behaviors as reciprocal grooming or cleaning. This occurs in numerous mammalian species, including many primates, where individuals can be seen picking lice and other parasites from each other's fur.

Cuckoo birds are brood parasites. These birds leave their eggs to be raised by other bird species, thereby avoiding the high energy expenditure required to monitor eggs and feed chicks.

The evolution of parasites and their hosts is also one of the best examples of **coevolution**, a situation in which there are two species, each of whose evolution depends upon and responds to the evolution of the other. Other pairs of species that may coevolve are predators and their prey, and flowering plants and their insect pollinators.

coevolution a situation in which two or more species evolve in response to each other

Coevolution between parasites and their hosts is antagonistic, and is sometimes described as an "evolutionary arms race," because each species attempts to evolve in such a way as to foil the other. That is, hosts are constantly evolving to avoid parasites, while parasites are evolving so that they can continue to exploit their hosts.

Another situation in which parasitism is hypothesized to play an important role is in the mating behaviors of species. One theory of **sexual selection**, called the handicap hypothesis, depends on parasitism as the critical evolutionary factor. The handicap hypothesis attempts to explain the evolution of brightly colored males, or males with elaborate ornamentation, in many species of animals. The peacock is a classic example of this—think of the gaudy coloration and elaborate tail of male peacocks.

sexual selection selection based on secondary sex characteristics that leads to greater sexual dimorphorphism or differences between the sexes

Why do males evolve these traits, which make them highly visible and hence vulnerable to predators? The explanation seems to be that colorful or ornamented males are preferred as mates by females, so that male reproduction depends on the evolution of these traits. Why do females prefer colorful males? The handicap hypothesis argues that only very healthy males would be able to develop and maintain bright colors or ornaments. It is believed that parasites would make males sickly, and prevent them from devoting the resources necessary to maintain their bright plumage.

Consequently, by mating with males who are brightly colored and in generally good shape, females are more likely to end up with mates that carry fewer parasites. These males may also be relatively parasite-free because they have "good genes," which might then be passed on to the female's offspring. SEE ALSO INTERSPECIES INTERACTIONS.

Jennifer Yeh

Bibliography

Askew, Richard Robinson. *Parasitic Insects.* New York: American Elsevier Publishing Company, 1971.

Cameron, Thomas W. M. *Parasites and Parasitism.* New York: Wiley, 1956.

Crewe, W., and David R. W. Haddock. *Parasites and Human Disease.* New York: Wiley, 1985.

Despommier, Dickson D., and John W. Karpelou. *Parasite Life-Cycles.* New York: Springer Verlag, 1987.

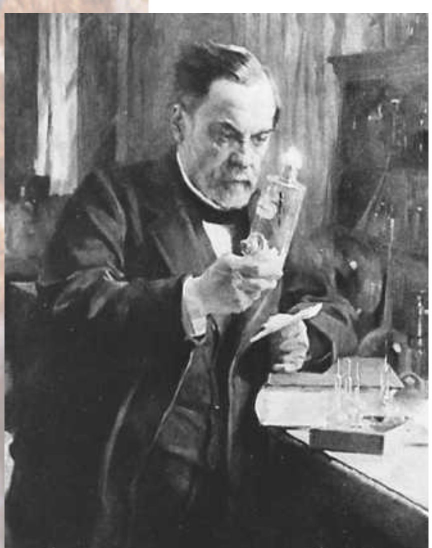
Kreier, Julius P., and John R. Baker, eds. *Parasitic Protozoa.* San Diego: Academic Press, 1991.

Lapage, Geoffrey. *Parasitic Animals.* Cambridge, U.K.: Cambridge University Press, 1951.

Rothstein, Stephen I., and Scott. K. Robinson, eds. *Parasitic Birds and Their Hosts: Studies in Coevolution.* New York: Oxford University Press, 1998.

Zimmer, Carl. *Parasite Rex: Inside the Bizarre World of Nature's Most Dangerous Creatures.* New York: Free Press, 2000.

Passive Transport *Transport.*



Louis Pasteur is known as the "father of bacteriology."

Pasteur, Louis

French Chemist and Microbiologist
1822–1895

Louis Pasteur, the father of modern bacteriology, was born on December 27, 1822, in Dôle in eastern France. Pasteur proved that microorganisms cause fermentation and disease; he also originated the process known as pasteurization. Pasteur created vaccinations for rabies, anthrax, and chicken cholera. He is also credited with saving the beer, wine, and silk industries in France during his time.

Pasteur, the son of a tanner, attended primary and secondary schools in Arbois and Besançon. As a boy he showed more interest in art than science. Pasteur attended the Royal College in Besançon, earning his bachelor of arts degree in 1840 and bachelor of science degree in 1842. The following year, he attended the École Normale Supérieure in Paris, earning his master of science degree in 1845, and his doctor of philosophy degree in 1847. By the age of twenty-six, Pasteur was famous for his work on the structure of crystals. In 1848 he received an appointment as professor of physics at the Dijon Lycée. Shortly thereafter, he became a professor of chemistry at the University of Strasbourg. This was the start of a distinguished career at various French universities. He married Marie Laurent, with whom he had five children. (Only two survived childhood.)

In 1854 Pasteur began his studies on fermentation, the chemical breakdown of substances by microbes. His work brought important improvements in brewing and winemaking. By the 1860s he had originated the process of pasteurization, applying controlled heat to kill disease-causing microbes in wine, beer, vinegar, and milk. This made it possible to produce, preserve, and transport these goods without their becoming ruined. Pasteur studied the mysteries of bacteriology and was the first to show that living things come only from living things. Before that, many scientists had believed in spontaneous generation, a theory that life could come from things that are not alive.

In 1865 Pasteur began studying a disease of silkworms that was devastating the silk industry. He isolated the germ that caused the disease and found methods of preventing contagion and detecting diseased stock, thus saving the silk industry. In the 1880s Pasteur began to realize that disease was spread by microorganisms (microscopic-sized organisms). His germ theory of disease was one of the greatest scientific discoveries of the nineteenth century. He went on to develop vaccinations for preventing the disease anthrax in sheep, chicken cholera in fowl, and rabies in humans. Pasteur was admired by his countrymen and honored by the French Parliament in many ways. He died on September 28, 1895.

Denise Prendergast

Bibliography

The New Encyclopedia Britannica, 15th ed. Chicago: Encyclopedia Britannica, Inc., 1993.

The World Book Encyclopedia. Chicago: World Book, Inc., 1995.

PCR

PCR (**polymerase** chain reaction) is a method used by scientists to increase the amount of purified DNA in a sample. It is a highly specific procedure that amplifies one particular gene from within a large sample of undesirable DNA, DNA that the scientist does not wish to replicate. Before PCR, it was very difficult and time consuming to obtain particular fragments of DNA from a sample, and practically impossible to amplify, produce many copies of, that fragment. With PCR, scientists can copy a specific stretch of DNA billions of times in a few hours.

polymerase an enzyme that links together nucleotides to form nucleic acid

PCR was invented in 1983 by American biochemist Kary B. Mullis, who received the 1993 Nobel Prize for chemistry (with Canadian biochemist Michael Smith) in recognition of this inestimable contribution to science. Mullis invented PCR while working for the Cetus Corporation, a biotechnology firm located in California. His discovery proved so essential to biological research that when Cetus closed down in 1991, the pharmaceutical company Hoffman-La Roche purchased the PCR patent for $300 million.

DNA Replication

Under most natural conditions, DNA exists in the form of two entwined single strands, and each strand is formed of smaller molecules called **nucleotides**. The word "polymerase" in the name polymerase chain reaction comes from the term "polymer," which refers to any large molecule composed of many smaller molecules. Thus DNA is a **polymer** of nucleotides. A polymerase is an enzyme that pieces together polymers from the smaller

nucleotides building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

polymer a compound made up of many identical smaller compounds linked together molecules. The strands of DNA must be separated before they can be copied, because the important information is contained along the center of the molecule, where the two strands are attached. Cells naturally synthesize new DNA in their nucleus through a process known as replication. During replication, the two parent strands unwind and separate and a new single daughter strand is built upon each of the existing parent strands. The two identical molecules of DNA that result from replication each contain one parent and one daughter strand. This is called semiconservative replication.

Scientists can find a particular gene (a sequence of nucleotides that encodes a unique protein) within a large sample of DNA by looking for the **nucleotide** sequences specific to that gene. The four basic nucleotides are adenine (A), guanine (G), thymine (T), and cytosine (C). An A on one strand always binds to a T on the other, and a G on one strand always binds to a C on the other. This makes it easy to determine the sequence of one strand of DNA when the sequence of the other strand is known. The beginnings and ends of all **genes** are defined by short sequences of three nucleotides called **codons**. The beginnings are marked by a "start" codon, and the ends by a "stop" codon. Special **enzymes** in the cell recognize the codons. These enzymes always begin at the start codon and end at the stop codon. Scientists can identify a particular gene by looking at the nucleotide sequence, and locate the place on the DNA where that gene begins by finding the start codon.

nucleotide the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

genes segments of DNA located on chromosomes that direct protein production

codons the genetic codes for an amino acid that are represented by three nitrogen bases

enzymes proteins that act as catalysts to start biochemical reactions

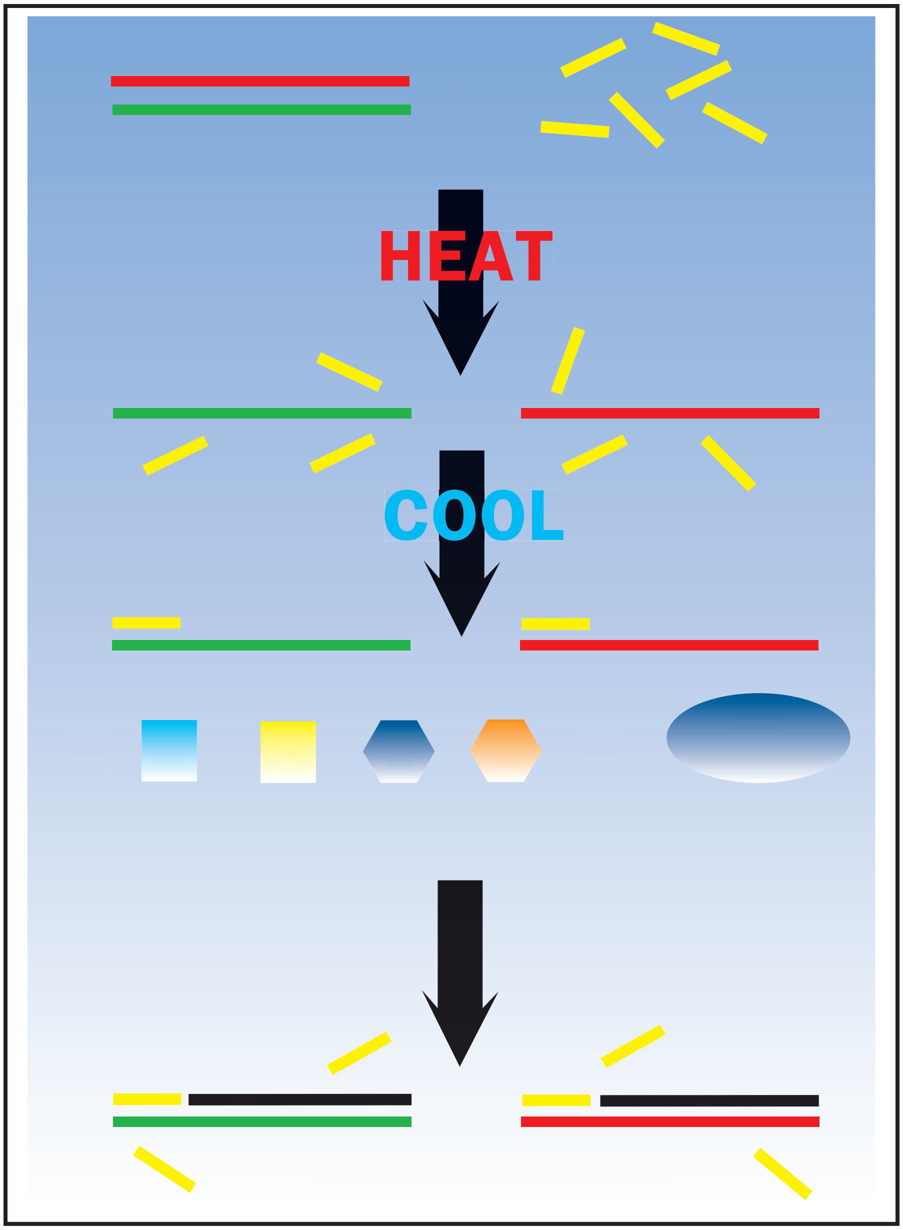
PCR Method

Almost any gene encoding almost any protein can be amplified using PCR. To replicate DNA in a laboratory environment, certain natural conditions must be reproduced. The necessary components are simple—the DNA to be replicated, DNA polymerase, **primers** complementary to both strands of DNA for that gene, and a mixture of the four nucleotides. DNA polymerase "reads" the nucleotide sequence and adds the correct nucleotides to the parent strand, thereby forming a complementary daughter strand. DNA polymerase can only build off a template, and it can add nucleotides only one by one, in one direction. DNA polymerase cannot begin without a primer, a short nucleotide sequence attached at one end of the DNA. For PCR, the primers must be present in very large quantities to increase the likelihood of replication. In a cell, a special enzyme builds primers for DNA, but the process is not specific for any one gene. By using synthetic primers that are complementary to the gene they want to replicate, scientists can replicate only that gene and not the remaining DNA.

primers short preexisting polynucleotide chains to which new deoxyribonucleotides can be added by DNA polymerase

PCR can be conducted with as little as one fragment of DNA in solution. By applying a high heat to the DNA solution, the bonds between the parent strands are broken, and the strands float apart. This process is called **denaturing** the DNA. In the first cycle of PCR amplification, the DNA is denatured, and the primers are added to the solution. The temperature is then lowered so that the primers can bind to the denatured strands. If the temperature is not lowered, the primers will not be able to function. After this, the temperature is raised slightly so that DNA polymerase can bind to the primer. Once it binds, the polymerase pulls nucleotides from the solution and adds them to the template parent strand to form a daughter strand. The polymerase drops away from the newly synthesized DNA at the stop

denaturing breaking down into small parts



Polymerase chain reaction. A mixture of DNA and primers is heated until the DNA denatures. After this, primers are added and the solution is allowed to cool. As the solution cools, the primers bind to the correct gene within the DNA. Nucleotides are added to the solution along with DNA polymerase. DNA polymerase adds nucleotides to the primer to form the daughter strands. Finally, the new strands of DNA are formed and the procedure may be repeated to create more DNA.

codon. This procedure creates two new molecules of DNA, which contain only the gene the scientist wants to replicate.

The first cycle of PCR generates twice the number of DNA molecules for the gene than there were in the original solution. Additional cycles are needed to greatly increase this number. The second cycle is very similar to the first—the DNA in solution is denatured in the presence of primers, which bind to the parent strands as they cool; polymerase builds the daughter strand with nucleotides from the solution; and the reaction completes itself. The result of this second cycle is that there are now four DNA molecules encoding the gene for every one original DNA molecule used. The cycles are repeated until the desired amount of DNA is attained. Scientists calculate the number of DNA molecules resulting from PCR amplification by employing the formula $a*2^n$, where *a* is the number of original molecules of DNA, and *n* is the number of cycles of PCR. When enough DNA is made, the scientist stops the reaction.

The DNA polymerase used for PCR must be able to function at a very high temperature, because a high temperature is needed to keep the parent strands apart so the daughter strands can be built upon them. Most DNA polymerases in nature cannot function at high temperatures, so PCR uses a polymerase found in certain archaebacteria that live in hot springs, where the water temperatures are often well above 90°C (194°F). The most commonly used polymerase is called *Taq* polymerase, because it was originally isolated from the archaebacterium *Thermus aquaticus.*

Applications of PCR

PCR is very useful for creating a large quantity of DNA from a very small initial sample. Applications of PCR can be used to identify a particular individual or even to map out the evolutionary history of a species. These applications are based on the concept that some DNA is unique to a particular individual, some genes are unique to a particular species, and certain genes are shared by all organisms. The unique DNA makes it possible to determine the exact individual from which a strand of DNA came, which is why PCR is used by forensic scientists to test skin cells and hair follicles found at crime scenes. Assuming that the DNA belongs to the person who carried out the crime, that person can be identified from among a group of suspects. PCR is used by archaeologists to determine the identity of ancient human remains and unidentifiable mummies, and by paleontologists to examine how the **genome** of an organism has changed over the course of evolution. PCR can also used to test the relatedness of different species when body characteristics alone do not provide enough evidence. For example, PCR analysis revealed that red panda bears are more closely related to raccoons than to greater panda bears, a distinction that had previously been impossible to determine.

genome an organism's genetic material

Other applications of PCR take advantage of its ability to accumulate large amounts of DNA to conduct statistically significant research experiments. The technique is often used in medical research, for example to amplify the DNA of a virus, such as HIV, to understand how it infects humans, or to replicate the DNA of a **hormone**, such as insulin, to understand how it functions. The biomedical industry relies on PCR for identifying viral and bacterial infections, especially for detecting infections like AIDS and leprosy in their early stages. PCR can also be used to detect hereditary medical conditions in babies or adults who do not yet show signs of impairment. The large quantities of DNA formed through PCR can be introduced into the genome of another organism to create a **transgenic organism**. Transgenic animals are important for creating animal models of human disease. For example, hereditary diseases such as Alzheimer's that do not normally occur in mice can be introduced into the mouse genome. When the mouse begins to show symptoms of the disease, scientists can administer different treatments to find out which is the most effective.

hormone a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

transgenic organism an organism that contains genes from another species

Transgenic plants can also be used instead of the application of toxic **pesticides**; the goal is to create a plant that can defend itself against insects by producing its own insecticides that are not harmful to humans. Then

pesticides substances that control the spread of harmful or destructive organisms fewer chemical pesticides would be needed, reducing the contamination of drinking water and harm to humans exposed to the chemicals.

Mark R. Hughes, deputy director of the National Center for Human Genome Research at the National Institutes of Health, the American base for the **Human Genome Project**, called PCR "the most important new scientific technology to come along in the last hundred years." (Powledge 1998). Its principle limitation is that the primer sequence must be known so that primers can be synthesized prior to the first cycle of PCR. Furthermore, PCR is less accurate when used to replicate large gene sequences (greater than approximately 5,000 nucleotides long), which means that it is difficult to study complex proteins. Additionally, the procedure is expensive and currently too technically demanding to be carried out by nonprofessionals. These drawbacks are being addressed by developments that would fully automate PCR, or provide simpler and less expensive kits. These kits could be used, for example, by people who suspect they are developing cancer. Indeed, PCR is expanding beyond the world of research and will be increasingly available to people for direct independent analyses. SEE ALSO Genes; Genetic Engineering; Genetics.

Human Genome Project a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

Rebecca M. Steinberg

Bibliography

Frank-Kamenetskii, M. D. *Unraveling DNA: The Most Important Molecule of Life*. Reading, MA: Addison-Wesley, 1997.

McPherson, M. J., S. G. Moller, R. Beynon, and C. Howe. *PCR (Basics: From Background to Bench)*. Oxford: BIOS; New York: Springer, 2000.

Nair, P. K. G., and K. Prabhaker Achar. *A Textbook of Genetics and Evolution*. New Delhi: Konark; New York: Distributed by Advent Books, 1990.

Sninsky, John J. *PCR Applications: Protocols for Functional Genomics*, Michael A. Innis and David H. Glefand, eds. San Diego, CA: Academic Press, 1999.

Peppered Moth

The peppered moth (*Biston botularia*) is an inconspicuous member of the family Geometridae, a night-flying species thought to spend its days resting camouflaged among the lichens that grow on tree trunks. The moth's predominant form has white wings, "peppered" with black specks or faint black lines, perfect for blending in with its tree bark environment. Less common is a variant, *carbonaria*, which is a black-winged moth, with increased levels of melanin (black pigment) causing the color change. The peppered moth has come to play a significant role in two important stories in science.

In 1859 British **naturalist** Charles Darwin proposed a theory of evolution in his book *On the Origin of Species*. He based his theory on three observations he made while collecting data on plants and animals during a five-year trip around the world in the survey ship *Beagle:* that living things vary, that they can pass on their characteristics, and that they are involved in a struggle for survival which favors genetic **mutations** that are better adapted to their environment.

naturalist a scientist who study nature and the relationships among the organisms

mutations abrupt changes in the genes of an organism

The **fossil record** is tantalizingly full of what appear to be gradual changes from one mineralized skeleton to the next, charting the evolution

fossil record a collection of all known fossils

Two variations of peppered moths. The camouflage achieved by the darker moth on the darker background will act to protect the moth from predators.

natural selection the process by which organisms best suited to their environment are most likely to survive and reproduce

of species. The only problem with Darwin's theory was that there was no evidence of **natural selection** in action. Then, in the mid-1800s a phenomenon occurred that seemed to indisputably prove natural selection. A small moth commonly called the peppered moth, common to British woodlands, underwent dramatic color changes with the advent of pollution-darkened skies. As the industrial revolution proceeded across Britain, covering towns and countryside with soot, blackening tree trunks, and killing the lichens, the melanic, or black, variety of the moth increased in number and the original peppered variety all but disappeared. Photographs of the two types of moths on sooty and clean tree bark were dramatic evidence of the power of camouflage, and experiments clearly showed birds predating the uncamouflaged moths when given a choice. Industrial melanism was the name given to this example of evolutionary adaptation to smoky air.

In the 1950s, Oxford University biologist H. B. D. Kettlewell bred peppered moths in a lab and released close to a thousand of them in polluted and nonpolluted woods. When the moths were recaptured several nights later, there was a clear correlation of more black moths in the dark woods and more white ones in the clean. Kettlewell further released hundreds of moths onto the bark of dark and light trees at dawn and photographed birds eating the more conspicuous species. He concluded, "The effects of natural selection on industrial melanism for crypsis (camouflage) in such areas can no longer be disputed. Birds act as selective agents as postulated by evolutionary theory. Had Darwin observed industrial melanism he would have seen evolution occurring not within thousands of years but in thousands of days." (Holdrege 1999, p. 66) By the 1970s, following the passage of legislation that resulted in cleaner air, the **population** of dark moths decreased and light ones made a dramatic comeback. This seemed to provide proof of natural selection.

population a group of individuals of one species that live in the same geographic area

Also during the 1970s, some surprising evidence was introduced by British biologist Cyril Clarke that called into question some of the previous research involving the peppered moth. In twenty-five years of studying the peppered moth, Clarke found only two in daylight. The moth is notoriously difficult to locate and in fact no one knows where it lives by day, but it is certainly not on the lower trunks of trees. The peppered moth is **nocturnal** and its chief predators are bats. All of the peppered moths experimented with had been collected in traps at night and many of the ones eaten from tree trunks had been glued to the trees where they were found by opportunistic birds. The ones not glued had been released in early morning when they typically would fall asleep on the bark. Further confounding the earlier research was the discovery that an increase in the original peppered variety around both Liverpool and Detroit, Michigan, occurred despite no increase in the dark lichens assumed to be their hiding place.

nocturnal active at night

The history of the peppered moth research is a reminder of how strongly people see what they look for. Kettlewell's field experiments showed that birds feed on moths released onto tree trunks preferentially by degree of camouflage. Since the moths are not normally found on lower tree trunks during the day, this experiment created, as all experiments do, an artificial situation and then appeared to prove a hypothesis. Some evolutionary scientists such as Stephen Jay Gould are highly critical of the unwillingness of researchers to consider alternative concepts. If Kettlewell had not been so convinced of the truth of bird predation, he might have been more willing to question his results. When scientists have an uncritical acceptance of a certain theory there is a real danger of seeing what one believes and turning science into dogma. Dogmatic knowledge, teaching what is only an opinion as absolute fact, is the antithesis of science's basic tenet of observation and questioning.

Biologist Craig Holdrege believes that instead of using experiments as a way of proving or disproving an idea, scientists could come to see them as a way of interacting with phenomena. To keep science alive, scientists need to remember to be aware of their own preconceptions and be wary of drawing general conclusions from a specific and contrived event. Experiments help scientists clarify ideas and formulate new questions. As such, they become more of a jumping-off point than an end. The peppered moth story points to the need for much greater basic natural history observation, difficult as that is. Where does the moth rest by day? How far does it fly? What do the larvae eat and could the melanism be an effect of a change in the larvae's diet?

The peppered moth is a reminder that science is an evolving process. Vitality comes from doubting conventional dogma, making new observations, and thinking with originality. Science is an ongoing exploration and renewal of ideas. Just as Darwin's hypotheses added to the richness of scientific thinking, so the peppered moth story is an excellent teacher of the evolution of the scientific process. SEE ALSO Camouflage; Genetic Variation in a Population; Selective Breeding.

Nancy Weaver

Bibliography

Burton, Dr. Maurice, and Robert Burton, eds. *International Wildlife Encyclopedia*, Vol. 13. New York: Marshall Cavendish, 1969.

Holdrege, Craig. "The Case of the Peppered Moth Illusion." *Whole Earth* Spring (1999):66.

Photo and Line Art Credits

The illustrations and tables featured in Animal Sciences were created by GGS Information Services. The photographs appearing in the text were reproduced by permission of the following sources:

Volume One

Acoustic Signals (**4**): Zig Leszczynski/Animals Animals; *Adaptation* (**7**): JLM Visuals, Ken Cole/Animals Animals; *African Cichlid Fish* (**9**): Gerard Lacz/Animals Animals; *Aggression* (**11**): Lynn Stone/Animals Animals; *Agnatha* (**14**): Omikron, National Audobon Society Collection/Photo Researchers, Inc.; *Allometry* (**16**): Redrawn from Scott Gilbert; *Allometry* (**15**): Redrawn from Scott Gilbert; *Altruism* (**18**): Robert J. Huffman/Field Mark Publications; *Amphibia* (**20**): Robert J. Huffman/ Field Mark Publications; *Animal Rights* (**25**): AP/Wide World Photos; *Animal Testing* (**29**): Yann Arthus-Bertrand/Corbis; *Annelida* (**31**): E. R. Degginger/Animals Animals; *Antibody* (**34**): Redrawn from Hans and Cassady; *Antlers and Horns* (**35**): Kennan Ward/Corbis; *Apiculture* (**37**): Breck P. Kent/Animals Animals; *Aposematism* (**39**): R. Andrew Odum, Toledo Zoological Society; *Aquaculture* (**42**): David Samuel Robbins/Corbis; *Aristotle* (**45**): UPI/Bettmann Newsphotos/Corbis; *Arthropoda* (**47**): Dr. Dennis Kunkel/ Phototake; *Arthropoda* (**50**): JLM Visuals; *Aves* (**53**): Joe McDonald/Animals Animals; *Bailey, Florence Augusta Merriam* (**57**): Courtesy of the Library of Congress; *Bates, Henry Walter* (**58**): Courtesy of the Library of Congress; *Behavior* (**60**): Ross, Edward S., Dr.; *Behavior* (**61**): Carl Purcell/Corbis; *Binomial (Linnaean System)* (**64**): Archive Photos, Inc.; *Biodiversity* (**68**): Joerg Sarback/AP/Wide World Photo; *Bioethics* (**71**): Jacques M. Chenet/Corbis; *Bioethics* (**70**): Robyn Beck/Corbis; *Biological Evolution* (**75**): Sally Morgan/Ecoscene/Corbis; *Biological Evolution* (**76**): P. Parks-OSF/ Animals Animals; *Biological Pest Control* (**80**): Bill Beatty/Animals Animals; *Biomechanics* (**84**): Brad Nelson/Phototake; *Biomes* (**88**): W. Wayne Lockwood, M.D./Corbis; *Biomes* (**89**): Robert J. Huffman/Field Mark Publications; *Blood* (**98**): Richard T. Nowitz/Phototake; *Body Cavities* (**100**): Redrawn from Holt, Rinehart and Winston; *Body Cavities* (**101**): Nancy Sefton, National Audobon Society Collection/ Photo Researchers, Inc.; *Body Plan* (**108**): JLM Visuals; *Bone* (**111**): CNRI/Phototake; *Burgess Shale and Ediacaran Faunas* (**113**): Lowell Laudon/JLM Visuals; *Cambrian Explosion* (**117**): Robert J. Huffman/Field Mark Publications; *Cambrian Period* (**119**): Mickey Gibson/Earth Scenes; *Camouflage* (**120**): Art Wolfe/The National Audubon Society Collection/Photo Researchers, Inc.; *Cancer* (**123**): Luis M. De La Maza/Phototake; *Carson, Rachel* (**128**): UPI/Bettmann Newsphotos/Corbis; *Cartilage* (**129**): Dr. Mary Notter/Phototake; *Cell Division* (**134**): Redrawn from Gale Research; *Cells* (**136**): Redrawn from New York Public Library Desk Reference; *Cephalization* (**139**): P. Parks-OSF/ Animals Animals; *Cestoda* (**142**): Custom Medical Stock Photo, Inc.; *Chitin* (**143**): Chris McLaughlin/Animals Animals; *Chondricthyes* (**145**): Joyce and Frank Burek/Animals Animals; *Chordata* (**147**): Ralph White/Corbis; *Circadian Rhythm* (**150**): George McCarthy/ Corbis; *Circulatory system* (**152**): GCA/CNRI/ Phototake; *Cnidaria* (**155**): Nancy Rotenberg/ Animals Animals; *Coevolution* (**161**): Robert J.

Huffman/Field Mark Publications; *Coevolution* (**159**): Michael and Patricia Fogden/Corbis; *Communication* (**165**): James E. Lloyd/Animals Animals; *Community Ecology* (**168**): Richard Baetson/U.S. Fish and Wildlife Service, Washington D.C.; *Competition* (**174**): Ross, Edward S., Dr.; *Conservation Biology* (**177**): Fred Whitehead/Animals Animals; *Constraints on Animal Development* (**179**): Robert Lubeck/ Animals Animals; *Convergence* (**185**): E. R. Degginger/Animals Animals; *Courtship* (**186**): Michael Fogden/Animals Animals.

Volume Two

Cretaceous (**2**): Richard P. Jacobs/JLM Visuals; *Cultures and Animals* (**6**): Duluth Convention and Visitor's Bureau; *Cultures And Animals* (**8**): Craig Lovell/Corbis; *Darwin, Charles* (**10**): Courtesy of the Library of Congress; *DDT* (**12**): AP/Wide World Photos; *Defense* (**14**): Mark N. Boulton/The National Audubon Society Collection/Photo Researchers, Inc.; *Diamond, Jared* (**18**): AP/Wide World Photos; *Digestive System* (**22**): Roger De La Harpe/ Animals Animals; *Dinosaurs* (**25**): Graves Museum of Archaeology and Natural History/ AP/Wide World Photos; *Domestic Animals* (**29**): Tim Thompson/Corbis; *Dominance Hierarchy* (**32**): Tim Wright/Corbis; *Drosophila* (**34**): UPI/Bettmann Newsphotos/Corbis; *Echinodermata* (**36**): Herb Segars/Animals Animals; *Ecology* (**42**): U.S. National Aeronautics and Space Administration (NASA); *Ecosystem* (**47**): James Watt/Animals Animals; *Elton, Charles Sutherland* (): Animals Animals/©; Scott Johnson; *Embryology* (**52**): Science Pictures Limited/Corbis; *Embryonic Development* (**54**): Redrawn from Scott Gilbert; *Embryonic Development* (**59**): Redrawn from Scott Gilbert; *Endangered Species* (**62**): Vince Streano/The Stock Market; *Entomology* (**72**): Doug Wechsler/Earth Scenes; *Environmental Degradation* (**74**): George H. H. Huey/Earth Scenes; *Environmental Impact* (**78**): David Barron/Earth Scenes; *Excretory and Reproductive Systems* (**88**): Joe McDonald/ Animals Animals; *Exotic Species* (**91**): C. C. Lockwood/Animals Animals; *Extinction* (**100**): Glen Smart/U.S. Fish and Wildlife Service/ Washington, D.C.; *Extremophile* (**103**): TC Nature/Animals Animals; *Farming* (**105**): Tim Page/Corbis; *Feeding* (**111**): Malcolm S. Kirk/Peter Arnold, Inc.; *Feeding Strategies* (**114**): Bruce Davidson/Animals Animals; *Fertilization* (**117**): Hank Morgan/National Audubon Society Collection/Photo Researchers, Inc.; *Flight* (**122**): Zefa Germany/ The Stock Market; *Foraging Strategies* (**130**): Suzanne Danegger/Photo Researchers, Inc.; *Fossey, Dian* (**131**): AP/Wide World Photos; *Fossil Fuels* (**133**): H. David Seawell/Corbis; *Functional Morphology* (**137**): Tim Davis/Photo Researchers; *Genes* (**140**): Biophoto Associates/ National Audobon Society Collection/Photo Researchers, Inc.; *Genetic Engineering* (**149**): Lowell Georgia/Corbis; *Genetic Variation In A Population* (**153**): Eastcott-Momatiuk/Animals Animals; *Genetically Engineered Foods* (**156**): Lowell Georgia/Corbis; *Geneticist* (**157**): Photo Researchers, Inc.; *Genetics* (**160**): AP/ Wide World Photos; *Gills* (**164**): Breck P. Kent/Animals Animals; *Global Warming* (**168**): Bernard Edmaier/Science Photo Library/ Photo Researchers, Inc.; *Goodall, Jane* (**171**): AP/Wide World Photos; *Gould, Steven Jay* (**172**): Wally McNamee/Corbis; *Habitat* (**178**): Johnny Johnson/Animals Animals; *Habitat Loss* (**180**): Ecoscene/Corbis; *Habitat Loss* (**182**): Francois Gohier/National Audubon Society Collection/Photo Researchers, Inc.

Volume Three

Habitat Restoration (**3**): Eastcott-Momatiuk/ Earth Scenes; *Haeckel's Law Of Recapitulation* (**5**): Courtesy of the Library of Congress; *Haldane, J. B. S.* (**6**): Courtesy of the Library of Congress; *Heterochrony* (**9**): Christian Testu/ BIOS; *Home Range* (**11**): Darren Bennet/ Animals Animals; *Hormones* (**17**): Barbra Leigh/Corbis; *Horse Trainer* (**19**): Jerry Cooke/Animals Animals; *Human Commensal and Mutual Organisms* (**31**): LSF OSF/Animals Animals; *Human Evolution* (**35**): John Reader/ Science Photo Library/Photo Researchers, Inc.; *Human Populations* (**41**): AP/Wide World Photos; *Human–Animal Conflicts* (**28**): John Nees/Animals Animals; *HunterGatherers* (**44**): Anthone Bannister/Earth Scenes; *Hunting* (**46**): Raymond Gehman/Corbis; *Imprinting* (**50**): Robert J. Huffman/Field Mark

Publications; *Instinct* (**52**): Anup Shah/Animals Animals; *Interspecies Interactions* (**55**): JLM Visuals; *Iteroparity And Semelparity* (**58**): Kennan Ward/The Stock Market; *Jurassic* (**60**): E. R. Degginger/Earth Scenes; *Keratin* (**63**): L. Lauber-OSF/Animals Animals; *Lamarck* (**69**): Courtesy of the Library of Congress; *Leakey, Louis And Mary* (**70**): UPI/Bettmann Newsphotos/Corbis; *Learning* (**72**): Erwin and Peggy Bauer/Animals Animals; *LeviMontalcini, Rita* (**74**): AP/Wide World Photos; *Linnaeus, Carolus* (**77**): U.S. National Library of Science; *Living Fossils* (**80**): Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc.; *Locomotion* (**88**): Jeffrey L. Rotman/Corbis, Richard Alan Wood/Animals Animals, Ross, Edward S., Dr., Robert Winslow/Animals Animals; *Lorenz, Konrad* (**91**): UPI/Bettmann Newsphotos/Corbis; *Malaria* (**95**): Redrawn from Hans and Cassady; *Malthus, Thomas Robert* (**98**): Archive Photos, Inc.; *Mammalia* (**103**): Leonard Lee Rue III/Animals Animals; *Mayr, Ernst* (**106**): AP/Wide World Photos; *Mendel, Gregor* (**108**): Archive Photos, Inc.; *Mesenchyme* (**110**): Lester V. Bergman/Corbis; *Migration* (**117**): AP/Wide World Photos; *Mimicry* (**122**): Breck P. Kent/Animals Animals; *Molecular Biologist* (**126**): Philippe Plailly/National Audubon Society Collection/Photo Researchers, Inc.; *Molting* (**135**): Ross, Edward S., Dr.; *Morphological Evolution in Whales* (**137**): Bomford/T.Borrill-OSF/Animals Animals; *Mouth, Pharynx, Teeth* (**141**): H. Pooley/OSF/Animals Animals; *Muscular System* (**143**): Custom Medical Stock Photo, Inc.; *Museum Curator* (**145**): Robert J. Huffman/Field Mark Publications; *Natural Resources* (**147**): Richard Hamilton Smith/Corbis; *Nematoda* (**151**): Eric V. Grave/Photo Researchers, Inc.; *Nervous System* (**157**): Redrawn from Neil Campbell.; *Nervous System* (**155**): Secchi-Lecague/Roussel-UCLAF/CNRI/Science Photo Library/National Audubon Society Collection/Photo Researchers, Inc.; *Osteichthyes* (**169**): A. Kuiter/OSF/Animals Animals; *Parasitism* (**179**): Frank Lane Picture Agency/Corbis; *Pasteur, Louis* (**180**): Courtesy of the Library of Congress; *Peppered Moth* (**186**): Breck P. Kent/Animals Animals.

Volume 4

Permian (**2**): Richard P. Jacobs/JLM Visuals; *Pesticide* (**4**): Arthur Gloor/Earth Scenes; *Phylogenetic Relationships of Major Groups* (**6**): Redrawn from Caroline Ladhani.; *Plankton* (**12**): Douglas P. Wilson/Frank Lane Picture Agency/Corbis; *Pleistocene* (**16**): Breck P. Kent/Earth Scenes; *Pollution* (**21**): Wesley Bocxe/National Audubon Society Collection/Photo Researchers, Inc.; *Population Dynamics* (**26**): Wolfgang Kaehler/Corbis; *Populations* (**32**): JLM Visuals; *Predation* (**37**): Johnny Johnson/Animals Animals; *Primates* (**40**): Barbara Vonn Hoffmann/Animals Animals; *Reproduction, Asexual and Sexual* (): Animals Animals/©; Zig Leszczynski; *Reptilia* (**52**): Animals Animals/©; Zig Leszczynski; *Respiration* (**55**): Ron Boardman, Frank Lane Picture Agency/Corbis; *Respiratory System* (**58**): Photo Researchers, Inc.; *Rotifera* (**60**): P. Parks/OSF/Animals Animals; *Scales, Feathers, and Hair* (**62**): Dr. Dennis Kunkel/Phototake; *Selective Breeding* (**65**): George Bernard/Animals Animals; *Sense Organs* (**68**): Robert J. Huffman/Field Mark Publications; *Sexual Dimorphism* (**74**): Gregory G. Dimijian/Photo Researchers, Inc.; *Sexual Selection* (**77**): Animals Animals/©; Darren Bennett; *Shells* (**81**): Spreitzer, A.E., Mr.; *Simpson, George Gaylord* (**85**): Courtesy of the Library of Congress; *Skeletons* (**86**): E. R. Degginger/Animals Animals; *Social Animals* (**91**): G. I. Bernard/OSF/Animals Animals; *Sociality* (**95**): JLM Visuals;*Stevens, Nettie Maria* (**99**): Science Photo Library/Photo Researchers, Inc.; *Sustainable Agriculture* (**101**): Michael Gadomski/Earth Scenes; *Territoriality* (**106**): Jack Wilburn/Animals Animals; *Threatened Species* (**113**): Kenneth W. Fink/Photo Researchers, Inc.; *Tool Use* (**115**): C. Bromhall/OSF/Animals Animals; *Trematoda* (**123**): Photo Researchers, Inc.; *Triassic* (**125**): Robert J. Huffmann/Field Mark Publications; *Urochordata* (**130**): Joyce and Frank Burek/Animals Animals; *Vertebrata* (**132**): Breck P. Kent/JLM Visuals; *Veterinarian* (**134**): Peter Weiman/Animals Animals; *Viruses* (**136**): Scott Camazinr/National Audubon Society Collection/Photo Researchers, Inc.; *Vision* (**139**): J. A. L. Cooke/OSF/Animals Animals;

Vocalization (**142**): Victoria McCormick/ Animals Animals; *Von Baer's Law* (**143**): Courtesy of the Library of Congress; *Water Economy In Desert Organisms* (**147**): Langley, Cory, Mr., (**148**): Maslowski/Photo Researchers, Inc.; *Wild Game Manager* (**150**): Raymond Gehman/Corbis; *Wildlife Biologist* (**152**): Mark Stouffer/Animals Animals; *Wildlife Photographer* (**153**): Johnny Johnson/ Animals Animals; *Wilson, E. O.* (**154**): AP/ Wide World Photos; *Xenopus* (**156**): Zig Leszczynski/Animals Animals, Dr. Dennis Kunkel/Phototake; *Zoological Parks* (**159**): Alfred B. Thomas/Animals Animals; *Zoologist* (**162**): N. Rosing/OSF/Animals Animals; *Zooplankton* (**164**): M. I. Walker/Science Photo Library/National Audubon Society Collection/Photo Researchers, Inc.

Glossary

abiogenic: pertaining to a nonliving origin

abiotic: nonliving parts of the environment

abiotic factors: pertaining to nonliving environmental factors such as temperature, water, and nutrients

absorption: the movement of water and nutrients

acid rain: acidic precipitation in the form of rain

acidic: having the properties of an acid

acoelomate: an animal without a body cavity

acoelomates: animals without a body cavity

acoustics: a science that deals with the production, control, transmission, reception, and effects of sound

actin: a protein in muscle cells that works with myosin in muscle contractions

action potential: a rapid change in the electric charge of the cell membrane

active transport: a process requiring energy where materials are moved from an area of lower to an area of higher concentration

adaptive radiation: a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

adenosine triphoshate: an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

aestivate: a state of lowered metabolism and activity that permits survival during hot and dry conditions

agnostic behavior: a type of behavior involving a contest of some kind that determines which competitor gains access to some resource such as food or mates

alkaline: having the properties of a base

allele: one of two or more alternate forms of a gene

alleles: two or more alternate forms of a gene

allometry: relative growth of one part of an organism with reference to another part

allopatry: populations separated by a barrier

alluvial: sediments from flowing water such as silt, sand, mud, and gravel

alpha: the dominant member of a group

altruistic behavior: the aiding of another individual at one's own risk or expense

alveoli: thin-walled sacs in the lungs where blood in capillaries and air in the lungs exchange gases

ameloblasts: cells that form dental enamel

amiote: embryo of a vertebrate that is surrounded by a fluid-filled sac

ammonites: an extinct group of cephalopods with a curled shell

amnion: the membrane that forms a sac around an embryo

amniote: a vertebrate which has a fluid-filled sac that surrounds the embryo

amniotes: vertebrates which have a fluid-filled sac that surrounds the embryo

anadromous: moving from the ocean up a river to spawn

analogous: a similarity in structures between two species that are not closely related

anemia: a condition that results from a decreased number of red blood cells

angiosperms: a flowering plant that produces seeds within an ovary

annelids: segmented worms

anoxic: an environment that lacks oxygen

anterior: referring to the head end of an organism

anterior pituitary: the front part of the pituitary gland that produces hormones that stimulate the production of sperm and testosterone in the testes

antibodies: proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

antigen: foreign substances that stimulate the production of antibodies in the blood

anurans: the order of amphibians that contains frogs and toads

aphrodisiac: a substance or object that is thought to arouse sexual desire

aphrodisiacs: substances or objects that are thought to arouse sexual desire

aposematic: a feature or signal that serves to warn

aposematic coloration: a bright coloration in animals with physical or chemical defenses that act as a warning to predators

appendicular: having to do with arms and legs

appendicular skeleton: part of the skeleton with the arms and legs

aquatic: living in water

aragonite: a mineral form of calcium carbonate

arboreal: living in trees

Archae: an ancient lineage of prokaryotes that live in extreme environments

arthropod: a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

arthropods: members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

artificial pollination: manual pollination methods

asexual reproduction: a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

asymmetrical: lacking symmetry, having an irregular shape

aural: related to hearing

autonomic nervous system: division of the nervous system that carries nerve impulses to muscles and glands

autotroph: an organism that makes its own food

autotrophs: organisms that make their own food

axial skeleton: the skeleton that makes up the head and trunk

axon: cytoplasmic extension of a neuron that transmits impulses away from the cell body

axons: cytoplasmic extensions of a neuron that transmit impulses away from the cell body

B-lymphocytes: specialized cells produced from stem cells in the bone marrow that secrete antibodies that bind with antigens to form a pathogen fighting complex

bacterium: a member of a large group of single-celled prokaryotes

baleen: fringed filter plates that hang from the roof of a whale's mouth

Batesian mimicry: a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

behavioral: relating to actions or a series of actions as a response to stimuli

benthic: living at the bottom of a water environment

bilateral symmetry: characteristic of an animal that can be separated into two identical mirror image halves

bilaterally symmetrical: describes an animal that can be separated into two identical mirror image halves

bilateria: animals with bilateral symmetry

bilipid membrane: a cell membrane that is made up of two layers of lipid or fat molecules

bio-accumulation: the build up of toxic chemicals in an organism

bioactive protein: a protein that takes part in a biological process

bioactive proteins: proteins that take part in biological processes

biodiversity: the variety of organisms found in an ecosystem

biogeography: the study of the distribution of animals over an area

biological control: the introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

biological controls: introduction of natural enemies such as parasites, predators, or pathogens as a method of controlling pests instead of using chemicals

biomagnification: increasing levels of toxic chemicals through each trophic level of a food chain

biomass: the dry weight of organic matter comprising a group of organisms in a particular habitat

biome: a major type of ecological community

biometry: the biological application of statistics to biology

biotic: pertaining to living organisms in an environment

biotic factors: biological or living aspects of an environment

bipedal: walking on two legs

bipedalism: describes the ability to walk on two legs

birthrate: a ratio of the number of births in an area in a year to the total population of the area

birthrates: ratios of the numbers of births in an area in a year to the total population of the area

bivalve mollusk: a mollusk with two shells such as a clam

bivalve mollusks: mollusks with two shells such as clams

bivalves: mollusks that have two shells

body plan: the overall organization of an animal's body

bone tissue: dense, hardened cells that makes up bones

botany: the scientific study of plants

bovid: a member of the family bovidae which is hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

bovids: members of the family bovidae which are hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

brachiopods: a phylum of marine bivalve mollusks

brackish: a mix of salt water and fresh water

brood parasites: birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

buccal: mouth

budding: a type of asexual reproduction where the offspring grow off the parent

buoyancy: the tendency of a body to float when submerged in a liquid

Burgess Shale: a 550 million year old geological formation found in Canada that is known for well preserved fossils

calcified: made hard through the deposition of calcium salts

calcite: a mineral form of calcium carbonate

calcium: a soft, silvery white metal with a chemical symbol of Ca

capture-recapture method: a method of estimating populations by capturing a number of individuals, marking them, and then seeing what percentage of newly captured individuals are captured again

cardiac: relating to the heart

cardiac muscle: type of muscle found in the heart

cardiopulmonary: of or relating to the heart and lungs

carnivorous: describes animals that eat other animals

carrying capacity: the maximum population that can be supported by the resources

cartilage: a flexible connective tissue

cartilaginous: made of cartilage

catadromous: living in freshwater but moving to saltwater to spawn

character displacement: a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

chelicerae: the biting appendages of arachnids

chemoreceptors: a receptor that responds to a specific type of chemical molecule

chemosynthesis: obtaining energy and making food from inorganic molecules

chemosynthetic autotrophs: an organism that uses carbon dioxide as a carbon source but obtains energy by oxidizing inorganic substances

chemotrophs: animals that make energy and produce food by breaking down inorganic molecules

chitin: a complex carbohydrate found in the exoskeleton of some animals

chitinous: made of a complex carbohydrate called chitin

chloroquine: a drug commonly used to treat malaria

chromosomes: structures in the cell that carry genetic information

cilia: hair-like projections used for moving

circadian rhythm: daily, 24-hour cycle of behavior in response to internal biological cues

clades: a branching diagram that shows evolutionary relationships of organisms

Class Branchiopoda: a group of marine bivalve mollusks

Class Malacostraca: crustaceans such as lobsters, crabs, and shrimp

Class Maxillopoda: crustaceans such as barnacles, ostracods, and copepods

Class Merostomata: crustaceans such as horseshoe crabs and eurypterids

Class Pycnogonida: crustaceans such as sea spiders

cleavage: the process of cytokinesis in animal cells; as cells multiply, the plasma membrane pinches off to make two cells from one

climate: long-term weather patterns for a particular region

cnidaria: a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

cnidarians: aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

codominance: an equal expression of two alleles in a heterozygous organism

codon: the genetic code for an amino acid that is represented by three nitrogen bases

codons: the genetic code for an amino acid that is represented by three nitrogen bases

coelom: a body cavity

coevolution: a situation in which two or more species evolve in response to each other

coexist: live together

commensal: a symbiotic relationship wherein which one species benefits and the other is neither helped nor harmed

competitive exclusion principle: the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

compound eye: a multifaceted eye that is made up of thousands of simple eyes

compound eyes: multifaceted eyes that are made up of thousands of simple eyes

concentric: having the same center

conchiolin: a protein that is the organic basis of mollusk shells

coniferous, conifers: having pine trees and other conifers

connective tissue: cells that make up bones, blood, ligaments, and tendons

consumers: animals that do not make their own food but instead eat other organisms

continental drift: the movement of the continents over geologic time

contour feather: a feather that covers a bird's body and gives shape to the wings or tail

contour feathers: feathers that cover a bird's body and give shape to the wings or tail

controversy: a discussion marked by the expression of opposing views

convergence: animals that are not closely related but they evolve similar structures

copulation: the act of sexual reproduction

crinoids: an echinoderm with radial symmetry that resembles a flower

critical period: a limited time in which learning can occur

critical periods: a limited time in which learning can occur

crustaceans: arthropods with hard shells, jointed bodies, and appendages that mainly live in the water

ctenoid scale: a scale with projections on the edge like the teeth on a comb

cumbersome: awkward

cytoplasm: fluid in eukaryotes that surrounds the nucleus and organelles

cytosolic: the semifluid portions of the cytoplasm

death rate: a ratio of the number of deaths in an area in a year to the total population of the area

deciduous: having leaves that fall off at the end of the growing season

denaturing: break down into small parts

dendrites: branched extensions of a nerve cell that transmit impulses to the cell body

described: a detailed description of a species that scientists can refer to identify that species from other similar species

dessication: drying out

detritus: dead organic matter

deuterostome: animal in which the first opening does not form the mouth, but becomes the anus

deuterostomes: animals in which the first opening does not form the mouth, but becomes the anus

diadromous: animals that migrate between freshwater and saltwater

differentiation: differences in structure and function of cells in multicellular organisms as the cells become specialized

diffusion: the movement of molecules from a region of higher concentration to a region of lower concentration

dioecious: having members of the species that are either male or female

diploblastic: having two germ layers; ectoderm and endoderm

diploid cells: cells with two sets of chromosomes

direct fitness: fitness gained through personal reproduction

diurnal: active in the daytime

DNA replication: the process by which two strands of a double helix separate and form two identical DNA molecules

dominance hierarchies: the structure of the pecking order of a group of individuals of a group where the multiple levels of dominance and submission occur

dominant: an allele that is always an expressed trait

dorsal: the back surface of an animal with bilateral symmetry

dorsal root ganglia: nervous tissue located near the backbone

dorsoventrally: flattened from the top and bottom

dysentery: inflammation of the intestines that is characterized by pain, diarrhea, and the passage of mucous and blood

ecdysis: shedding the outer layer of skin or exoskeleton

ecdysone: hormone that triggers molting in arthropods

echinoderms: sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

ecological: relating to an organism's interaction with its environment

ecology: study of how organisms interact with their environment

ecosystem: a self-sustaining collection of organisms and their environment

ecosystems: self-sustaining collections of organisms and their environments

ecotourism: tourism that involves travel to areas of ecological or natural interest usually with a naturalist guide

ectodermal: relating to the outermost of the three germ layers in animal embryos

ectoparasite: an organism that lives on the surface of another organism and derives its nutrients directly from that organism

ectoparasites: organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

edentates: lacking teeth

El Niño: a periodic condition characterized by a warming of the central Pacific Ocean and the changes in global weather patterns that are brought about

emit: to send out or give off

endocrine system: the grouping of organs or glands that secrete hormones into the bloodstream

endoparasite: an organism that lives inside another organism and derives its nutrients directly from that organism

endoparasites: organisms that live inside other organisms and derive their nutrients directly from those organisms

endoskeleton: a skeleton that is surrounded by muscle tissue

endosymbionts: the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

endotrophic: deriving nourishment from within

enterocoelous: a cavity formed by the in-folding of the wall of the intestinal cavity in a gastrula

enzyme: a protein that acts as a catalyst to start a biochemical reaction

enzymes: proteins that act as catalysts to start biochemical reactions

epidermis: the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

epistasis: a phenomenon in which one gene alters the expression of another gene that is independently inherited

epithelial cells: cells that occur in tightly packed sheets that line organs and body cavities

epithelial lining: sheets of tightly packed cells that cover organs and body cavities

epitope: a localized region on an antigen that is recognized chemically by antibodies

equilibrium: a state of balance

erythrocytes: red blood cells, cells containing hemoglobin that carry oxygen throughout the body

estuaries: an area of brackish water where a river meets the ocean

ethology: animal behavior

eucoelomates: animals that have a true body cavity that is completely surrounded by mesoderm

eukaryota: a group of organisms containing a membrane bound-nucleus and membrane-bound organelles

eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles

eukaryotic cells: contains a membrane-bound nucleus and membrane-bound organelles

euryhaline: animals that can live in a wide range of salt concentrations

eusocial: animals that show a true social organization

evaporites: rocks formed from evaporation of salty and mineral-rich liquid

excrescence: an abnormal growth

excrescences: abnormal growths

exons: the coding region in a eukaryotic gene that is expressed

exoskeleton: a hard outer protective covering common in invertebrates such as insects

exoskeletons: hard outer protective coverings common in invertebrates such as insects

exponential growth: a population growing at the fastest possible rate under ideal conditions

extant: still living

facilitated diffusion: the spontaneous passing of molecules attached to a carrier protein across a membrane

facultative parasites: organisms that can survive either as a parasite or free-living

falconry: a sport where falcons are used for hunting

fascicle: a close cluster

fauna: animals

fertilization: the fusion of male and female gametes

fibroblasts: type of cells found in loose connective tissue that secretes the proteins for connective fibers

fight or flight response: an automatic, chemically controlled response to a stimulus that causes increased heart and breathing rates for increased activity

filter feeders: animals that strain small food particles out of water

fission: dividing into two parts

fixed action pattern: behaviors that are common to all members of a species

flagella (flagellum): cellular tail that allows the cell to move

flagellae: cellular tails that allow cells to move

flora: plants

fossil record: a collection of all known fossils

frequency-dependant selection: a decline in the reproductive success of a particular body type due to that body type becoming common in the population

frugivores: fruit-eating animals

functional morphology: studying form and function

fusion: coming together

gametes: reproductive cells that only have one set of chromosomes

gametocyte: cell that produces gametes through division

gametocytes: cells that produce gametes through division

ganoid scale: hard, bony, and enamel covered scales

gastropods: mollusks that are commonly known as snails

gastrovascular cavity: a single cavity where digestion occurs

gastrulation: the formation of a gastrula from a blastula

gene therapy: a process where normal genes are inserted into DNA to correct a genetic disorder

genes: segments of DNA located on chromosomes that direct protein production

genetic trait: trait related to biological inheritance

genetics: the branch of biology that studies heredity

genome: an organism's genetic material

genomes: the sum of all genes in a set of chromosomes

genotype: the genetic makeup of an organism

germ cell: an egg or sperm cell, a gamete

germ cells: egg or sperm cells, gametes

gill arches: arches of cartilage that support the gills of fishes and some amphibians

gill filaments: the site of gas exchange in aquatic animals such as fish and some amphibians

gills: site of gas exchange between the blood of aquatic animals such as fish and the water

gizzard: the muscular part of the stomach of some animals where food is ground

global warming: a slow and steady increase in the global temperature

glycoprotein: an organic molecule that contains a carbohydrate and a protein

gonad: the male and female sex organs that produce sex cells

gonads: the male and female sex organs that produce sex cells

granulocytes: a type of white blood cell where its cytoplasm contains granules

green house effect: a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

habitat: the physical location where organisms live in an ecosystem

habitat loss: the destruction of habitats through natural or artificial means

habitat requirement: necessary conditions or resources needed by an organism in its habitat

habitats: physical locations where organisms live in an ecosystem

Hamilton's Rule: individuals show less agression to closely related kin than to more distantly related kin

haplodiploidy: the sharing of half the chromosomes between a parent and an offspring

haploid cells: cells with only one set of chromosomes

hemocoel: a cavity between organs in arthropods and mollusks through which blood circulates

hemocyanin: respiratory pigment found in some crustaceans, mollusks, and arachnids

hemoglobin: an iron-containing protein found in red blood cells that binds with oxygen

hemolymph: the body fluid found in invertebrates with open circulatory systems

herbivore: an animal that eats plants only

herbivores: animals that eat only plants

herbivorous: animals that eat plants

heredity: the passing on of characteristics from parents to offspring

heritability: the ability to pass characteristics from a parent to the offspring

hermaphodite: an animals with both male and female sex organs

hermaphroditic: having both male and female sex organs

heterodont: teeth differentiated for various uses

heterotrophic eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles and do not make their own food

heterotrophs: organisms that do not make their own food

heteroxenous: a life cycle in which more than one host individual is parasitized

heterozygote: an organism whose chromosomes contain both genes of a contrasting pair

heterozygote advantage: a condition where a heterozygous individual has a reproductive advantage over a homozygous individual

Hippocrates: a central figure in medicine in ancient Greece, he is considered the father of modern medicine

home range: the area where an animal lives and eats

homeostasis: a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

homeothermic: describes animals able to maintain their body temperatures

hominid: belonging to the family of primates

hominids: belonging to the family of primates

homodont: teeth with a uniform size and shape

homologous: similar but not identical

homology: correspondence in the type of structure and its origin

homoplastic: similar but of different origins

homozygote: an animal with two identical alleles for one trait

hormone: a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

hormones: chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

Horseshoe crabs: "living fossils" in the class of arthropods

Hox genes: also known as selector genes because their expression leads embryonic cells through specific morphologic development

Human Genome Project: a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

hunting season: a period of time during which hunting is permited

hunting seasons: periods of time during which hunting is permited

hybrid: offspring resulting from the cross of two different species

hydrostatic skeleton: a pressurized, fluid-filled skeleton

hyperpolarizing potential: any change in membrane potential that makes the inside of the membrane more negatively charged

hypothalamus: part of the upper end of the brain stem that regulates activities in the nervous and endrocrine systems

IgA: imunoglobin A; a class of proteins that make up antibodies

IgD: imunoglobin D; a class of proteins that make up antibodies

IgE: imunoglobin E; a class of proteins that make up antibodies

IgG: imunoglobin G; a class of proteins that make up antibodies

IgM: imunoglobin M; a class of proteins that make up antibodies

inbreeding depression: loss of fitness due to breeding with close relatives

incomplete dominance: a type of inheritance where the offspring have an intermediate appearance of a trait from the parents

incus: one of three small bones in the inner ear

indirect fitness: fitness gained through aiding the survival of non-descendant kin

infrared: an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red; heat is carried on infrared waves

innate behavior: behavior that develops without influence from the environment

innervate: supplied with nerves

inoculation: introduction into surroundings that support growth

insectivore: an animal that eats insects

insectivores: animals that eat insects

instars: the particular stage of an insect's or arthropod growth cycle between moltings

integument: a natural outer covering

intercalation: placing or inserting between

intraspecific: involving members of the same species

introns: a non-coding sequence of base pairs in a chromosome

invagination: a stage in embryonic development where a cell layer buckles inward

invertebrates: animals without a backbone

involuntary muscles: muscles that are not controlled by will

isthmus: a narrow strip of land

iteroparous: animals with several or many reproductive events in their lives

***k*-selected species:** a species that natural selection has favored at the carrying capacity

***k*-selecting habitat:** habitat where there is a high cost of reproduction and is sensitive to the size of the offspring

key innovation: a modification that permits an individual to exploit a resource in a new way

keystone species: a species that controls the environment and thereby determines the other species that can survive in its presence

krill: an order of crustaceans that serves as a food source for many fish, whales, and birds

lancelet: a type of primitive vertebrate

lancelets: primitive vertebrates

lateral inhibition: phenomenon that amplifies the differences between light and dark

lateral line: a row of pressure sensitive sensory cells in a line on both sides of a fish

learned behavior: behavior that develops with influence from the environment

learning: modifications to behavior motivated by experience

leukocytes: a type of white blood cells that are part of the immune system

life history strategies: methods used to overcome pressures for foraging and breeding

life history strategy: methods used to overcome pressures for foraging and breeding

lipids: fats and oils; organic compounds that are insoluble in water

logistic growth: in a population showing exponential growth the individuals are not limited by food or disease

lungs: sac-like, spongy organs where gas exchange takes place

lymphocytes: white blood cell that completes development in bone marrow

macroparsite: a parasite that is large in size

macroparasites: parasites that are large in size

macrophages: white blood cell that attacks anything foreign such as microbes

malleus: the outermost of the inner ear bones

mantle: the tissue in mollusks that drapes over the internal organs and may secrete the shell

mantles: tissues in mollusks that drape over the internal organs and may secrete the shell

matrix: the nonliving component of connective tissue

megachiroptera: fruit bats and flying foxes

meiosis: a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

merozoite: a motile stage in some parastic protozoa

mesenchyme: the part of the mesoderm from which the connective tissues (bone, cartilage, and vascular system) arise

mesenteries: the membrane that suspends many internal organs in the fluid-filled body cavity of vertebrates

mesoderm: the middle layer of cells in embryonic tissue

messenger RNA: a type of RNA that carries protein synthesis information from the DNA in to the nucleus to the ribosomes

metamorphose: to change drastically from a larva to an adult

metamorphoses: changes drastically from its larval form to its adult form

metamorphosing: changing drastically from a larva to an adult

metamorphosis: a drastic change from a larva to an adult

metazoan: a subphylum of animals that have many cells, some of which are organized into tissues

metazoans: a subphylum of animals that have many cells, some of which are organized into tissues

microchiroptera: small bats that use echolocation

microparasite: very small parasite

microparasites: very small parasites

midoceanic ridge: a long chain of mountains found on the ocean floor where tectonic plates are pulling apart

mitochondria: organelles in eukaryotic cells that are the site of energy production for the cell

Mitochondrial DNA: DNA found within the mitochondria that control protein development in the mitochondria

mitosis: a type of cell division that results in two identical daughter cells from a single parent cell

modalities: to conform to a general pattern or belong to a particular group or category

modality: to conform to a general pattern or belong to a particular group or category

molecular clock: using the rate of mutation in DNA to determine when two genetic groups spilt off

molecular clocks: using the rate of mutation in DNA to determine when two genetic groups spilt off

mollusks: large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

molted: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

molting: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

monoculture: cultivation of a single crop over a large area

monocultures: cultivation of single crops over large areas

monocytes: the largest type of white blood cell

monophyletic: a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

monotremes: egg-laying mammals such as the platypus and echidna

monoxenous: a life cycle in which only a single host is used

morphogenesis: the development of body shape and organization during ontogeny

morphological: the structure and form of an organism at any stage in its life history

morphological adaptation: an adaptation in form and function for specific conditions

morphological adaptations: adaptations in form and function for specific conditions

morphologies: the forms and structures of an animal

mutation: an abrupt change in the genes of an organism

mutations: abrupt changes in the genes of an organism

mutualism: ecological relationship beneficial to all involved organisms

mutualisms: ecological relationships beneficial to all involved organisms

mutualistic relationship: symbiotic relationship where both organisms benefit

mutualistic relationships: symbiotic relationships where both organisms benefit

mutualists: a symbiotic relationship where both organisms benefit

myofibril: longitudinal bundles of muscle fibers

myofilament: any of the ultramicroscopic filaments, made up of actin and myosin, that are the structural units of a myofibril

myosin: the most common protein in muscle cells, responsible for the elastic and contractile properties of muscle; it combines with actin to form actomyosin

natural selection: the process by which organisms best suited to their environment are most likely to survive and reproduce

naturalist: a scientist who studies nature and the relationships among the organisms

naturalists: scientists who study nature and the relationships among the organisms

neuromuscular junction: the point where a nerve and muscle connect

neuron: a nerve cell

neurons: nerve cells

neurotransmitters: chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

niche: how an organism uses the biotic and abiotic resources of its environment

nocturnal: active at night

notochord: a rod of cartilage that runs down the back of Chordates

nucleotide: the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

nucleotide chain: a chain composed of five-carbon sugar groups that forms the basis for nucleic acid

nucleotides: building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

obligative mutualism: an animal that must exist as part of a mutually beneficial relationship

obligatory parasites: an animal that can only exist as a parasite

olfactory: relates to the sense of smell

omnivorous: eating both plants and animals

ontogeny: the embryonic development of an organism

oocyst: a cyst in sporozoans that contains developing sporozoites

operculum: a flap covering an opening

operculum chamber: space covered by a flap

organelles: membrane-bound structures found within a cell

ornithology: the study of birds

osmoregulatory functions: controlling the water balance within an animal

osmoregulatory system: system that regulates the water balance between an organism and its environment

osmosis: the diffusion of water across a membrane

ossification: deposition of calcium salts to form hardened tissue such as bone

osteoblasts: potential bone forming cells found in cartilage

oviparous: having offspring that hatch from eggs external to the body

ovoviparity: having offspring that hatch from eggs retained in the mother's uterus

ovoviviparous: having offspring that hatch from eggs retained in the mother's uterus

paleoanthropology: the study of ancient humans

parasitology: the study of parasites

parasympathetic division: part of the nervous system that generally enhances body activities that gain and conserve energy such as digestion and heart rate

parental imprinting: a process by which a gene's expression in a child depends on which parent donated it before development

passive diffusion: the passing of molecules across a membrane from an area of higher concentration to an area of lower concentration without any energy input

pathogens: disease-causing agents such as bacteria, fungi, and viruses

pecking order: the position of individuals of a group wherein multiple levels of dominance and submission occur

pectoral: of, in, or on the chest

pedipapls: one pair of short appendages near the mouth in some arthropods used for feeding and copulation

pericardial cavity: the space within the membrane that surrounds the heart

peripheral nervous system: the sensory and motor nerves that connect to the central nervous system

peritoneum: the thin membrane that lines the abdomen and covers the organs in it

pesticide: any substance that controls the spread of harmful or destructive organisms

pesticides: substances that control the spread of harmful or destructive organisms

pH: a measure of how acidic or basic a substance is by measuring the concentration of hydrogen ions

phalanges: bones of the fingers and toes

pharyngeal: having to do with the tube that connects the stomach and the esophagus

phenotype: physical and physiological traits of an animal

phenotypes: the physical and physiological traits of an animal

phenotypic: describes the physical and physiological traits of an animal

phenotypic trait: physical and physiological variations within a population

phenotypic variation: differences in physical and physiological traits within a population

pheromones: small, volatile chemicals that act as signals between animals that influence physiology or behavior

phlogenetic: relating to the evolutionary history

phospholipid: molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water

photoreceptors: specialized cells that detect the presence or absence of light

photosynthesis: the combination of chemical compounds in the presence of sunlight

photosynthesizing autotrophs: animals that produce their own food by converting sunlight to food

phyla: broad, principle divisions of a kingdom

phylogenetic: relating to the evolutionary history of species or group of related species

phylogeny: the evolutionary history of a species or group of related species

physiological: relating to the basic activities that occur in the cells and tissues of an animal

physiology: the study of the normal function of living things or their parts

placenta: the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placental: having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placoid scale: a scale composed of three layers and a pulp cavity

placoid scales: scales composed of three layers and a pulp cavity

plankton: microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

plate tectonics: the theory that Earth's surface is divided into plates that move

platelet: cell fragment in plasma that aids clotting

platelets: cell fragments in plasma that aid in clotting

pleural cavity: the space where the lungs are found

plumose: having feathers

pluripotent: a cell in bone marrow that gives rise to any other type of cell

poaching: hunting game outside of hunting season or by using illegal means

poikilothermic: an animal that cannot regulate its internal temperature; also called cold blooded

polymer: a compound made up of many identical smaller compounds linked together

polymerase: an enzyme that links together nucleotides to form nucleic acid

polymerases: enzymes that link together nucleotides to form nucleic acid

polymodal: having many different modes or ways

polymorphic: referring to a population with two or more distinct forms present

polymorphism: having two or more distinct forms in the same population

polymorphisms: having two or more distinct forms in the same population

polyploid: having three or more sets of chromosomes

polysaccharide: a class of carbohydrates that break down into two or more single sugars

polysaccharides: carbohydrates that break down into two or more single sugars

population: a group of individuals of one species that live in the same geographic area

population density: the number of individuals of one species that live in a given area

population dynamics: changes in a population brought about by changes in resources or other factors

population parameters: a quantity that is constant for a particular distribution of a population but varies for the other distrubutions

populations: groups of individuals of one species that live in the same geographic area

posterior: behind or the back

precursor: a substance that gives rise to a useful substance

prehensile: adapted for siezing, grasping, or holding on

primer: short preexisting polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase

producers: organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

progeny: offspring

prokaryota: a group of organisms that lack a membrane-bound nucleus and membrane-bound organelles

prokaryotes: single-celled organisms that lack a true cell nucleus

prokaryotic endosymbionts: single-celled organisms that lack a true cell nucleus that live inside of other cells

proprioceptors: sense organs that receive signals from within the body

protostome: animal in which the initial depression that starts during gastrulation becomes the mouth

protostomes: animals in which the initial depression that starts during gastrulation becomes the mouth

protozoa: a phylum of single-celled eukaryotes

protozoan: a member of the phylum of single-celled organisms

pseudocoelom: a body cavity that is not entirely surrounded by mesoderm

pseudocoelomates: animals with a body cavity that is not entirely surrounded by mesoderm

pterylae: feather tracks

quadrupedal: describes an animal with four legs

quadrupeds: animals with four legs

quinine: substance used to treat malaria

***r*-selected species:** a species that shows the following characteristics: short lifespan; early reproduction; low biomass; and the potential to produce large numbers of usually small offspring in a short period of time

***r*-selecting habitat:** the concept where a high reproductive rate is the chief determinant of life history

radially symmetric: wheel-like symmetry in which body parts radiate out from a central point

radially symmetrical: describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

recessive: a hidden trait that is masked by a dominant trait

recombinant DNA: DNA that is formed when a fragment of DNA is incorporated into the DNA of a plasmid or virus

regeneration: regrowing body parts that are lost due to injury

relative abundance: an estimate of population over an area

rennin: an enzyme used in coagulating cheese; is obtained from milk-fed calves

resorbed: absorption of materials already in the body

resorption: absorbing materials that are already in the body

respiratory pigments: any of the various proteins that carry oxygen

restriction enzymes: bacterial proteins that cut DNA at specific points in the nucleotide sequence

retina: a layer of rods and cones that line the inner surface of the eye

riparian: habitats in rivers and streams

ruminants: plant-eating animals with a multicompartment stomach such as cows and sheep

sagital plane: a plane that runs long-ways through the body

salamanders: four-legged amphibians with elongated bodies

sarcomere: one of the segments into which a fibril of striated muscle is divided by thin dark bands

scavengers: animals that feed on the remains of animals it did not kill

schizocoelous: the mesoderm originates from existing cell layers when the cells migrate

scleroblasts: cells that give rise to mineralized connective tissue

sedimentary rock: rock that forms when sediments are compacted and cemented together

semelparous: animals that only breed once and then die

serial homology: a rhythmic repetition

sessile: not mobile, attached

sexual reproduction: a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

sexual selection: selection based on secondary sex characteristics that leads to greater sexual dimorphorphism or differences between the sexes

sexual size dimorphism: a noticeable difference in size between the sexes

shoals: shallow waters

single-lens eyes: an eye that has a single lens for focusing the image

skeletal muscle: muscle attached to the bones and responsible for movement

smooth muscle: muscles of internal organs which is not under conscious control

somatic: having to do with the body

somatic nervous system: part of the nervous system that controls the voluntary movement of skeletal muscles

somatosensory information: sensory information from different parts of the body except for the eyesm tongue, ears, and other primary sense organs

somites: a block of mesoderm along each side of a chordate embryo

sonar: the bouncing of sound off distant objects as a method of navigation or finding food

spinal cord: thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

splicing: spliting

spongocoel: the central cavity in a sponge

sporozoa: a group of parasitic protozoa

sporozoans: parasitic protozoans

sporozoite: an infective stage in the life cycle of sporozoans

stapes: innermost of the three bones found in the inner ear

stimuli: anything that excites the body or part of the body to produce a specific response

stimulus: anything that excites the body or part of the body to produce a specific response

strata: layers of sedimentary rock consisting of approximately the same kinds of material

striated muscle: a type of muscle with fibers of cross bands usually contracted by voluntary action

striated muscles: muscles with fibers of cross bands usually contracted by voluntary actions

superposition: the order in which sedimentary layers are found with the youngest being on top

symbiosis: any prolonged association or living together of two or more organisms of different species

symbiotic relationship: close, long-term relationship where two species live together in direct contact

symbiotic relationships: close, long-term relationships where two species live together in direct contact

symmetrical: a balance in body proportions

synapse: the space between nerve cells across which impulses are chemically transmitted

systematic: study of the diversity of life

tactile: the sense of touch

tapetum: a reflective layer in the eye of nocturnal animals

taxa: named taxonomic units at any given level

taxon: named taxonomic unit at any given level

taxonomy: the science of classifying living organisms

terraria: a small enclosure or closed container in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrariums: small enclosures or closed containers in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrestrial: living on land

thoracic: the chest area

thromboplastin: a protein found in blood and tissues that promotes the conversion of prothrombin to thrombin

torpid: a hibernation strategy where the body temperature drops in relation to the external temperature

trachea: the tube in air-breathing vertebrates that extends from the larynx to the bronchi

transcription: process where enzymes are used to make an RNA copy of a strand of DNA

transgenic: an organism that contains genes from another species

transgenic organism: an organism that contains genes from another species

translation: process where the order of bases in messenger RNA codes for the order of amino acids in a protein

transverse plane: a plane perpendicular to the body

trilobites: an extinct class of arthropods

triploblasts: having three germ layers; ectoderm, mesoderm, and endoderm

trophic level: the division of species in an ecosystem by their main source of nutrition

trophic levels: divisions of species in an ecosystem by their main source of nutrition

ungulates: animals with hooves

urea: soluble form of nitrogenous waste excreted by many different types of animals

urethra: a tube that releases urine from the body

uric acid: insoluble form of nitrogenous waste excreted by many different types of animals

ventral: the belly surface of an animal with bilateral symmetry

vertebrates: animals with a backbone

viviparity: having young born alive after being nourished by a placenta between the mother and offspring

viviparous: having young born alive after being nourished by a placenta between the mother and offspring

vocalization: the sounds used for communications

voluntary muscles: a type of muscle with fibers of cross bands usually contracted by voluntary action

wavelength: distance between the peaks or crests of waves

zooplankton: small animals who float or weakly move through the water

zygote: a fertilized egg

zygotes: fertilized eggs

zymogens: inactive building-block of an enzyme

Topic Outline

ADAPTATIONS

Adaptation
Antlers and Horns
Aposematism
Biological Evolution
Biomechanics
Blood
Camouflage
Catadromous—Diadromous and Anadromous Fishes
Colonization
Communication
Community Ecology
Comparative Biology
Defense
Echolocation
Egg
Extremophile
Locomotion
Mimicry
Peppered Moth
Tool Use
Water Economy in Desert Organisms

AGRICULTURE

Apiculture
Aquaculture
Classification Systems
Dinosaurs
Domestic Animals
Farmer
Farming
Selective Breeding
Sustainable Agriculture

ANIMAL DIVERSITY

Animal
Biodiversity
Biogeography
Biological Evolution
Cambrian Explosion
Camouflage
Cephalization
Coevolution
Colonization
Community Ecology
Constraints on Animal Development
Diversity of Major Groups
Extremophile
Functional Morphology
Kingdoms of Life
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Prokaryota
Sexual Dimorphism
Taxonomy

ANIMAL GROUPS

Agnatha
Amphibia
Annelida
Arthropoda
Aves
Cephalochordata
Cestoda
Chondricthyes
Chordata
Cnidaria
Dinosaurs
Echinodermata

Eukaryota
Mammalia
Metazoan
Molluska
Nematoda
Osteicthyes
Platyhelmithes
Porifera
Primates
Prokaryota
Reptilia
Rotifera
Trematoda
Turbellaria
Urochordata
Vertebrata

ANIMAL HISTORY

African Cichlid Fishes
Animal
Burgess Shale and Ediacaran Faunas
Cambrian Explosion
Coevolution
Colonization
Constraints on Animal Development
Domestic Animals
Eukaryota
Extinction
Fossil Record
Horses
Kingdoms of Life
Living Fossils
Paleontologist
Paleontology
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Tetropods—From Water to Land
Xenopus

ANATOMY

Acoustic Signals
Biomechanics
Body Cavities
Body Plan
Bone
Cartilage
Cells
Cephalization
Comparative Biology
Echolocation
Embryology
Embryonic Development
Feeding
Functional Morphology
Gills
Growth And Differentiation of the Nervous System
Homology
Keratin
Locomotion
Mouth, Pharynx, and Teeth
Muscular System
Neuron
Scales, Feathers, and Hair
Sense Organs
Skeletons
Vision

BEHAVIOR

Acoustic Signals
Aggression
Altruism
Behavior
Behavioral Ecology
Circadian Rhythm
Courtship
Crepuscular
Diurnal
Dominance Hierarchy
Ethology
Homeostasis
Imprinting
Instinct
Learning
Migration
Nocturnal
Social Animals
Sociality
Sociobiology
Territoriality

BIOCHEMISTRY AND PHYSIOLOGY

Absorption
Allometry
Antibody

Blood
Cancer
Cell Division
Cells
Digestion
Egg
Homeostasis
Hormones
Keratin
Molecular Biologist
Molecular Biology
Molecular Systematics
Physiologist
Physiology
Respiration
Transport

BIODIVERSITY

Biodiversity
Biogeography
Biomass
Biomes
Colonization
Community Ecology
Diversity of Major Groups
Eukaryota
Habitat
Habitat Loss
Habitat Restoration
Zooplankton

CAREERS IN ANIMAL SCIENCE

Ecologist
Environmental Lawyer
Farmer
Functional Morphologist
Geneticist
Horse Trainer
Human Evolution
Livestock Manager
Marine Biologist
Medical Doctor
Molecular Biologist
Museum Curator
Paleontologist
Physiologist
Scientific Illustrator
Service Animal Trainer
Systematist
Taxonomist
Veterinarian
Wild Game Manager
Wildlife Biologist
Wildlife Photographer
Zoologist

CELL BIOLOGY

Absorption
Blood
Cell Division
Cells
Viruses

ECOLOGY

African Cichlid Fishes
Behavioral Ecology
Biotic Factors
Camouflage
Community Ecology
Competition
Competitive Exclusion
Conservation Biology
DDT
Ecologist
Ecology
Ecosystem
Evolutionary Stable Strategy
Exotic Species
Expenditure per Progeny
Feeding Strategies
Fitness
Food Web
Foraging Strategies
Growth And Differentiation of the Nervous System
Habitat
Habitat Loss
Habitat Restoration
Home Range
Human Commensals and Mutual Organisms
Interspecies Interactions
Iteroparity and Semelparity
Keystone Species
Life History Strategies

Malthus, Thomas Robert
Parasitism
Plankton
Population Dynamics
Populations
Predation
Territoriality
Trophic Level
Zooplankton

ENVIRONMENT

Biological Pest Control
Biomass
Biomes
Biotic Factors
Carson, Rachel
DDT
Ecosystem
Endangered Species
Environment
Environmental Degradation
Environmental Impact
Environmental Lawyer
Fossil Fuels
Global Warming
Human Populations
Natural Resources
Pesticide
Pollution
Silent Spring
Threatened Species

ETHICS

Animal Rights
Animal Testing
Bioethics

EVOLUTION

Adaptation
African Cichlid Fishes
Aposematism
Biological Evolution
Camouflage
Coevolution
Constraints on Animal Development
Continental Drift
Convergence
Darwin, Charles
Genetic Variation in a Population
Heterochrony
Homology
Human Evolution
Lamarck
Leakey, Louis and Mary
Modern Synthesis
Morphological Evolution in Whales
Morphology
Natural Selection
Peppered Moth
Sexual Dimorphism
Sexual Selection
Spontaneous Generation

FORM AND FUNCTION

Acoustic Signals
Adaptation
African Cichlid Fishes
Antlers and Horns
Aposematism
Biomechanics
Blood
Body Cavities
Body Plan
Bone
Burgess Shale and Ediacaran Faunas
Camouflage
Cell Division
Cells
Cephalization
Chitin
Circulatory System
Communication
Defense
Digestion
Digestive System
Echolocation
Endocrine System
Excretory and Reproductive Systems
Feeding
Flight
Gills
Gliding and Parachuting
Locomotion
Mimicry

Nervous System
Respiratory System
Sexual Selection
Shells
Vision
Vocalization

GENETICS

Drosophila
Genes
Genetic Engineering
Genetic Variation in a Population
Genetically Engineered Foods
Geneticist
Genetics
Mendel, Gregor
Modern Synthesis
PCR
Viruses

GEOLOGIC HISTORY

Cambrian Period
Carboniferous
Continental Drift
Cretaceous
Devonian
Geological Time Scale
Jurassic
K/T Boundary
Oligocene
Ordovician
Permian
Pleistocene
Quaternary
Silurian
Tertiary
Triassic

GROWTH AND DEVELOPMENT

Allometry
Antlers and Horns
Body Cavities
Body Plan
Bone
Cartilage
Cell Division
Cells
Comparative Biology
Constraints on Animal Development
Egg
Embryology
Embryonic Development
Haeckel's Law of Recapitulation
Heterochrony
Mesenchyme
Metamorphosis
Molting
Ontogeny
Serial Homology
Von Baer's Law

HISTORICAL FIGURES IN SCIENCE

Aristotle
Bailey, Florence Augusta Merriam
Bates, Henry Walter
Carson, Rachel
Darwin, Charles
Diamond, Jared
Elton, Charles Sutherland
Fausto–Sterling, Anne
Fossey, Dian
Goodall, Jane
Gould, Steven Jay
Haldane, J. B. S.
Lamarck, Jean-Baptiste
Leakey, Louis and Mary
Linnaeus, Carolus
Lorenz, Konrad
Malthus, Thomas Robert
Mayr, Ernst
McArthur, Robert
Mendel, Gregor
Montalcini, Rita Levi
Pasteur, Louis
Simpson, George Gaylord
Stevens, Nettie Maria
Wallace, Alfred Russel
Wilson, E. O.

HUMANS AND THE ANIMAL WORLD

Cultures and Animals
Human Commensals and Mutual Organisms
Human Populations
Human–Animal Conflicts

Hunter-Gatherers
Hunting
Malaria

LIFE CYCLES

Catadromous—Diadromous and Anadromous Fishes
Cell Division
Colonization
Courtship
Endosymbiosis
Iteroparity and Semelparity
Malaria
Metamorphosis
Parasitism

REPRODUCTION

Antlers and Horns
Asexual And Sexual Reproduction
Cell Division
Excretory and Reproductive Systems
Fertilization

SCIENTIFIC FIELDS OF STUDY

Behavioral Ecology
Community Ecology
Comparative Biology
Conservation Biology
Ecology
Embryology
Entomology
Functional Morphology
Herpetology
Icthyology
Molecular Biology
Morphology
Mouth, Pharynx, and Teeth
Paleontology
Physiology
Sociobiology
Taxonomy

animal sciences

VOLUME 4
Per–Zoo

The Macmillan Science Library

animal sciences

animal sciences

VOLUME 4
Per–Zoo

Allan B. Cobb, Editor in Chief

MACMILLAN REFERENCE USA™

THOMSON GALE™

New York • Detroit • San Diego • San Francisco • Cleveland • New Haven, Conn. • Waterville, Maine • London • Munich

Macmillan Reference USA
1633 Broadway
New York, NY 10019

The Gale Group
27500 Drake Rd.
Farmington Hills, 48331-3535

Printed in the United States of America
1 2 3 4 5 6 7 8 9 10

Library of Congress Cataloging-in-Publication Data
Animal Sciences / Allan B. Cobb, editor in chief.
p. cm.
Includes bibliographical references and index.
ISBN: 0-02-865556-7 (set) - ISBN 0-02-865557-5 (vol. 1) - ISBN 0-02-865558-3 (vol. 2) - ISBN 0-02-865559-1 (vol. 3) - ISBN 0-02-865560-5 (vol. 4)
1. Animal Culture. 2. Livestock. I. Title.
SF61.C585 2001
590.3-dc21 2001026627
Rev

Preface

Six hundred million years of animal evolution and adaptation have produced a stunning range and variety of life on Earth. From the oldest, single-celled creatures to the most complex mammalian forms, animal diversity defies easy categorization or explanation. The Macmillan *Animal Sciences* encyclopedia provides a clear and comprehensive resource for better understanding this vast domain. By the nature of its interdisciplinary scope, the subject of animal sciences demands an approach that is both specific and general, detailed and thematic. *Animal Sciences* achieves this end in the course of nearly three hundred well-researched, clearly presented entries that explore the wide ranging diversity that exists within the animal kingdom.

Students will learn how animals develop throughout their lives, how they adapt to their changing environments, and how they develop specialized structures over time. Entries in this category explain how animals develop from fertilized eggs to adults. While some forms of development are straightforward—like a puppy maturing to become a dog—other changes are more dramatic—like a caterpillar changing its body forms over the course of its metamorphosis into a butterfly. Other entries study the various forms of animals and how body parts function.

The encyclopedia gives significant attention to animal ecology and behavior. Entries show how animals are part of the world environment while exhibiting unique behaviors within their own particular environments. Animal ecology addresses how animals are a part of ecosystems and how they interact with plants and other animals, both within and beyond their individual species. Given the close relationship of animal behavior and ecology, a number of entries discuss how animals select mates, whether they live alone or as members of groups, or how they share resources within an ecosystem, to give just a few examples.

Finally, *Animal Sciences* surveys the connection between animals and humans. Humans are unique in the animal kingdom because of their ability to alter environments significantly. Agriculture, which includes the domestication of animals and farming, serves as the chief example of such human-inspired environmental change and its impact on animal life worldwide. In addition, humans are the most social of animals and have developed complex social interactions. As human populations grow, habitat once occupied

by other animals is converted to human use. One consequence of such socialization is the pollution generated from an expanding human population and its deleterious effect on animal environments.

Animal Sciences also presents biographies of selected scientists who have made significant contributions to the many related fields, and introduces readers to the myriad career opportunities in the discipline.

The authors who contributed entries to *Animal Sciences* represent diverse backgrounds, and include members of academic and research institutions, as well as practicing scientists. The editorial board sought informative, up-to-date, and engaging articles, most of which include cross references, photographs or illustrations that prove helpful in understanding challenging concepts. A generous collection of sidebars accent related subjects. Every attempt has been made to avoid overly technical terms or scientific jargon, and whenever necessary such terms are highlighted and defined in the margin. Selected bibliographies guide readers to additional up-to-date resources, including those found on the Internet. Each of the four volumes also includes a geologic time scale, with particular emphasis on animals, as well as a phylogenetic tree and an alternative table of contents that groups articles under more general topic headings.

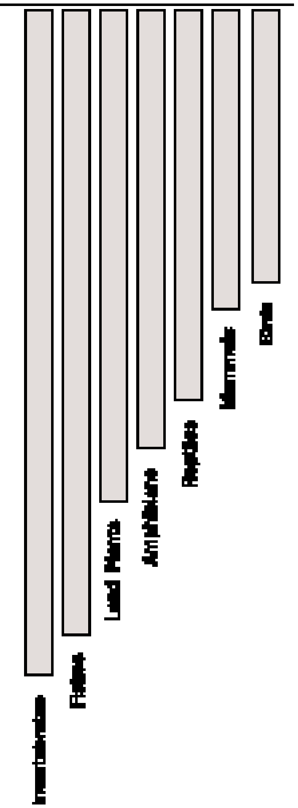
I wish to thank the staff at Macmillan Reference USA and the Gale Group for their hard work and attention to detail. In particular, I would like to thank Hélène Potter, Elly Dickason, Linda Hubbard, and Christa Brelin. I want to offer special thanks to Kate Millson for all her efforts and long hours in helping guide this project to fruition. I wish to thank the editorial board members—Amy Bryan, Andrew Gluesenkamp, and Marvin Elliot Richmond—for their vast knowledge and hard work. Finally, it is my hope that *Animal Sciences* can spark the interest of the next generation of committed scholars, researchers, and laypersons.

Allan B. Cobb
Editor in Chief

Geological Time Scale

Eon	Era	Period	Epoch	Significant Events	Million Years Before Present
Phanerozoic	Cenozoic	Quaternary	Holocene	recorded human history, rise and fall of civilizations, global warming, habitat destruction, pollution mass extinction	0.01
			Pleistocene	Homo sapiens, ice ages	1.6
		Tertiary	Pliocene	global cooling, savannahs, grazing mammals	5.3
			Miocene	global warming, grasslands, Chalicotherium	24
			Oligocene		37
			Eocene	modern mammals flourish, ungulates	58
			Paleocene		66
	Mesozoic	Cretaceous		last of age of dinosaurs, modern mammals appear, flowering plants, insects	144
		Jurassic		large plant-eating dinosaurs, carnivorous dinosaurs, first birds, breakup of Pangea	208
		Triassic		lycophytes, glossopterids, and dicynodonts, and the dinosaurs	245
	Paleozoic	Permian		Permian ends with largest mass extinction in history of Earth, most marine invertebrates extinct	286
		Pennsylvanian		vast coal swamps, evolution of amniote egg allowing exploitation of land	320
		Mississippian		shallow seas cover most of Earth	360
		Devonian		vascular plants, the first tetrapods, wingless insects, arachnids, brachiopods, corals, and ammonite were also common, many new kinds of fish appeared	408
		Silurian		Coral reefs, rapid spread of jawless fish, first freshwater fish, first fish with jaws, first good evidence of life on land, including relatives of spiders and centipedes	438
		Ordovician		most dry land collected into Gondwana, many marine invertebrates, including graptolites, trilobites, brachiopods, and the conodonts (early vertebrates), red and green algae, primitive fish, cephalopods, corals, crinoids, and gastropods, possibly first land plants	505
		Cambrian		most major groups of animals first appear, Cambrian explosion	570
Precambrian	Proterozoic			stable continents first appear, first abundant fossils of living organisms, mostly bacteria and archaebacteria, first eukaryotes, first evidence of oxygen build-up	2500
	Archean			atmosphere of methane, ammonia, rocks and continental plates begin to form, oldest fossils consist of bacteria microfossils stromatolites, colonies of photosynthetic bacteria	3800
	Hadean			pre-geologic time, Earth in formation	4600

Time Range of Several Groups of Plants & Animals



COMPARISON OF THE FIVE-KINGDOM AND SIX-KINGDOM CLASSIFICATION OF ORGANISMS

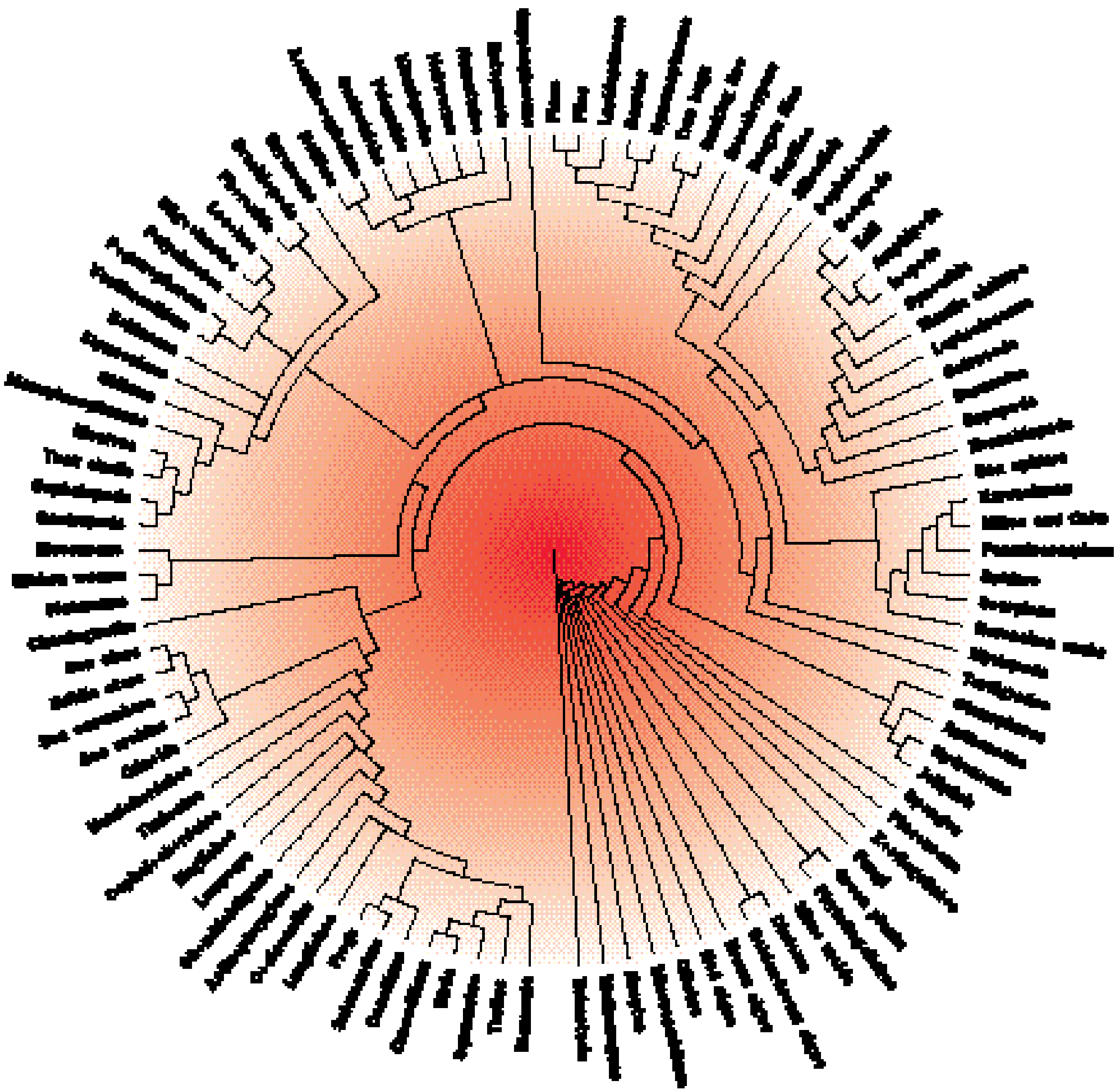
Five Kingdom	Six Kingdom

Kingdom: Monera
    Phylum: Bacteria
    Phylum: Blue-green algae (cyanobacteria)
	Kingdom: Archaebacteria
	Kingdom: Eubacteria

- Kingdom: Protista
  - Phylum: Protozoans
    - Class: Ciliophora
    - Class: Mastigophora
    - Class: Sarcodina
    - Class: Sporozoa
  - Phylum: Euglenas
  - Phylum: Golden algae and diatoms
  - Phylum: Fire or golden brown algae
  - Phylum: Green algae
  - Phylum: Brown algae
  - Phylum: Red algae
  - Phylum: Slime molds
- Kingdom: Fungi
  - Phylum: Zygomycetes
  - Phylum: Ascomycetes
  - Phylum: Basidiomycetes
- Kingdom: Plants
  - Phylum: Mosses and liverworms
  - Phylum: Club mosses
  - Phylum: Horsetails
  - Phylum: Ferns
  - Phylum: Conifers
  - Phylum: Cone-bearing desert plants
  - Phylum: Cycads
  - Phylum: Ginko
  - Phylum: Flowering plants
    - Subphylum: Dicots (two seed leaves)
    - Subphylum: Monocots (single seed leaves)
- Kingdom: Animals
  - Phylum: Porifera
  - Phylum: Cnidaria
  - Phylum: Platyhelminthes
  - Phylum: Nematodes
  - Phylum: Rotifers
  - Phylum: Bryozoa
  - Phylum: Brachiopods
  - Phylum: Phoronida
  - Phylum: Annelids
  - Phylum: Mollusks
    - Class: Chitons
    - Class: Bivalves
    - Class: Scaphopoda
    - Class: Gastropods
    - Class: Cephalopods
  - Phylum: Arthropods
    - Class: Horseshoe crabs
    - Class: Crustaceans
    - Class: Arachnids
    - Class: Insects
    - Class: Millipedes and centipedes
  - Phylum: Echinoderms
  - Phylum: Hemichordata
  - Phylum: Cordates
    - Subphylum: Tunicates
    - Subphylum: Lancelets
    - Subphylum: Vertebrates
      - Class: Agnatha (lampreys)
      - Class: Sharks and rays
      - Class: Bony fishes
      - Class: Amphibians
      - Class: Reptiles
      - Class: Birds
      - Class: Mammals
          - Order: Monotremes
          - Order: Marsupials
        - Subclass: Placentals
          - Order: Insectivores
          - Order: Flying lemurs
          - Order: Bats
          - Order: Primates (including humans)
          - Order: Edentates
          - Order: Pangolins
          - Order: Lagomorphs
          - Order: Rodents
          - Order: Cetaceans
          - Order: Carnivores
          - Order: Seals and walruses
          - Order: Aardvark
          - Order: Elephants
          - Order: Hyraxes
          - Order: Sirenians
          - Order: Odd-toed ungulates
          - Order: Even-toed ungulates

PHYLOGENETIC TREE OF LIFE

This diagram represents the phylogenetic relationship of living organisms, and is sometimes called a "tree of life." Often, these diagrams are drawn as a traditional "tree" with "branches" that represent significant changes in the development of a line of organisms. This phylogenetic tree, however, is arranged in a circle to conserve space. The center of the circle represents the earliest form of life. The fewer the branches between the organism's name and the center of the diagram indicate that it is a "lower" or "simpler" organism. Likewise, an organism with more branches between its name and the center of the diagram indicates a "higher" or "more complex" organism. All of the organism names are written on the outside of the circle to reinforce the idea that all organisms are highly evolved forms of life.



SI BASE AND SUPPLEMENTARY UNIT NAMES AND SYMBOLS

Physical Quality	Name	Symbol
Length	meter	m
Mass	kilogram	kg
Time	second	s
Electric current	ampere	A
Thermodynamic temperature	kelvin	K
Amount of substance	mole	mol
Luminous intensity	candela	cd
Plane angle	radian	rad
Solid angle	steradian	sr

Temperature

Scientists commonly use the Celsius system. Although not recommended for scientific and technical use, earth scientists also use the familiar Fahrenheit temperature scale (ºF). 1ºF = 1.8ºC or K. The triple point of H_2O, where gas, liquid, and solid water coexist, is 32ºF.

- To change from Fahrenheit (F) to Celsius (C):
  ºC = (ºF-32)/(1.8)
- To change from Celsius (C) to Fahrenheit (F):
  ºF = (ºC x 1.8) + 32
- To change from Celsius (C) to Kelvin (K):
  K = ºC + 273.15
- To change from Fahrenheit (F) to Kelvin (K):
  K = (ºF-32)/(1.8) + 273.15

UNITS DERIVED FROM SI, WITH SPECIAL NAMES AND SYMBOLS

Derived Quantity	Name of SI Unit	Symbol for SI Unit	Expression in Terms of SI Base Units
Frequency	hertz	Hz	s-1
Force	newton	N	m kg s-2
Pressure, stress	Pascal	Pa	N m-2 =m-1 kg s-2
Energy, work, heat	Joule	J	N m =m2 kg s-2
Power, radiant flux	watt	W	J s-1 =m2 kg s-3
Electric charge	coulomb	C	A s
Electric potential, electromotive force	volt	V	J C-1 =m-2 kg s-3 A-1
Electric resistance	ohm	_	V A-1 =m2 kg s-3 A-2
Celsius temperature	degree Celsius	C	K
Luminous flux	lumen	lm	cd sr
Illuminance	lux	lx	cd sr m-2

UNITS USED WITH SI, WITH NAME, SYMBOL, AND VALUES IN SI UNITS

The following units, not part of the SI, will continue to be used in appropriate contexts (e.g., angtsrom):

Physical Quantity	Name of Unit	Symbol for Unit	Value in SI Units
Time	minute	min	60 s
	hour	h	3,600 s
	day	d	86,400 s
Plane angle	degree	˚	(π/180) rad
	minute	'	(π/10,800) rad
	second	"	(π/648,000) rad
Length	angstrom	Å	10^{-10} m
Volume	liter	l, L	1 dm^3 = 10^{-3} m^3
Mass	ton	t	1 mg = 10^3 kg
	unified atomic mass unit	u (=$m_a(^{12}C)/12$)	≈1.66054 x 10^{-27} kg
Pressure	bar	bar	10^5 Pa = 10^5 N m^{-2}
Energy	electronvolt	eV (= e X V)	≈1.60218 x 10^{-19} J

CONVERSIONS FOR STANDARD, DERIVED, AND CUSTOMARY MEASUREMENTS

Length

1 angstrom (Å)	0.1 nanometer (exactly) 0.000000004 inch
1 centimeter (cm)	0.3937 inches
1 foot (ft)	0.3048 meter (exactly)
1 inch (in)	2.54 centimeters (exactly)
1 kilometer (km)	0.621 mile
1 meter (m)	39.37 inches 1.094 yards
1 mile (mi)	5,280 feet (exactly) 1.609 kilometers
1 astronomical unit (AU)	1.495979×10^{13} cm
1 parsec (pc)	206,264.806 AU 3.085678×10^{18} cm 3.261633 light-years
1 light-year	9.460530×10^{17} cm

Area

1 acre	43,560 square feet (exactly) 0.405 hectare
1 hectare	2.471 acres
1 square centimeter (cm^2)	0.155 square inch
1 square foot (ft^2)	929.030 square centimeters
1 square inch (in^2)	6.4516 square centimeters (exactly)
1 square kilometer (km^2)	247.104 acres 0.386 square mile
1 square meter (m^2)	1.196 square yards 10.764 square feet
1 square mile (mi^2)	258.999 hectares

MEASUREMENTS AND ABBREVIATIONS

Volume

1 barrel (bbl)*, liquid	31 to 42 gallons
1 cubic centimeter (cm^3)	0.061 cubic inch
1 cubic foot (ft^3)	7.481 gallons 28.316 cubic decimeters
1 cubic inch (in^3)	0.554 fluid ounce
1 dram, fluid (or liquid)	⅛ fluid ounce (exactly) 0.226 cubic inch 3.697 milliliters
1 gallon (gal) (U.S.)	231 cubic inches (exactly) 3.785 liters 128 U.S. fluid ounces (exactly)
1 gallon (gal) (British Imperial)	277.42 cubic inches 1.201 U.S. gallons 4.546 liters
1 liter	1 cubic decimeter (exactly) 1.057 liquid quarts 0.908 dry quart 61.025 cubic inches
1 ounce, fluid (or liquid)	1.805 cubic inches 29.573 milliliters
1 ounce, fluid (fl oz) (British)	0.961 U.S. fluid ounce 1.734 cubic inches 28.412 milliliters
1 quart (qt), dry (U.S.)	67.201 cubic inches 1.101 liters
1 quart (qt), liquid (U.S.)	57.75 cubic inches (exactly) 0.946 liter

* There are a variety of "barrels" established by law or usage. For example, U.S. federal taxes on fermented liquors are based on a barrel of 31 gallons (141 liters); many state laws fix the "barrel for liquids" as 31½ gallons (119.2 liters); one state fixes a 36-gallon (160.5 liters) barrel for cistern measurement; federal law recognizes a 40-gallon (178 liters) barrel for "proof spirits"; by custom, 42 gallons (159 liters) comprise a barrel of crude oil or petroleum products for statistical purposes, and this equivalent is recognized "for liquids" by four states.

Units of mass

1 carat (ct)	200 milligrams (exactly) 3.086 grains
1 grain	64.79891 milligrams (exactly)
1 gram (g)	15.432 grains 0.035 ounce
1 kilogram (kg)	2.205 pounds
1 microgram (μg)	0.000001 gram (exactly)
1 milligram (mg)	0.015 grain
1 ounce (oz)	437.5 grains (exactly) 28.350 grams
1 pound (lb)	7,000 grains (exactly) 453.59237 grams (exactly)
1 ton, gross or long	2,240 pounds (exactly) 1.12 net tons (exactly) 1.016 metric tons
1 ton, metric (t)	2,204.623 pounds 0.984 gross ton 1.102 net tons
1 ton, net or short	2,000 pounds (exactly) 0.893 gross ton 0.907 metric ton

Pressure

1 kilogram/square centimeter (kg/cm^2)	0.96784 atmosphere (atm) 14.2233 pounds/square inch (lb/in^2) 0.98067 bar
1 bar	0.98692 atmosphere (atm) 1.02 kilograms/square centimeter (kg/cm^2)

Contributors

Allan B. Cobb
Austin, Texas
Jes Marie Creech
University of Texas, Austin
Emily H. DuVal
University of California, Berkeley
Andrew G. Gluesenkamp
University of Texas, Austin
Ann Guidry
Austin, Texas
Brook Ellen Hall
California State University, Sacramento
Laura A. Higgins
University of Texas, Austin
Ryan I. Hill
University of Texas, Austin
Alisha K. Holloway
University of Texas, Austin
Leslie Hutchinson
Flagstaff, Arizona
Jean Krejca
University of Texas, Austin
Stephanie A. Lanoue
Panama City Beach, Florida
Denise Prendergast
Austin, Texas
Ian Quigley
University of Texas, Austin
Elliot Richmond
Austin Community College
Karen Rogowski
University of Texas, Austin
Gil G. Rosenthal
University of California, San Diego
Todd A. Schlenke
University of Texas, Austin
Danielle Schnur
Austin, Texas
Judy P. Sheen
University of California, Berkeley
Kathrin F. Stanger-Hall
University of Texas, Austin
Rebecca M. Steinberg
University of Texas, Austin
Nancy Weaver
Driftwood, Texas
Brian R. West
University of Texas, Austin
Jennifer Yeh
University of Texas, Austin

Table of Contents

VOLUME 1:

VOLUME TWO:

D

E

F

G

Permian

P

The Permian period, 280 to 230 million years ago, was named for the Perm Province of the Ural Mountains in Russia. The Permian signaled the end of the "ancient life" Paleozoic era.

In the Permian, the close ties between geology and evolution were especially apparent. The two great land masses of the Paleozoic drifted close enough together to form one supercontinent, Pangaea. Collisions in the tectonic plates created extensive volcanic activity and heaved up the Urals, Alps, Appalachians, and Rocky Mountains. The shallow inland seas drained to leave deposits of gypsum and salt. Vast sand dunes throughout much of what is now North America and Europe were recorded by massive yellow sandstones (hardened sand dunes) that contained few fossils other than scorpions.

Great glaciers scoured the southern regions of Africa, India, and Australia, further inhibiting life. **Conifers** and a few cold-hardy plants grew along the fringes of the immense ice cap.

The long stable **climate** of the Carboniferous gave way to dryness, with severe fluctuations of heat and cold. Only in the tropics of Pangaea did anything remain of the great Carboniferous rain forests, and there insects and amphibians continued to evolve.

Insects, members of the **arthropod** or "jointed leg" animals whose ancestors were the first to explore both land and air, continued to flourish in every new ecological opportunity. Several new groups appeared—the bugs, cicadas, and beetles. Thanks possibly to their diminutive size and adaptable **metamorphosis,** in which young live and feed in a totally different

coniferous having pine trees and other conifers

climate long-term weather patterns for a particular region

arthropod a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

metamorphosis a drastic change from a larva to an adult

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

The permian period and surrounding time periods.

An amphibian fossil from the Permian era on display at the Field Museum in Chicago, Illinois.

environment from adults, the arthropods became the most evolutionarily successful animals on Earth. Amphibians fared less well, mostly just hanging on in those areas still hospitable to their warm, moist requirements.

ammonites an extinct group of cephalopods with a curled shell

brachiopods a phylum of marine bivalve mollusks

trilobites an extinct class of arthropods

herbivores animals who eat plants only

insectivores animals who eats insects

Many marine species thrived in the shallow seas. Thousands of types of sponges, corals, **ammonites**, bryozoans, **brachiopods**, and snails left their remains in the rocks that now make up the mountains of west Texas and southern New Mexico. Bony fishes remained plentiful. However, spiny fishes, the fleshy-finned rhipidistians (organisms who originally gave rise to amphibians), and the once-dominant **trilobites** disappeared.

Reptiles flourished in the semidesert regions that made up much of Pangaea. Their leathery-skinned, cold-blooded bodies were ideal for the hotter, drier climate. Reptile adaptations led to **herbivores** and **insectivores** who could exploit new food resources. As their legs continued to become stronger and more upright, the reptiles increased in body size and mobility. *Coelorosauravus* joined the flying insects, gliding from tree to tree by means of a sail-like membrane. And *Mesosaurus*, a 1 meter (3 feet) long fish eater, returned to living underwater. Virtually the whole of Pangaea was dominated by the reptiles.

habitats physical locations where an organism lives in an ecosystem

genes segments of DNA located on chromosomes that direct protein production

However, all this exuberance ended. The close of the Permian was marked by the worst extinction ever recorded. More than 75 percent of all plant and animal groups disappeared forever from the land, and in the ocean only about 5 percent of existing species survived. As devastating as these losses were, evolution and extinction are a recurring theme: the emptying of **habitats**, the reshuffling of **genes**, and a new start. Survival of the fittest might really be said to be survival of the luckiest. SEE ALSO Geological Time Scale.

Nancy Weaver

Bibliography

Asimov, Isaac. *Life and Time.* Garden City, NY: Doubleday & Company, 1978.

Fortey, Richard. *Fossils: The Key to the Past.* Cambridge, MA: Harvard University Press, 1991.

———. *Life: A Natural History of the First Four Billion Years of Life on Earth.* New York: Viking Press, 1998.

Friday, Adrian, and David S. Ingram, eds. *The Cambridge Encyclopedia of Life Sciences.* London: Cambridge University, 1985.

Gould, Stephen Jay, ed. *The Book of Life.* New York: W. W. Norton & Company, 1993.

McLoughlan, John C. *Synapsida: A New Look Into the Origin of Mammals.* New York: Viking Press, 1980.

Steele, Rodney, and Anthony Harvey, eds. *The Encyclopedia of Prehistoric Life.* New York: McGraw Hill, 1979.

Wade, Nicholas, ed. *The Science Times Book of Fossils and Evolution.* New York: The Lyons Press, 1998.

Pesticide

Pesticides are natural or human-made substances used to kill pest species such as rodents and insects. It is not surprising that many of these substances are highly toxic not only to the pests, but to other biological organisms as well. Pesticides are used in forests, agricultural regions, parks, residential areas, and within the home.

The bulk of **pesticide** use is related to agricultural pest control. In fact, pesticide application increased dramatically when intensive agricultural methods began to be used near the start of the twentieth century. Although pesticides clearly help to increase agricultural production, they also harm humans and other animal species. In addition, they contaminate the environment, often persisting in water, air, and soil for long periods of time. The World Health Organization reports over one million human pesticide poisonings every year, including twenty thousand that result in death.

pesticide any substance that controls the spread of harmful or destructive organisms

These numbers do not include the slower and more subtle effects that exposure to pesticides can have on human health. Many pesticides, for example, are carcinogenic, or cancer-causing. Finally, because pest species always evolve resistance to pesticides over time, ever-increasing amounts or different types of pesticides are constantly required to maintain the same effect.

Some pesticides are inorganic, containing naturally toxic compounds such as lead, arsenic, or mercury. Because these chemicals cannot be broken down, they accumulate in the environment. Natural pesticides include substances produced by plants such as tobacco and certain conifer trees. These are used by the plant species that produce them to ward off herbivores. The majority of pesticides, however, are human-made organic chemicals that function by affecting some essential **physiological** function of pest species.

physiological describes the basic activities that occur in the cells and tissues of an animal

One of the best-known pesticides is dichloro-diphenyl-trichloroethane, commonly known as DDT. When DDT was first invented in 1939, by Swiss chemist Paul Muller, it was hailed as a major breakthrough in pesticide

Pesticides are sprayed over farmland in Florida.

development. In fact, Muller received a Nobel Prize for the achievement. DDT found its first use in World War II, when it was sprayed in malarial areas to kill disease-carrying insects to safeguard U.S. troops.

After the war, DDT was widely used in the United States for agricultural control, and like many pesticides seemed highly effective at first. DDT was praised particularly for being highly toxic to insects while comparatively harmless for other species. DDT also had the advantages of being inexpensive to produce and easy to spray. By the 1950s, however, there was evidence that insect pests were evolving resistance to DDT. There were also hints that DDT might not be so harmless after all.

Rachel Carson's monumental book, *Silent Spring* (1962), was critical in bringing public attention to the serious side effects of DDT use for all living species. The title of the book refers to the absence of birdsong, a result of countless massive bird deaths throughout the country that Carson traced to DDT spraying. Studies of the impact of DDT have shown that the chemical breaks down very slowly, often lingering in the environment for decades after application. DDT is taken up by organisms through diet, and then accumulates in the fatty tissues. This effect is magnified higher up the food chain because any time a predator eats a prey item, the predator takes in all the DDT stored in the tissues of that prey, and then stores it in its own body.

bio-accumulation the build up of toxic chemicals in an organism

endocrine systems groupings of organs or glands that secrete hormones into the bloodstream

This process is called **bio-accumulation**. Bio-accumulation explains why birds high in the food chain, such as eagles, owls, and other birds of prey, are particularly vulnerable to DDT poisoning. DDT affects the **endocrine systems** of birds, throwing off the hormonal control of reproduction. Therefore, large amounts of bio-accumulated DDT cause the delay or cessation of egg laying. When eggs are produced, they are characterized by extremely thin eggshells that break easily during incubation. Although birds appear to be particularly vulnerable to DDT, numerous other species are affected as well.

Carson also showed that there were causal links between pesticides, genetic **mutations**, and diseases such as cancer. Concerns regarding the tremendous health risks posed by DDT contributed to its being banned in the United States in 1972. Since then, many once-threatened species are now returning. *Silent Spring* is often credited not only with the ban of DDT, but with initiating awareness that toxic substances can be extremely harmful not only to the environment but to all the species that live within it, including humans. *Silent Spring* was crucial to the beginnings of environmentalism, as well as to the creation of the Environmental Protection Agency (EPA) in 1970.

mutations abrupt changes in the genes of an organism

Numerous pesticides are still in use now, including many that are even more toxic than DDT. Some of these break down more easily, however, and therefore do not remain in the environment for as long a period. Nonetheless, as awareness of some of the damaging cumulative effects of pesticides has increased, the popularity of and demand for organic foods has also increased.

In addition to toxicity, another problem with pesticide application is that pests inevitably evolve resistance. Pesticide resistance is a striking example of how efficiently **natural selection** can operate. In many cases, **alleles** that offer resistance to particular pesticides already exist in the **population** at very low frequencies. The application of pesticides selects strongly for these resistant alleles and causes them to spread quickly throughout the population. A classic example of the evolution of pesticide resistance is that of rats and warfarin. Warfarin is a pesticide that interferes with vitamin K and prevents blood coagulation, resulting in internal bleeding and death. Resistance to warfarin is conferred by a single gene, which spreads quickly through the rat population upon large-scale application of warfarin.

natural selection the process by which organisms best suited to their environment are most likely to survive and reproduce

alleles two or more alternate forms of a gene

population a group of individuals of one species that live in the same geographic area

Because of the many harmful side effects of pesticide use, scientists have worked to develop alternative means for pest control. These include mechanical strategies such as screens or traps, the development of pest-resistant plants, crop cycling, and **biological control**, which aims to control pest populations by releasing large numbers of predators or parasites of a pest. In general, thorough information on the natural history of pest species, such as its life cycle requirements and natural enemies, helps to provide insight into the sort of strategies that may be effective in controlling it. SEE ALSO CARSON, RACHEL; DDT; SILENT SPRING.

biological control the introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

Jennifer Yeh

Bibliography

Carson, Rachel. *Silent Spring.* Boston: Houghton Mifflin, 1962.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

Internet Resources

Office of Pesticide Programs. United States Environment Protection Agency. <http://www.epa.gov/pesticides/>.

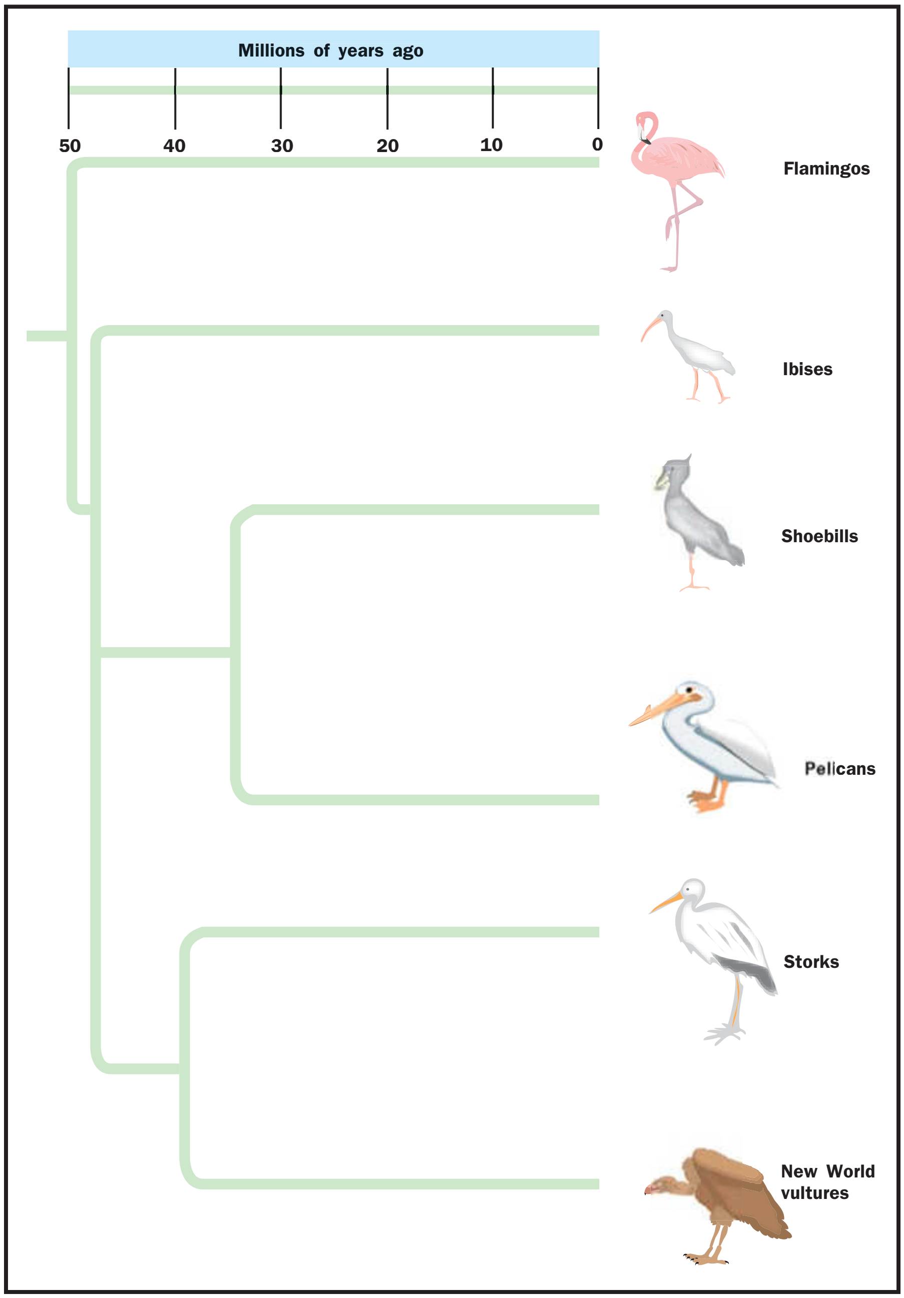
Phylogenetic Relationships of Major Groups

phylogeny the evolutionary history of a species or group of related species

systematic study of the diversity of life

The evolutionary history of a species or group of related species is called its **phylogeny**. When the evolutionary history is diagrammed, it is shown in the shape of a tree that traces evolutionary relationships as they have changed over time. The reconstruction of phylogenetic history is part of the field of **systematics**. The diversity of the phylogenetic tree is a reflection of speciation.

A phylogenetic tree shows not only how closely related two groups are but also how once-related species evolved independently. The further back in time a group branched represents a greater amount of time for divergent evolution to occur. When systematists construct a phylogenetic tree, they



Study of the DNA sequences of these birds explains their evolutionary relationships.

consider as much data as possible. Whenever possible, they take the **fossil record** into account to identify when branching occurred. Scientists can compare ribosomal RNA or **mitochondrial DNA** of different organisms to pinpoint branches in the evolutionary history. After all the available data are compiled, the relationship can be drawn as a phylogenetic tree. Scientists often revise phylogenetic trees as new techniques or new data further clarify evolutionary relationships.

fossil record a collection of all known fossils

mitochondrial DNA DNA found within the mitochondria that control protein development in the mitochondria

A phylogenetic tree can be used to show the evolutionary relationships of different groups. The figure (opposite) shows a simple phylogenetic tree of selected bird families. The first branch of the tree, which branched off about fifty million years ago, leads to the modern flamingo family on one branch and the other families off the other branch. The shoebill and the pelican families branched off about forty-five million years ago. It is important to realize that even though flamingos branched off much earlier than pelicans, each family has been influenced by evolutionary change. As environmental pressures such as climate change took place, each family adapted to the changes. This phylogenetic tree does not show any branches that became extinct.

Using a phylogenetic tree to find how closely related animals are is a relatively simple task. The closer together two **phyla** are on the tree, the more closely related the phyla. On the phylogenetic tree within the front-matter of this book, only the phyla are shown. Each phyla can be further divided into classes, orders, families, genera, and species. Also note that phyla that branch very close to the edge of the circle are closely related, while those that branch closer to the center of the tree are more distantly related. For example, frogs and **salamanders** are very closely related because they branch close to the outer edge of the circle. Eubacteria and methanogens are close together, but they branch close to the center of the tree. This means that they are distantly related.

phyla the broad, principal divisions of a kingdom

salamander a four-legged amphibian with an elongated body

Allan B. Cobb

Bibliography

Barnes-Svarney, ed. *The New York Public Library Science Desk Reference.* New York: Macmillan, 1995.

Rupert, Edward R., and Robert D. Barns. *Invertebrate Zoology.* New York: Oxford University Press, 1994.

Phylogenetics Systematics

This is a field of study that allows biologists to reconstruct a pattern of evolutionary events resulting in the distribution and diversity of present-day life. Achieving this goal requires classifying organisms into groups in a meaningful and universal manner. This classification is based on evolutionary events that occurred long before human civilization appeared on Earth. **Taxonomy** is the system used to name organisms based on their evolutionary relationships. A **taxon** is a hierarchical category used in the naming process, and taxa is the plural form of the word. The main taxa, in order of broadest to most specific designation, are: kingdom, phylum, class, order, family, genus, and species. For example, a domestic cat's kingdom is Animalia because it is an animal, its class is Mammalia because it is a mammal, and its genus and species are *Felis domesticus*. Phylogenetics refers to the study of

taxonomy the science of classifying living organisms an organism's evolutionary history: when it first appeared on Earth, what it evolved from, where it lived, and when and why it went extinct (or survived). Systematics, then, refers to naming and organizing these biological taxa into meaningful relationships. For example, if two species of deer that are alive today are both thought to have evolved from a different species that subsequently went extinct, the taxonomic nomenclature (scientific name) of the deer should reflect that relationship.

Cladistics is an important tool for forming hypotheses about the relationships among organisms. Cladistics is a mechanism for providing a testable phylogenetic tree, a diagram representing the relationships of different organisms as a tree, with the oldest ancestors at the trunk of the tree and later descendants at the branch ends. The underlying assumption of cladistic analysis is that members of a single group are more closely related to each other than to members of a different group. When several organisms share a suite of features, they are grouped together because these shared features are likely to have belonged to a common ancestor of all the group members. When common features are thought to have this sort of evolutionary relevance, they are called "synapomorphies."

Conversely, those features that distinguish each member within a group from each other are called "apomorphies". These are derived characters, meaning that they evolved anew in the descendant and did not belong to the ancestor. As an example, both owls and sparrows have feathers and a beak because they share the synapomorphies of being birdlike; however, owls have very large eyes at the front of their head whereas sparrows have small eyes on either side of their head, and these are apomorphies. Cladistic analysis sums up the number of apomorphies and synapomorphies among different organisms and produces possible phylogenetic trees that minimize the apomorphies in particular groups. This is one method by which evolutionary relationships are estimated.

morphological related to the structure and form of an organism at any stage in its life history

The information that is used in cladistic analysis can be **morphological** or molecular. Morphological measurements are taken from fossils or from living animals. In fossil evidence, imprints of an organism or the fossilized organism itself provide evidence for the size and connectivity of hard body parts. Extant, or living, organisms make it possible also to measure the organism's soft parts, those that are unlikely to be fossilized. This is the most common type of cladistic study. Molecular evidence comes from comparing the genetic codes of extant species. Because DNA is thought to evolve at a constant rate, the **molecular clock** can be set at a particular, confidently estimated evolutionary event such as the divergence of **placental** from marsupial mammals. Then the amount of time since the divergence of two groups of organisms can be estimated based on the number of differences between their genetic codes. SEE ALSO Phylogenetic Relationships of Major Groups.

molecular clock using the rate of mutation in DNA to determine when two genetic groups spilt off

placental having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

Rebecca M. Steinberg

Bibliography

Lincoln, Roger J., Geoffrey Allan Boxshall, and Paul F. Clark. *A Dictionary of Ecology, Evolution and Systematics.* Cambridge, U.K., and New York: Cambridge University Press, 1998.

Winston, Judith E. *Describing Species.* New York: Columbia University Press, 1999.

Physiologist

Physiologists study the functions and activities of organisms—the way plants and animals are designed as well as how they interact with their environment. This includes functions and activities at the cellular and molecular level, both under normal and abnormal conditions. Physiologists may choose to specialize in any of the life processes, including growth, reproduction, aging, and metabolism, or the circulatory, nervous, or immune systems.

Notable physiologists include scientists such as American Dr. Matilda Brooks, who developed antidotes for cyanide and carbon monoxide poisoning. The Scottish physiologist Sir Charles Bell (1774–1842) described the central nervous system in human beings. A British physiologist, Edgar Adrian, shared a Nobel prize in 1932 for his work in determining the electrical nature of nerves and muscles, and later went on to codevelop the electroencephalograph which measures brain activity.

All physiologists require a background in physics and computer science with an emphasis on biological sciences such as microbiology, **ecology**, evolution, **genetics**, and **behavioral** biology. Physiologists work in either applied or basic research. Physiologists with a masters degree generally do applied research at companies interested in developing specific solutions to health problems or restoring the environment. They should be familiar with high-tech laboratory equipment such as electron microscopes, thermal cyclers, and nuclear magnetic resonance machines. They must also be able to communicate well with nonscientists.

ecology the study of how organisms interact with their environment

genetics the branch of biology that studies heredity

behavioral relating to actions or a series of actions as a response to stimuli

Physiologists who pursue a Ph.D. spend additional time in laboratory research and in writing a dissertation. Frequently they go on for several years of post-doctorate work in their area of interest. Physiologists who specialize in basic research tend to work at universities, where they are funded by scientific grant money. Usually their work consists of doing original research, overseeing graduate students, and teaching. Unlike applied researchers, basic researchers are free to pursue knowledge for its own sake without the constraints of producing a practical product. This can lead to exciting discoveries, as they follow their curiosity into the mysteries of the world within and without.

Nancy Weaver

Bibliography

Occupational Outlook Handbook. Washington, D.C.: U.S. Dept. of Labor/Bureau of Labor Statistics, 2000.

Physiology

Physiology is the study of how living things function. It encompasses the most basic unit of living things, the cell, and the most complex organs and organ systems, such as the brain or endocrine system.

The word "physiology" was first used by the Greeks around 600 B.C.E. to describe a philosophical inquiry into the nature of things in general. Around the sixteenth century, the word began to be used with specific reference to the vital activities of healthy humans. By the nineteenth century, curiosity and medical necessity stimulated research concerning the physiology of all living things. Discoveries of similar structures and functions common to living things resulted in the development of the concept of general physiology. Since the mid-nineteenth century, physiology has used experimental methods, as well as techniques and concepts of the physical sciences, to investigate the causes and mechanisms of the activities of living things. Today there are many specialized areas of study within the field of physiology including cellular, vertebrate, and invertebrate physiology, as well as medical specialties such as endocrinology.

Scientists who study physiology are called physiologists. They investigate how different parts or organs of a living thing work together to perform a particular function. In humans, for example, the circulation of blood in the body involves the action of the heart and other structures such as veins, arteries, and capillaries. Special nerve centers known as nodes trigger the ventricles of the heart to contract in a predictable rhythm, which causes the blood to flow in and out of the heart. By learning how organs such as the heart function normally, physiologists (and physicians) can better understand what happens when organs function abnormally and learn how to treat them. In their studies, physiologists pay close attention to structure, information transfer, metabolism, regulation, and transport.

Structure

The structures of living things are often related to their function. For example, the shape and structure of a bird's beak is related to how it uses the beak. Eagles have a large, sharp beak for ripping and tearing prey. Hummingbirds have long, slender beaks for sipping nectar from flowers. Physiologists often study and compare animal structures such as appendages (projecting structures or parts of an animal's body that are used in movement or for grasping objects) to determine similarities, differences, and evolutionary etiology (origin) among species.

Information Transfer

vertebrates animals with a backbone

neurons nerve cells

spinal cord a thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

Animals react quickly to external stimuli such as temperature change, touch, light, and vibration. Information from an organism's external environment is rapidly transferred to its internal environment. In **vertebrates**, nerve impulses initiated in sensory **neurons**, or nerve cells, are transferred to the center of the brain or **spinal cord**. Sensory neurons are nerve cells that transmit impulses from a receptor such as those in the eye or ear to a more central location in the nervous system. From the brain or spinal cord, impulses initiated in motor neurons (nerve cells that transmit impulses from a central area of the nervous system to an effector such as a muscle) are transferred to muscles and induce a reflex response. The brain and spinal cord receive incoming messages and initiate, or trigger, the motor neurons so that animals, including humans, can move.

> The reflex response is an automatic reaction, such as your knee jerking when the tendon below the knee cap is tapped; the impulse provoked by the tap, after travelling to the spinal cord, travels directly back to the leg muscle.

Metabolism

Metabolism is the processing of matter and energy within the cells, tissues, and organs of living organisms. There are four major questions to be answered in the study of metabolism: How do matter and energy move into the cells? How are substances and forms of energy transformed within the cell? What function does each transformation serve? What controls and coordinates all the processes?

All animals require the atoms and molecules from food to build their bodies. Animals also require the energy released when chemical bonds are broken and new bonds are formed. This energy is required to do work and to maintain body temperature. Plants manufacture their own food by harvesting the energy of sunlight and storing the energy in the chemical bonds of carbohydrates, fats, and proteins. Animals cannot make their own food, so they obtain the energy of sunlight indirectly by eating plants or other animals.

The bodies of animals are composed of many different chemical compounds, including specialized proteins found in muscle tissue and in red blood cells. These proteins are not present in the food animals eat, so metabolism is the process of disassembling the proteins found in plant tissue into amino acids, then reassembling those amino acids in to the proteins that animals need.

Animals must use energy to assemble new molecules. Animals also require energy to pump blood, contract muscles, and maintain body temperature. This energy comes from the carbohydrates, **lipids**, and proteins animals eat. A complex series of reactions called the Kreb's cycle is the primary mechanism for the controlled release of energy from these molecules.

lipids fats and oils; organic compounds that are insoluble in water

Regulation

Animals maintain their internal environments at a constant level. This process, called **homeostasis**, depends on the action of **hormones**. In humans, metabolic functions and hormone interactions expend energy and help to maintain a constant body temperature of 37°C (98.6°F). Comparative studies of neurosecretory cells, special nerve cells capable of secreting hormones, indicate that the cells are also important in the developmental and regulatory functions of most animals. In insects and **crustaceans**, hormones control the cycles of growth, **molting**, and development. By identifying the hormones that regulate these cycles in insects, scientists may be able to control insect pests by interfering with hormone production and thus, with the insect's processes of growth and development.

homeostasis a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

molting the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

Transport

Most animals have a transport or circulatory system that involves the movement of oxygen and carbon dioxide through blood. In vertebrates and a few invertebrates, notably **annelids** and cephalopod **mollusks**, blood flows entirely in closed channels or vessels. In most other invertebrates, blood flows for part of its course in large sinuses (cavities or opening), or lacunae, and comes directly into contact with tissues. SEE ALSO BIOMECHANICS.

Stephanie A. Lanoue

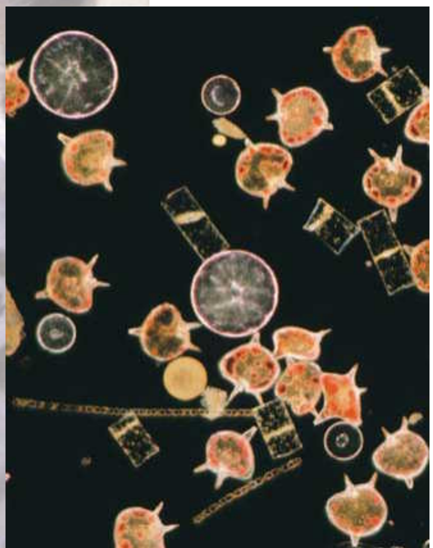
annelids segmented worms

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

Bibliography

Alexander, R. McNeil. *Animal Mechanics.* Seattle, WA: University of Washington Press, 1998.

Plankton



Marine plankton.

Plankton (from the Greek word *planktos*, which means "wandering") are communities of mostly microscopic organisms that inhabit watery environments, from oceans to muddy regions. Some plankton drift passively or swim weakly near the surfaces of oceans, ponds, and lakes, while others exist as bottom-dwellers, attaching to rocks or creeping on the ground through sand and silt.

Plankton are classified under the kingdom Protista. During the genesis of protists, a true nucleus, as well as the other components of **eukaryotic cells** (mitochondria, chloroplasts, endoplasmic reticulum, Golgi bodies, 9+2 **flagella** and **cilia**, the functions **mitosis** and **meiosis**) arose. Thus these organisms are considered to be ancestral to plants, fungi and animals. While the majority of plankton are unicellular and therefore considered to be simple eukaryotic organisms, at the cellular level they are extremely complex. Plankton should be considered an organism in itself and not be compared to a single cell from a multicellular organism.

Despite their small size, plankton are the very basis for life in the earth's various **ecosystems**. An ecosystem is comprised of all the organisms living in a community and all **abiotic factors** with which the organisms interact.

The two main processes within an ecosystem are energy flow and chemical cycling. Energy enters most systems in the form of sunlight and is converted to chemical energy by **autotrophs**. The chemical energy is then passed to **heterotrophs** in organic compounds of food, and finally dissipates into the system as heat. **Trophic levels** are based on an organism's main source of nutrition. Autotrophs, also called primary producers, are generally photosynthetic organisms that use light energy to synthesize sugars and other organic compounds. Heterotrophs, or consumers, are supported by these photosynthetic organisms. The primary consumers are herbivores, who gain sustenance directly from autotrophs. Secondary consumers feed on the herbivores and tertiary consumers feed on the secondary ones. Those organisms that feed off of dead organisms are known as detritovores. An understanding of this pyramid within an ecosystem explains why the extent of photosynthetic activity determines the energy supply of the entire ecosystem.

Algae, as freshwater and marine phytoplankton and intertidal seaweeds, are responsible for nearly half of all photosynthetic production of organic material, rendering them extremely significant in the aquatic food webs where they support countless suspension-feeding and predatory animals. All algae, except prokaryotic cyanobacteria (formerly called blue-green algae), belong to the kingdom Protista. Algae all contain chlorophyll A, a primary pigment in cyanobacteria and plants, but differ in accessory pigments, which trap **wavelengths** of light to which chlorophyll A is not as sensitive. These accessory pigments include other chlorophylls (green), carotenoids (yellow-orange), xanthophylls (brown), and phycobilins (red and blue).

These differences in pigments point to different roles and effects of algae on the ecosystem. An overabundance of dinoflagellates (algae containing phycobilins) results in the blooming of red tides. When shellfish such as oysters feed on the dinoflagellates, they concentrate the algae along with

eukaryotic cells contain a membrane-bound nucleus and membrane-bound organelles

flagella cellular tails that allow the cell to move

cilia hair-like projections used for moving

mitosis a type of cell division that results in two identical daughter cells from a single parent cell

meiosis a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

ecosystems self-sustaining collections of organisms and their environments

abiotic factors pertaining to nonliving environmental factors such as temperature, water, and nutrients

autotrophs organisms that make their own food

heterotrophs organisms that do not make their own food

toxic compounds released by the dinoflagellate cells. Because these toxins are dangerous to humans, collection of shellfish is restricted during red tides to reduce the risk of paralytic shellfish poisoning. Seaweed is the large marine algae that inhabits intertidal and subtidal zones of coastal waters. Coastal people, especially in Asia, harvest seaweed for food since it is high in iodine and other essential minerals. The brown alga laminaria is used in soups and the red alga porphyra is used to wrap sushi.

trophic levels divisions of species in an ecosystem by their main sources of nutrition

wavelengths distance between the peaks or crests of waves

With so much dependent on the existence of plankton, the fight against water pollution aims to prevent not only the destruction of plankton, but of other species as well. SEE ALSO Food Web; Zooplankton.

Danielle Schnur

Bibliography

Campbell, Neil A. *Biology*, 3rd ed. Berkeley, CA: Benjamin/Cummings Publishing Company, Inc, 1993.

Odum, Howard T. *Systems Ecology: An Introduction*. New York: Wiley, 1984.

Plate Tectonics *See Continental Drift.*

Platyhelminthes

bilateral symmetry characteristic of an animal that can be separated into two identical mirror image halves

mesoderm the middle layer of cells in embryonic cells

ventral the belly surface of an animal with bilateral symmetry

diffusion the movement of molecules from a region of higher concentration to a region of lower concentrations

fission dividing into two parts

terrestrial living on land

scavengers animals that feed on the remains of animals that they did not kill

endoparasites organisms that live inside other organisms and derive their nutrients directly from those organisms

ectoparasites organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

Animals in the phylum Platyhelminthes are called flatworms because they are flattened from head to tail. Flatworms share several features with more derived animal phyla. They are the most primitive group to exhibit **bilateral symmetry**. Flatworms have three embryonic tissue layers: ectoderm, **mesoderm**, and endoderm.

Animals within Platyhelminthes show more complexity than ancestral phyla, but are not as complex as more derived animal phyla. They are acoelomates, which means they do not have a body cavity. Platyhelminthes are unsegmented. They have muscles and a simple nervous system that includes a primitive brainlike structure which is formed from a thickening of the **ventral** nerve cords in the head region. They have a mouth, but no anus, and a primitive digestive cavity. They also have a primitive excretory system. They do not have a respiratory or circulatory system and are limited to simple **diffusion** for gas exchange. They can regenerate by **fission** as well as reproduce sexually, sometimes with complex life cycles passing through more than one host. Flatworms move about using cilia and by undulating movements of the whole body.

Almost all Platyhelminthes are aquatic, both fresh water and marine, but a few **terrestrial** species live in moist, warm areas. Species vary in size from microscopic to over 60 feet (20 meters) long for some tapeworms.

There are four major classes of Platyhelminthes and over twenty-five thousand species. Flatworms in the class Turbellaria are marine and freshwater free-living **scavengers**. The other three classes are parasitic and include some of the most harmful human parasites. The classes Trematoda, commonly called flukes, and Momogea are both **endoparasites** and **ectoparasites**. Momogea are parasites of aquatic vertebrates such as fish.

Flatworms in the class Cestoda are endoparasites known as tapeworms. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS

Laura A. Higgins

Bibliography

Anderson, D. T., ed. *Invertebrate Zoology.* Oxford: Oxford University Press, 1998.

Barnes, Robert D. *Invertebrate Zoology*, 5th ed. New York: Saunders College Publishing, 1987.

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Purves, William K., Gordon H. Orians, H. Craig Heller, and David Sadava. *Life the Science of Biology*, 5th ed. Sunderland, MA: Sinauer Associates Inc. Publishers, 1998.

Pleistocene

This most recent sequence of geologic time is somewhat complicated to describe in terms of animal science since there is much more information available from the fossil record. Scientifically, it is described as the period of time from 1.9 million year ago to 10,000 years ago. It is identified with a noticeable change in the animal fossils, which usually indicates some kind of extinction or massive change in the environment. It is difficult to summarize what happened from region to region since there was as much climatic variety then as there is today. However, the general consensus among scientists is that the beginning of the Pleistocene epoch began with an overall global cooling. This cooling was significant in that many cold-intolerant species disappeared and some new more resistant species appear in the fossil record.

Every geologic time period is defined by what scientists call a type section. A type section is a place that is considered to be the first discovered well-defined area in which evidence of a time-period shift, or difference between plant and animal communities, can be observed. In short, it is the first discovery of some important geological event characterized by a change in the kinds of species and populations of plant and animal fossils.

Sir Charles Lyell (1797-1875) was a British geologist who opposed the catastrophic theory advanced at the time to account for great geologic changes. A proponent of uniformitarianism, Lyell is considered the father of modern geology.

The type section for the Pleistocene was first proposed in 1839 by British geologist Charles Lyell after he examined a sequence (one of many layers) of rocks in southern Italy. He noticed that within and between the layers of rock, there was a distinct change between fossils of marine mollusks of warm-water species to fossils of species which were similar to modern cold-water species. After further investigation it was determined that this new set of geologic strata contained almost 70 percent living or historical species. Later studies in Europe by other geologists revealed that glaciation had occurred at about the same time as the strata in Italy were deposited. Eventually researchers pieced together evidence that indicated the Pleistocene was a time of great global cooling. During the epoch, immense glaciers and ice sheets occurred at the North and South Poles and at all high altitudes.

The Pleisocene was a relatively short span of geologic time that fluctuated between episodes of warming and cooling, but the general climate was very cold for much of the seas and regions of the continents.

faunas animals

The Pleistocene cooling had a tremendous effect on animal life on Earth; **faunas**, or ecological populations of animals, were severely disrupted or

Era	Period	Epoch	Million Years Before Present
Cenozoic	Quaternary	Holocene	0.01
		Pleistocene	1.6
	Tertiary	Pliocene	5.3
		Miocene	24
		Oligocene	37
		Eocene	58
		Paleocene	65

The Pleistocene epoch and surrounding time periods.

eliminated altogether. Some species became extinct, while others flourished. Many new species have been identified as occurring around this time change and after. New species appeared both on land and at sea. As the ice sheets bound up more and more water, sea levels dropped. Land bridges appeared from beneath the sea, the most famous of which were the Bering land bridge and the land bridge between North and South America. Waves of animal migrations occurred on the continents.

Animal Migrations to the Americas

Before the Pleistocene, North and South America contained their own distinctive sets of animals. Marsupials abounded in South America and the horse flourished in North America. With the emergence of the Panamanian land bridge between the two Americas, a great migration, or swapping of animal species, began. Marsupials (mammals with no **placenta** but with a pouch in which their young develop), sloths, and other animals such as glyptodonts, which looked like an armadillo, headed north. The proboscideans—including a group called the gomphotheres, with elongated lower jaws that looked like shovels—as well as mammoths, and mastodons, moved south. Relatives of modern horses, lions, camels, and wolves migrated after the gomphotheres.

placenta a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

The Bering land bridge that connects Russia and Alaska supported the invasion from Asia of animals such as the mammoth, deer and their relatives, and bison to the Americas. Perhaps the most influential animal to come across the land bridge was another mammal, *Homo sapiens*.

Animal Adaptations to Climate

Animals were also on the move in other parts of the world. The mammoths continued to migrate over Europe and Asia. The woolly mammoth developed a thick fur and began to graze in the spruce forests that bordered the ice. The rhinoceros also moved into Europe and central Asia and developed a coat of thick fur for surviving in the cold conditions. Its front horn grew to extreme lengths, reaching nearly a meter, and some researchers have suggested that legends describing the survivors of this species may have led to the myth of the unicorn. The massive and dangerous archaeocyonids, or bear dogs, were enormous predators whose bones are still found in caves today. In Europe, *Panthera leo spelaea*, a large species of cave lion, roamed the mountains in search of bison and other prey. In North America, *Smilodon*, the saber-toothed cats, traveled over the more warm and savanna-like regions of what is now the southwest United States.

A fossil beetle of the Pleistocene period.

Pleistocene Extinctions

terrestrial living on land

Terrestrial invertebrates flourished and died with the fluctuating climate. Records of species of snails show scientists how the climate cooled and warmed throughout the period. Scientists identify these changes by the silt deposits left by the advancing and retreating glaciers in the North. They also use tree ring thicknesses (a part of dendrochronology) to determine periods of dry or wet years. The best data for calculating oxygen and carbon dioxide isotopes (different numbers of electrons) come from ice cores in Greenland. Small, single-celled marine animals called foraminifera were able to secrete specialized shells. These small eukaryotes are extremely sensitive to temperature change and their tiny fossils leave an excellent record of shifting climate for paleontologists to observe. The records of these animals, found in mud recovered from oil wells off coastal waters read like a book of temperature fluctuations. When the water is warm a certain species will abound. They die and sink to the mud where they are fossilized. When the water is colder other species survive. These also leave their fossils in the mud. An expert can read the sequence of fossils in the mud.

Curiously, amphibians and reptiles of the Pleistocene did not suffer the extinctions that befell the mammals. Since these animals appear to be very sensitive to climate today, it was assumed they would be affected by changes in climate during the ice ages. Apparently they were not, and the fossils of these animals did not change over time either in species or abundance. Their geographic distribution may have changed as climates fluctuated, but there are very few known extinctions of species. Birds also managed to survive. Most of the birds that disappeared did so as a result of human interference in recent times. The great moa of New Zealand was hunted to extinction in the Holocene and is not considered a Pleistocene casualty.

The Pleistocene is famous for its extinctions rather than for its migrations. Some researchers believe the extinction event is not over and point

to the increasing list of endangered species throughout the world. Scientists are still not sure what caused the Pleistocene extinctions. Some hypothesize that many species could simply not tolerate the continuous climate fluctuations, others that temperatures were too cold. This is called the "Overchill Hypothesis." Other scientists note that wherever evidence of human migration is discovered, the large animals, or megafauna, disappear. These scientists believe that humans overhunted, and although not all the bison, deer, mammoths, and other large herbivores were killed for food, their disappearance led to the starvation of predators that relied on these animals. This is the "Overkill Hypothesis." Both hypotheses have merit, but still raise many questions. We may never know what caused the Pleistocene extinctions, but today, loss of habitat and increasing pollution are the most lethal killers of animal life on Earth. SEE ALSO Phylogenetic Relationships of Major Groups.

Brook Ellen Hall

Bibliography

Carroll, Robert. *Vertebrate Paleontology and Evolution.* New York: W. H. Freeman and Company, 1988.

Macdonald, D. *The Encyclopedia of Mammals.* New York: Facts on File Publications, 1987.

Martin, Paul, and Richard Klein. *Quaternary Extinctions: A Prehistoric Revolution.* Tucson, University of Arizona Press, 1989.

Woodburne, M. *Cenozoic Mammals of North America.* Berkeley: University of California Press, 1987.

Pollution

Pollution can be defined as a change in the physical, chemical, or biological characteristics of the air, water, soil, or other parts of the environment that adversely affects the health, survival, or other activities of humans or other organisms. After pollution occurs, the polluted resource is no longer suitable for its intended use. Most pollutants are solid, liquid, or gaseous chemicals created as byproducts of the extractive or manufacturing industries. Pollution can also take the form of excessive heat, noise, light, or other electromagnetic radiation.

Pollution is also a complex political problem and affects people's lives in numerous ways other than health. Determining an acceptable level of pollution is often more of a political problem than a scientific problem. This is especially true when jobs are at stake, as when a manufacturing plant is forced to close or to modify its operations.

Air Pollution

Air pollution is the contamination of air by unwanted gases, smoke particles, and other substances. Air pollution has been around since the beginning of the Industrial Revolution. In the United States, smoke pollution was at its worst in the first half of the twentieth century. The smoke was so thick in the winter in some industrial cities that street lights had to be left on all day. However, air pollution was considered a local problem. The burning of fossil fuels produced the most smoke, so some cities restricted the type of coal that could be burned to hard coal, which burns cleaner than soft coal. More efficient burners were installed and devices were attached to smokestacks to remove soot. Diesel locomotives replaced steam locomotives, which had burned coal or oil to heat the water to make the steam. These changes all led to a gradual reduction in smoke pollution during the last half of the twentieth century.

However, a new type of air pollution, smog, became a problem beginning in the 1940s. Smog is not the same as smoke pollution, although this was not immediately apparent. When Los Angeles had its first major smog attack, it became obvious that some phenomenon other than smoke was responsible. Los Angeles did not burn coal or oil to generate heat or electricity, yet its smog problem worsened. Scientists now know that smog is the result of the action of sunlight on unburned hydrocarbons and other compounds in the air. These unburned hydrocarbons come from the exhaust of motor vehicles with internal combustion engines.

acid rain rain that is more acidic than non-polluted rain

Rapid industrial growth, urban and suburban development, dependence on motor vehicles, construction and operation of large facilities using fossil fuels for generating electricity, production of iron and steel, petrochemicals, and petroleum refining converted what had been a local problem into a regional or national problem. Many areas of the United States now suffer seasonal episodes of unhealthy air, including smog, haze, and **acid rain**. A wide range of pollutants currently poses an ecological threat in cities all over the United States and in other industrialized nations. Since pollution does not recognize national borders, the problem can spread around the world.

Costs of Air Pollution

The costs of air pollution in the United State are difficult to estimate. The economic benefits from the control of pollution are even harder to estimate. Business and industry bear the direct costs of compliance with regulations designed to control air pollution. Ultimately, consumers bear these costs through increased prices and reduced stock dividends. However, the economic benefits of cleaner air may be returned to the consumer in the form of lower health costs and longer-lasting and more reliable products.

Types of Pollutants and Controls

There are six principal classes of air pollutants: particulate matter (soot), carbon monoxide, sulfur oxides, nitrogen oxides, unburned hydrocarbons, and ozone. Billions of metric tons of these compounds are discharged into the air each year.

Particulates. Suspended particulate matter such as soot and aerosols, are particulates. These particles of solids or liquids range in size from those that are visible as soot and smoke, to those that are so small they can only be seen through a microscope. Aerosols can remain suspended in the air for long periods and can be carried over great distances by the wind. Most particulates are produced by burning fossil fuels in power plants and other stationary sources. Controlling particulates usually involves washing, centrifugal separation, or electrostatic precipitation.

Particulates are harmful for a number of reasons. Some particles contribute to acid rain. Toxic materials such as lead or mercury can appear as particulates. However, the greatest health risk comes from breathing particulates. Some particles can lodge deep in the **lungs** and cause inflammation or chronic lung disease.

lungs sac-like, spongy organs where gas exchange takes place

Carbon monoxide. Carbon monoxide is a colorless, odorless, flammable, poisonous gas. The incomplete burning of carbon fuels produces carbon monoxide. Carbon monoxide comes largely from motor vehicles, with lesser amounts from other internal combustion engines such as those on lawnmowers and leafblowers, and from open fires and industrial processes. Carbon monoxide emissions can be controlled by more efficient burners or improved combustion chambers. Modern computer-controlled engines with catalytic converters successfully remove most carbon monoxide from automobile exhaust.

Sulfur oxides. Sulfur oxides are the major contributor to acid rain in the United States. Sulfur oxides include sulfur dioxide, sulfuric acid, and various sulfate compounds. Sulfur oxides are produced when fuel that contains sulfur is burned, or when metal ores are processed. Sulfur oxide emissions in the United States come primarily from plants that use fuels containing sulfur to generate electricity. The best way to reduce sulfur oxide emissions is to use fuels that naturally contain less than 1 percent sulfur, but these fuels are more expensive. Other techniques include removing sulfur from fuels and sulfur oxides from the combustion gases. Removing sulfur from stack gases after fuel is burned is difficult and expensive. However, the by-product, sulfuric acid, can be sold to recover some of the cost.

Nitrogen oxides. Nitrogen oxides are also contributors to acid rain and are a principal component of photochemical smog. Nitrogen oxides primarily result from the high-temperature combustion of gasoline or diesel in internal combustion engines. During combustion, nitrogen in the air chemically combines with oxygen to produce nitric oxide. Much of the nitric oxide is converted to nitrogen dioxide in a chemical reaction promoted by sunlight. Computer-controlled combustion and optimally designed combustion chambers can partially reduce the formation of nitrogen oxides. Special catalytic converters can combine nitric oxide with carbon monoxide and unburned hydrocarbons to produce nitrogen, carbon dioxide, and water.

Unburned hydrocarbons. Unburned hydrocarbons in air also represent wasted fuel. Gaseous hydrocarbons are not toxic at concentrations normally found in the atmosphere, but unburned hydrocarbons are a major contributor to the formation of ozone and smog. Catalytic converters on automobile engines have substantially reduced the emission of unburned hydrocarbons.

Ozone. Ozone is a form of oxygen in which the molecule contains three atoms instead of two. Ozone is beneficial when it is high in the atmosphere, but near the surface, ozone can damage rubber and paint as well as damage lung tissue. Ozone is a constituent of smog, and is produced from the reaction of nitrogen oxides with gaseous hydrocarbons in the presence of sunlight. A small amount of ozone is also produced by lightning storms. The control of ozone and other photochemical oxidants depends on the effective control of both nitrogen oxides and gaseous hydrocarbons.

Water Pollution

Water pollution is caused by any chemical, physical, or biological substance that affects the natural condition of water or its intended use. We rarely stop to think about how important a reliable and safe water supply is until it is restricted or damaged. Water pollutants are produced primarily by the activities of humans. Our fresh water supply is under worldwide threat from pollution.

Water in lakes and rivers (surface water) throughout the world must satisfy a wide variety of different needs. Some of these needs partially conflict with others:

- The public wants lakes and rivers preserved in their natural state.
- Lakes and rivers must support a healthy population of fish and wildlife.
- Surface water must be safe for recreational uses such as swimming.
- Many localities depend on surface water for a safe drinking water supply.
- Surface water must be safe for agricultural use.
- Surface water must accommodate a variety of industrial purposes
- Surface water is used to generate power or cool power plants.
- Surface water is counted upon to dilute and transport human and industrial waste.

Because of the complex factors involved, there is no precise definition of water pollution. Instead, the intended use of the water must be considered. Once the intended use of the water is specified, pollutants can be grouped as not permissible, as undesirable and objectionable, as permissible but not necessarily desirable, or as desirable. For example, if water is to be used for wildlife support and enhancement, toxic compounds are not permissible, but oxygen is desirable. If the water is to be converted to steam in a power plant, some toxic materials might be desirable (because they reduce zebra mussel infestations), while excess oxygen that could corrode equipment would be undesirable.

> In the United States, concern for the natural condition of water was first expressed in the 1899 Rivers and Harbors Appropriation Act. The measure made it illegal to dump waste into waters used by any kind of vessels, except by special permission.

Another method of classifying water pollutants is to distinguish between pollutants that are not altered by the biological processes occurring in natural waters, and those that will eventually break down into other, perhaps less objectionable, compounds. Inorganic chemicals are diluted by water but do not chemically change. Industrial waste often contains this sort of pollutant (for example, mercury). On the other hand, domestic sewage can be converted into inorganic materials, such as bicarbonates, sulfates, and phosphates, by the action of bacteria and other microorganisms in the water. If the water is not too heavily laden with waste, bacteria can break down the waste to safe levels.

Until early in the twentieth century, efforts to control water pollution were directed toward eliminating potential disease-causing organisms, such as typhoid. This led to treatment plants to provide safe drinking water and measures to enhance the natural biological activity of streams and rivers in order to assimilate and break down waste. By the middle of the twentieth

Two men attempt to clean a bird caught up in the oil spilled into the Persian Gulf during the 1991 Gulf War. Feathers soaked with oil lose their waterproofing characteristics—the feature birds need to stay afloat in the water.

century, the focus had shifted to the treatment of chemical pollutants not removed by conventional water-treatment methods.

By the middle of the twentieth century, the situation was changing. Rapidly growing urban areas generated large quantities of waste that had to be processed. Increased manufacturing capacity greatly increased the amount and variety of industrial waste. Commercial fertilizers and pesticides created many new pollution problems. Sewer systems were often unable to keep pace with rapid urban growth. Today, virtually every body of water on Earth has some degree of water pollution. Even the oceans, which were once thought to be able to absorb an unlimited amount of waste, are now showing significant stress due to pollution.

Major Water Pollutants

Water is considered polluted if it contains an amount of any substance that renders the water unsuitable for a particular purpose. The list of substances that may pollute water is very long, and only a few major pollutants can be discussed here.

Organic waste. Organic waste comes from domestic sewage, agricultural runoff, feedlot operations, and industrial waste of animal and plant origin, such as from a paper mill. Domestic sewage is the largest and most widespread source of organic waste. Industrial organic waste tends to occur in larger quantities at fewer locations. Industries that make food and paper (and wood pulp) produce the largest amounts of industrial organic waste.

Bacteria can efficiently break down organic waste. However, bacterial action also removes oxygen from the water. Because fishes and other forms of **aquatic** life depend on dissolved oxygen, the bacterial action necessary to break down the waste damages the aquatic environment. If organic waste consumes oxygen at a rate greater than it can be replenished, then anaerobic bacteria dominate the decay process. Anaerobic decomposition by bacteria is smelly and aesthetically unpleasant.

aquatic living in water

Plant nutrients. Nitrogen and phosphorus are the two main plant nutrients acting as polluting agents. If plant nutrients get into water, they stimulate the growth of algae and other water plants. When these plants die and decay, they consume oxygen, just like any other organic waste. The excess plant growth caused by fertilization and subsequent build up of dead plant matter is called eutrophication. If the oxygen level drops even a small amount, desirable species of fishes, such as trout and bass, will be replaced by less desirable species such as carp and catfish. If the oxygen level drops low enough, all species of fishes, crayfishes, shrimp, and other organisms may die.

Synthetic organic chemicals. The water pollution problem causing the greatest concern is the ever-increasing variety of new chemical compounds. Often new compounds are developed and old ones abandoned before their environmental impact is known. Some of these compounds will remain in water for decades, or longer. The presence of these synthetic chemicals adversely affect fishes and other aquatic life. Many researchers think that some synthetic chemicals mimic natural hormones, disrupting growth and reproductive cycles in affected populations.

Inorganic chemicals. Inorganic chemicals such as mercury, nitrates, phosphates, and other compounds may also enter surface water. Many of these chemicals destroy fish and aquatic life, cause excessive hardness of water supply, and corrode machinery. This adds to the cost of water treatment.

Mercury pollution has been recognized as a serious, chronic, and widespread danger in many waterways. Even very small amounts of mercury can cause serious physiological effects or even death. Because mercury is not normally found in food or water, no organisms have developed the ability to process and excrete mercury. So it collects in tissues until toxic levels are reached. Mercury also undergoes **biomagnification**. Organisms at higher trophic levels consume a large number of organisms at lower trophic levels. The concentration of mercury becomes progressively higher at higher trophic levels. Predators at the highest trophic levels can accumulate dangerously high levels of mercury in this way.

biomagnification increasing levels of toxic chemicals through each trophic level of a food chain

Radioactive materials. Radioactive materials are a recent addition to the list of potential water pollutants. Radioactive waste comes from the mining and processing of radioactive ores, from the refining of radioactive materials, from the industrial, medical, and research uses of radioactive materials,

and from nuclear-powered reactors. Some radioactive waste still remains from the atmospheric testing of nuclear weapons in the 1940s and 1950s. The two most common radioactive materials found in water are strontium-90 and radium-226.

Oil. Oil pollution can enter water through bilge flushing, from accidental or deliberate discharge from ships, or from accidental spills of crude oil during transport. Some experts estimate that 1.5 million tons of oil are spilled into the oceans each year. Water polluted by oil greatly damages aquatic life and other wildlife such as birds that depend on the water for food and nesting areas. Waterfowl alighting on oil-covered waters usually become so oil soaked that they are unable to fly. One speck of oil on a bird's feathers can poison the bird if it ingests the oil while preening. Oil destroys much of the aquatic life of oceans. It is particularly damaging to shellfish and other **filter feeders**. It also damages the small shrimp and other organisms that serve as food for larger fish.

filter feeders animals that strain small food particles out of water

Thermal pollution. Thermal pollution is caused by the release of heat into the water or air. Electric power plants are a major source of thermal pollution, since they convert only about one-third of fuel energy into electricity. The remaining heat is discharged to the local environment as heated water or air. This can alter the ecological balance of a large area. For example, if warm water is discharged into a lake, the warm water will not be able to dissolve as much oxygen. This may result in more desirable species of fishes being replaced by less desirable species.

Land and Soil Pollution

One of the miracles of technology in the late twentieth century has been the extraordinary ability of agriculture to increase the productivity of croplands to previously unheard of levels. However, this increased productivity requires the heavy use of pesticides and fertilizer. Most pesticides today are designed to decompose very quickly into harmless compounds. Thousands of pesticides are currently in use, and in most cases their agricultural value balances their risks. However, many scientists think that we may be in an unbreakable cycle of having to continually develop new and more potent pesticides to overcome pests that are resistant to older pesticides.

Noise Pollution

Noise pollution is a recently identified source of environmental degradation. The hearing apparatus of living things is sensitive to certain frequency ranges and sound intensities. Sound intensities are measured in decibels. A sound at or above the 120 decibel level is painful and can injure the ear. Noise pollution is present even in the open ocean. Researchers have shown that whales communicate over great distances using low frequency sound waves. Unfortunately, the noise generated by engines and screws of ships falls in the same frequency range and can interfere with the whale's communication.

Light Pollution

Professional and amateur astronomers have recently identified a problem that did not exist a generation ago: light pollution. This form of pollution

has spread so widely in the last few decades that many people are only able to see a few of the brightest stars. From many of our big cities, no stars at all are visible. Light pollution is not an inevitable consequence of making our streets and neighborhoods safer. Most light pollution comes from wasted light. At least 75 percent of the sky glow in most cities comes from poorly designed or improperly installed light fixtures. According to a study conducted by the International Dark-Sky Association in 1997, about $1.5 billion per year is spent on wasted light that does nothing to improve security or safety.

Efforts to Control Pollution

Because pollution does not recognize national borders, the solution to many pollution problems requires cooperation at regional, national, and international levels. For example, smokestacks of coal-burning power plants in the United States cause some of the acid rain that falls in Canada.

In the United States, the Environmental Protection Agency (EPA) is charged with enforcing the many and complex laws, rules, executive orders, and agency regulations regarding the environment. The EPA came into being in 1969 with the passage of the National Environmental Policy Act (NEPA). This act also required the filing of environmental impact statements. Almost all government agencies and many businesses are required by law to file these statements, which state the potential harmful environmental effects of such activities as opening new factories, building dams, and drilling new oil wells.

> The 1990 Pollution Prevention Act created a new office in the Environmental Protection Agency, with the mission to help industries limit pollutants.

Additional laws to protect the environment were passed in the 1970s and 1980s, including the Clean Air Act, the Safe Drinking Water Act, and the Comprehensive Environmental Response, Compensation, and Liability Act, known as Superfund. Then-president George Bush signed the Clean Air Act of 1990. This new law called for substantial reductions in emissions of all types. The act also added to the list of potentially toxic chemicals that must be monitored by the EPA. The pace of new environmental legislation has waned since 1990, but congress enacted the Food Quality Protection Act in 1996 and the Chemical Safety Information, Site Security and Fuels Regulatory Relief Act in 1999. SEE ALSO Habitat Loss; Trophic Level.

Elliot Richmond

Bibliography

Art, Henry W., ed. *The Dictionary of Ecology and Environmental Science.* New York: Holt, 1993.

Bowler, Peter J. *Norton History of Environmental Sciences.* New York: Norton, 1993.

Caplan, Ruth. *Our Earth, Ourselves: The Action-Oriented Guide to Help You Protect and Preserve Our Planet.* Toronto, Canada: Bantam, 1990.

Carson, Rachel. *Silent Spring.* Boston: Houghton Mifflin, 1994.

Chiras, Daniel D. *Environmental Science: Action for a Sustainable Future*, 4th ed. Menlo Park, CA: Benjamin-Cummings Publishing Company, 1993.

Franck, Irene M., and David Brownstone. *The Green Encyclopedia.* New York: Prentice Hall General Reference, 1992.

Harms, Valerie. *The National Audubon Society Almanac of the Environment.* New York: Putnam Publishing, 1994.

Luoma, Jon R. *The Air Around Us: An Air Pollution Primer.* Raleigh, NC: Acid Rain Foundation, 1989.

Miller Jr., G. Tyler. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth Publishing Company, 1990.

Mott, Lawrie, and Karen Snyder. *Pesticide Alert: A Guide to Pesticides in Fruits and Vegetables.* San Francisco: Sierra Club Books, 1997.

Newton, David. *Taking a Stand Against Environmental Pollution.* Danbury, CA: Franklin Watts Incorporated, 1990.

Rubin, Charles T. *The Green Crusade: Rethinking the Roots of Environmentalism.* New York: Free Press, 1994.

Population Dynamics

A population describes a group of individuals of the same species occupying a specific area at a specific time. Some characteristics of populations that are of interest to biologists include the **population density**, the **birthrate**, and the **death rate**. If there is immigration into the population, or emigration out of it, then the immigration rate and emigration rate are also of interest. Together, these **population parameters,** or characteristics, describe how the population density changes over time. The ways in which population densities fluctuate—increasing, decreasing, or both over time—is the subject of population dynamics.

population density the number of individuals of one species that live in an given area

birthrate a ratio of the number of births in an area in a year to the total population of the area

death rate a ratio of the number of deaths in an area in a year to the total population of the area

population parameters a quantity that is constant for a particular distribution of a population but varies for the other distrubutions

Population density measures the number of individuals per unit area, for example, the number of deer per square kilometer. Although this is straightforward in theory, determining population densities for many species can be challenging in practice.

Measuring Population Density

One way to measure population density is simply to count all the individuals. This, however, can be laborious. Alternatively, good estimates of population density can often be obtained via the quadrat method. In the quadrat method, all the individuals of a given species are counted in some subplot of the total area. Then that data is used to figure out what the total number of individuals across the entire habitat should be.

The quadrat method is particularly suited to measuring the population densities of species that are fairly uniformly distributed over the habitat. For example, it has been used to determine the population density of soil species such as nematode worms. It is also commonly used to measure the population density of plants.

For more mobile organisms, the **capture-recapture method** may be used. With this technique, a number of individuals are captured, marked, and released. After some time has passed, enough time to allow for the mixing of the population, a second set of individuals is captured. The total population size may be estimated by looking at the proportion of individuals in the second capture set that are marked. Obviously, this method works only if one can expect individuals in the population to move around a lot and to mix. It would not work, for example, in territorial species, where individuals tend to remain near their territories.

capture-recapture method a method of estimating populations by capturing a number of individuals, marking and releasing them, and then seeing what percentage of newly captured individuals are captured again

The birthrate of a population describes the number of new individuals produced in that population per unit time. The death rate, also called mortality rate, describes the number of individuals who die in a population per

King penguins survey the scene at St. Andrews Bay, South Georgia Island.

unit time. The immigration rate is the number of individuals who move into a population from a different area per unit time. The emigration rates describe the numbers of individuals who migrate out of the population per unit time.

The values of these four population parameters allow us to determine whether a population will increase or decrease in size. The "intrinsic rate of increase r" of a population is defined as r = (*birth rate* + *immigration rate*) − (*death rate* + *emigration rate*).

If r is positive, then more individuals will be added to the population than lost from it. Consequently, the population will increase in size. If r is negative, more individuals will be lost from the population than are being added to it, so the population will decrease in size. If r is exactly zero, then the population size is stable and does not change. A population whose density is not changing is said to be at **equilibrium**.

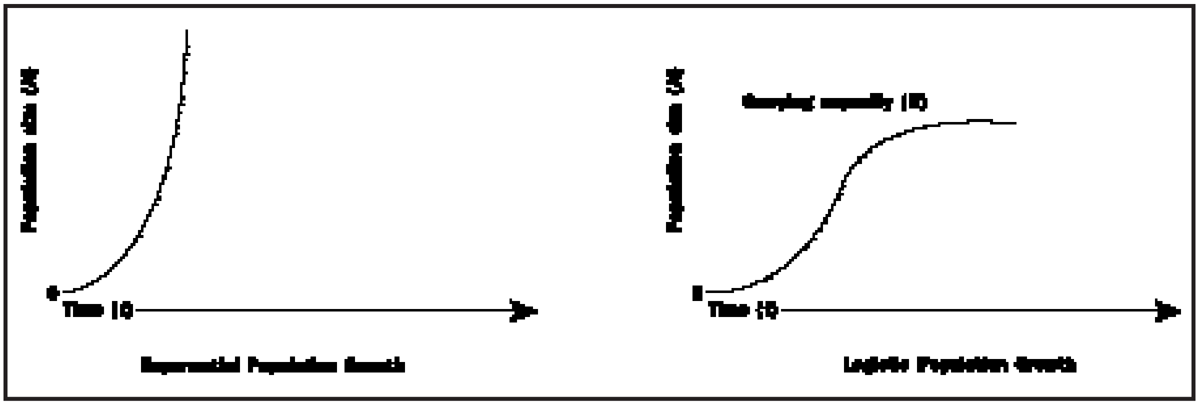
equilibrium a state of balance

Population Models

We will now examine a series of population models, each of which is applicable to different environmental circumstances. We will also consider how closely population data from laboratory experiments and from studies of natural populations in the wild fit these models.

Exponential growth. The first and most basic model of population dynamics assumes that an environment has unlimited resources and can support an unlimited number of individuals. Although this assumption is clearly unrealistic in many circumstances, there are situations in which resources are in fact plentiful enough so that this model is applicable. Under these circumstances, the rate of growth of the population is constant and equal to the intrinsic rate of increase r. This is also known as **exponential growth**.

exponential growth a population growing at the fastest possible rate under ideal conditions



Population growth predicted by exponential and logistical models.

What happens to population size over time under exponential growth? If *r* is negative, the population declines quickly to extinction. However, if *r* is positive, the population increases in size, slowly at first and then ever more quickly. Exponential growth is also known as "J-shaped growth" because the shape of the curve of population size over time resembles the letter "J." Also, because the rate of growth of the population is constant, and does not depend on population density, exponential growth is also called "density-independent growth." Exponential growth is often seen in small populations, which are likely to experience abundant resources. J-shaped growth is not sustainable however, and a population crash is ultimately inevitable.

There are numerous species that do in fact go through cycles of exponential growth followed by population crashes. A classic example of exponential growth resulted from the introduction of reindeer on the small island of Saint Paul, off the coast of Alaska. This reindeer population increased from an initial twenty-five individuals to a staggering two thousand individuals in twenty-seven years. However, after exhausting their food supply of lichens, the population crashed to only eight. A similar pattern was seen following the introduction of reindeer on Saint Matthew Island, also off the Alaskan coast, some years later. Over the course of history, human population growth has also been J-shaped.

Logistic growth. A different model of population increase is called **logistic growth**. Logistic growth is also called "S-shaped growth" because the curve describing population density over time is S-shaped. In S-shaped growth, the rate of growth of a population depends on the population's density. When the population size is small, the rate of growth is high. As population density increases, however, the rate of growth slows. Finally, when the population density reaches a certain point, the population stops growing and starts to decrease in size. Because the rate of growth of the population depends on the density of the population, logistic growth is also described as "density-dependent growth".

logistic growth in a population showing exponential growth the individuals are not limited by food or disease

Under logistic growth, an examination of population size over time shows that, like J-shaped growth, population size increases slowly at first, then more quickly. Unlike exponential growth, however, this increase does not continue. Instead, growth slows and the population comes to a stable equilibrium at a fixed, maximum population density. This fixed maximum is called the **carrying capacity**, and represents the maximum number of in-

carrying capacity the maximum population that can be supported by the resources

dividuals that can be supported by the resources available in the given habitat. Carrying capacity is denoted by the variable *K.*

The fact that the carrying capacity represents a stable equilibrium for a population means that if individuals are added to a population above and beyond the carrying capacity, population size will decrease until it returns to *K*. On the other hand, if a population is smaller than the carrying capacity, it will increase in size until it reaches that carrying capacity. Note, however, that the carrying capacity may change over time. *K* depends on a wealth of factors, including both **abiotic** conditions and the impact of other biological organisms.

abiotic nonliving parts of the environment

Logistic growth provides an accurate picture of the population dynamics of many species. It has been produced in laboratory situations in single-celled organisms and in fruit flies, often when populations are maintained in a limited space under constant environmental conditions.

Perhaps surprisingly, however, there are fewer examples of logistic growth in natural populations. This may be because the model assumes that the reaction of population growth to population density (that is, that population growth slows with greater and greater population densities, and that populations actually decrease in size when density is above the carrying capacity) is instantaneous. In actuality, there is almost always a time lag before the effects of high population density are felt. The time lag may also explain why it is easier to obtain logistic growth patterns in the laboratory, since most of the species used in laboratory experiments have fairly simple life cycles in which reproduction is comparatively rapid.

Biological species are sometimes placed on a continuum between *r*-selected and *k*-selected, depending on whether their population dynamics tend to correspond more to exponential or logistic growth. In *r*-selected species, there tend to be dramatic fluctuations, including periods of exponential growth followed by population crashes. These species are particularly suited to taking advantage of brief periods of great resource abundance, and are specialized for rapid growth and reproduction along with good capabilities for dispersing.

In *k*-selected species, population density is more stable, often because these species occupy fairly stable habitats. Because *k*-selected species exist at densities close to the carrying capacity of the environment, there is tremendous competition between individuals of the same species for limited resources. Consequently, *k*-selected individuals often have traits that maximize their competitive ability. Numerous biological traits are correlated to these two **life history strategies**.

life history strategies methods used to overcome pressures for foraging and breeding

Lotka-Volterra models. Up to now we have been focusing on the population dynamics of a single species in isolation. The roles of competing species, potential prey items, and potential predators are included in the logistic model of growth only in that they affect the carrying capacity of the environment. However, it is also possible directly to consider between-species interactions in population dynamics models. Two that have been studied extensively are the Lotka-Volterra models, one for competition between two species and the other for interactions between predators and prey.

Competition describes a situation in which populations of two species utilize a resource that is in short supply. The Lotka-Volterra models of the population dynamics of competition show that there are two possible results: either the two competing species are able to **coexist**, or one species drives the other to extinction. These models have been tested thoroughly in the laboratory, often with competing yeasts or grain beetles.

coexist to both be present

Many examples of competitive elimination were observed in lab experiments. A species that survived fine in isolation would decline and then go extinct when another species was introduced into the same environment. Coexistence between two species was also produced in the laboratory. Interestingly, these experiments showed that the outcome of competition experiments depended greatly on the precise environmental circumstances provided. Slight changes in the environment—for example, in temperature—often affected the outcome in competitions between yeasts.

Studies in natural populations have shown that competition is fairly common. For example, the removal of one species often causes the abundance of species that share the same resources to increase. Another important result that has been derived from the Lotka-Volterra competition equations is that two species can never share the same **niche**. If they use resources in exactly the same way, one will inevitably drive the other to extinction. This is called the **competitive exclusion principle**. The Lotka-Volterra models for the dynamics of interacting predator and prey populations yields four possible results. First, predator and prey populations may both reach stable equilibrium points. Second, predators and prey may each have never-ending, oscillating (alternating) cycles of increase and decrease. Third, the predator species can go extinct, leaving the prey species to achieve a stable population density equal to its carrying capacity. Fourth, the predator can drive the prey to extinction and then go extinct itself because of starvation.

niche how an organism uses the biotic and abiotic resources of its environment

competitive exclusion principle the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

As with competition dynamics, biologists have tried to produce each of these effects in laboratory settings. One interesting result revealed in these experiments was that with fairly simple, limited environments, the predator would always eliminate the prey, and then starve to death. The persistence of both predator and prey species seemed to be dependent on living in a fairly complex environment, including hiding places for the prey.

In natural populations, studies of predator-prey interactions have involved predator removal experiments. Perhaps surprisingly, it has often proven difficult to demonstrate conclusively that predators limit prey density. This may be because in many predator-prey systems, the predators focus on old, sick, or weak individuals. However, one convincing example of a predator limiting prey density involved the removal of dingoes in parts of Australia. In these areas, the density of kangaroos skyrocketed after the removal of the predators.

Continuing oscillations between predators and prey do not appear to be common in natural populations. However, there is one example of oscillations in the populations of the Canada lynx and its prey species, the snowshoe hare. There are peaks of abundance of both species approximately every ten years. SEE ALSO Populations.

Jennifer Yeh

Bibliography

Curtis, Helena. *Biology.* New York: Worth Publishers, 1989.

Gould, James L., and William T. Keeton, and Carol Grant Gould. *Biological Science*, 6th ed. New York: W. W. Norton & Co., 1996.

Krebs, Charles J. *Ecology: The Experimental Analysis of Distribution and Abundance.* New York: Harper Collins College Publishers, 1994.

Murray, Bertram G., Jr. *Population Dynamics: Alternative Models.* New York: Academic Press, 1979.

Pianka, Eric R. *Evolutionary Ecology.* New York: Addison Wesley Longman, 2000.

Ricklefs, Robert E., and Gary L. Miller. *Ecology*, 4th ed. New York: W. H. Freeman, 2000.

Soloman, Maurice E. *Population Dynamics.* London: Edward Arnold, 1969.

Populations

The study of populations and population ecology is a growing field of biology. Plants and animals are studied both singly and in relationship to one another. Factors that affect population growth and overall health are constantly being sought and analyzed.

Animal populations are a bit easier to discuss since the genetic basis from which animal populations arise is not as complicated as the genetic basis of plants. Animal populations are more constrained by genetic variation than are plants. No haploid or **polyploid** animal exists or reproduces. Population dynamics (growth, death, and reproduction rate) are more easily explained in animals and many models, or predictions of population success, can be used to examine and learn from animal populations. Insects, in particular, provide a wealth of interesting population models since they tend to reproduce rapidly and in high numbers and their life cycles are fairly short.

polyploid having three or more sets of chromosomes

A great deal of healthy debate exists regarding the definition of a population. Not all species fit neatly into any one definition. In general, a population is described as a group of individuals of a species that lives in a particular geographic area. It is a sexually reproducing species in which individuals add to the continued growth or sustenance of the population. The sexually reproducing component of the definition is critical in that many endangered populations are at risk simply because they are not reproducing effectively enough to sustain their populations.

An example of this was found in the remnant population of the California condor. Its numbers in the wild had dwindled to approximately twenty individuals. The condors were not successfully reproducing in their natural habitat. Each year the eggs were infertile or crushed and no offspring were being reared. The population continued to dwindle as the older birds died and no young birds were born to replace them. Eventually, they were all captured and artificially bred in hopes of preserving the species. The population has increased in captivity, but California condors still face the challenge of becoming a viable biological population in the wild.

> Raising captive baby condors requires all sorts of skills. After feeding the young birds had become an issue, their caretakers started to wear hand puppets designed in the image of the head of a female California condor. The babies quickly adjusted to taking their food from the mouth of their fabricated "mother." This gimmick made a difference in the number of babies surviving in captivity.

A population can exist over a broad geographic expanse, such as the North American continent or even the Earth, but it can also exist in one small pond. Many different populations of desert pupfish live only in their own small pond throughout the Mojave Desert. Populations of mites or parasites may live on one specific host or they may prefer one area of the host organism. For instance, a population of tapeworms may live only in the intestinal tract of the host while a louse population exists in the external environment. Most often a population for biological study is one in which a

distinct geographical range can be assessed, such as a valley, plain, or forest, and a definite **genotype** can be identified.

genotype the genetic makeup of an organism

A great deal of genetic variation exists within a population and the predictions of how this variation may be expressed is the fascinating work of population geneticists. Mathematics is used to help predict how a trait will move through a population or how a population will respond to an environmental pressure. Mathematical models that help scientists study population response to internal (genetic) and external (environmental) pressures are predictive only and are never entirely correct.

It is the very nature of scientific models to be incorrect. No human or computer can ever account for all the existing variables or potential variables that may affect a population. How would one anticipate an intensely cold and violent storm three years from now? How would it be possible to predict a specific genetic mutation? None of this can be done, but all natural variables eventually affect populations in some way or another.

Environmental Variables

All populations are ultimately controlled by the carrying capacity of their environment. The carrying capacity is the sum of all resources needed by a specific species in order to survive. The abundance of food is a major control. When food is short, young, old, and unfit members will die.

If two or more species are competing for one food source, additional pressure is placed on both populations. If two species of birds rely heavily on a certain insect for protein and nutrition, the availability and abundance of that insect is crucial. Any reduction in the population of insects will result in a loss of species from either bird population. There may not be enough food to feed and rear the young. Older birds unable to fly long distances for alternate food will also perish.

Food is not the only limiting factor that affects carrying capacity. Shelter and places to safely rear young are also part of the limits for many populations. Ground squirrels often rear their young underground or in rock shelters. This protects the young from predators, such as foxes or birds of prey. If there is a lack of adequate shelter the young are in peril. The rock squirrel lives in the crevices of rocks. If there are no rocks in a particular feeding area the squirrel may be able to eat out in the open or under a tree, but hiding from snakes and birds would be difficult under such circumstances. Rock squirrels in an area without the necessary physical habitat would be unable to successfully raise young to replenish the next generation.

Climate variables can also affect carrying capacity. If normal weather conditions change significantly over a period of time, certain plant species may not survive. Animals living on those plants will also perish. Pollution may also prevent populations from surviving; water and food may become toxic and make the environment unsuitable for existing populations.

Ultimately, the carrying capacity of an area affects the growth of a population since the numbers of species will not grow if there are not enough resources for the individuals to survive. The population will be regulated by the availability of food and other resources. Numbers of individuals will not increase, but in all likelihood remain the same.

The health of this group of minnows, also known as shiners, can be greatly dependant upon environmental conditions.

Population Regulation

Population regulation is achieved through several mechanisms. The environment is always at the top of the list of population regulation factors for reasons just mentioned. Another factor is the number of predators in any given area. If an animal that feeds on other animals is maintaining a stable population, it will only eat so many prey species every year. If, however, the prey species begins to flourish and increase in numbers, there will be more food for the predator. The predator population will also become more successful and increase in numbers. Eventually the predators will eat all the available prey and they will have reached the limits or carrying capacity of their environment.

The classic example of this type of population regulation is the Canadian lynx and the snowshoe hare. With regular cyclicity, hare populations increase in their habitats. As they rear more and more young, the available food for the Canadian lynx increases. With readily available food, the lynx is also more successful at raising young, so its population grows in response. Eventually the limit of how many snowshoe hares can exist in a particular region is reached. The lynx eat more and more hares, thus regulating and even reducing the population of hares. As the snowshoe hare population declines so does the population of Canadian lynx. Each population is regulating the growth of the other.

Density Dependence and Independence

Density-dependent and density-independent populations are the focus of many scientific models. A density-dependent population is one in which the number of individuals in the population is dependent on a variety of factors including genetic variability and the carrying capacity of its environment. In a density-dependent population the ability to find a mate is critical. When population numbers are low this may be a critical factor in the survival of the species. If no mates are found during a season there will be no offspring.

Another effect of density-dependency is **intraspecific** (within the species) competition. When members of a population are all competing for food resources or adequate habitat, the less fit (unhealthy, young, or old) members will lose out and perish. As a population grows, this type of intraspecific competition serves as a self-regulating mechanism, eliminating many members of the population.

intraspecific involving members of the same species

Density-independent populations are those that are regulated by catastrophic or unusual events. Hurricanes constantly provide population controls on the coasts of North America or neighboring islands. Winds bring down trees where birds and other animals find shelter. Water drowns populations of squirrels or other mammals. Freshwater fish are inundated by saltwater.

The list of catastrophic effects is long, but the end result is that the local populations suffer and must rebuild until the next hurricane comes along. Other catastrophic events may include climatic changes or the accidental dumping of toxic waste. Oil spills have become an increasing threat to coastal populations of all types. In a truly severe event the populations may never return and the members that survive may not be able to live in the wasted environment.

Human Populations

Human populations defy the ecological rules imposed on other animal populations. Because we can modify our environment, humans can live beyond the carrying capacity of our environment by growing extra food and building shelter. Medicine has helped the survivorship of our young and elderly. It is hard to describe human populations in terms of density dependence or independence. We are a highly successful species that is increasingly intelligent about survival in formerly inhospitable habitats.

Most scientists agree, however, that there is a limit to which the human population can grow. Eventually all the food that can be produced may still be inadequate to support the population. Resources like water and energy may reach their limits. There is no reason to believe that human populations will not also be regulated by environment. Mass starvation has already occurred in regions where natural catastrophes destroy food resources and hinder the attempts of other populations to help. There are scientists and governments that advocate population regulation on a voluntary basis to keep the human population from exceeding the carrying capacity of the Earth.

Extinction

Extinction is a part of population biology. It is a natural process that has been or will be experienced by every population. The fossil record is full of animals that flourished for millions of years and then vanished.

Extinction and the mechanisms that compose it are not always well understood. The Earth is still experiencing extinctions at an amazing rate. The mammoths and saber-toothed cats are among the better known populations to have vanished in the last ten to twenty thousand years. Animal populations still disappear every day. However, when one population disappears, quite often another grows. Humans are blamed for the loss of many species. As human populations stabilize, additional populations will begin to flourish. This is the nature of population ecology cycles. SEE ALSO Human Populations; Population Dynamics.

Brook Ellen Hall

Bibliography

Gutierrez, A. P. *Applied Population Ecology: A Supply-Demand Approach.* New York: John Wiley & Sons, 1996.

MacArthur, Robert H., and Joseph H. Connell. *The Biology of Populations.* New York: Wiley, 1996.

Porifera

The phylum Porifera contains all the species of sponges. Phylogenetically, Porifera is most closely related to Protista, making it the first animal phylum to have evolved to be multicellular. This also makes Porifera the simplest in form and function. Sponges arose 550 million years ago in the pre-Cambrian period, evolving from colonial protists, groups of identical single cell organisms that live together. Evidence for this comes from specialized cells called choanocytes which sponges use in feeding. Although sponges are made up of many cells with specialized functions, their cells are not organized into true tissues.This lack of true tissue layers makes sponges different from all other animals except protozoans, which are not multicellular. Sponges also lack symmetry, true organs, a digestive or respiratory system, a nervous system, muscles, and a true mouth.

sessile not mobile, attached

budding a type of asexual reproduction where the offspring grow off the parent

naturalists scientists who study nature and the relationships among the organisms

Sponges are **sessile**; they are attached to one place and do not move around. They range in size from over 1 meter (3 feet) long to 2 millimeters (less than 1/8 of an inch) long. All sponges live in water, from the deepest seas to the shallow coastal waters. Most species are marine and can be found in all the oceans; only 3 percent live in fresh water. All sponges have the ability to completely regenerate an adult from fragments or even single cells. Sponges reproduce sexually, with one sponge producing both sperm and eggs from the choanocytes at different times, giving rise to a larvae that is free living (not sessile). A very few species reproduce asexually by **budding**. Some of the first **naturalists** like Aristotle mistakenly thought sponges were plants because they do not move and can regenerate.

Sponges depend on the water currents flowing through them for food and gas exchange. Sponges have specialized cells for gathering small particles of food from the water and distributing the food around the organism. Water comes in through pores along the body wall into the **spongocoel**, the main cavity of a sponge, and flows out a large opening in the top called an osculum. Choanocytes, also called collar cells, are specialized feeding cells which line the spongocoel. Choanocytes have a **flagellum** that extends out of the cell and sweeps food particles into a sticky, collarlike opening. They are similar in shape and function to certain colonial protists, such as the choanoflagellates. Amoebocytes, which digest food and transport it around the sponge, are specialized cells that move around the sponge's body under the **epidermis**, the outer layer of cells, through a jellylike middle cell layer. Amoebocytes move in a way that is similar to how amoebae move. Amoebocytes secrete hard structural fibers called spicules, which are made of calcium carbonate or silica. In some sponges, amoebocytes secrete other materials that make up the skeleton called spongin which are flexible fibers made of collagen. Only sponges have spicules. This structural feature is part of what divides sponges into different classes.

spongocoel the central cavity in a sponge

flagellum a cellular tail that allows cells to move

epidermis the protective element of the outer portion of the skin found in some animals; it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

There are over nine thousand identified species of sponges, and more are identified all the time. These species are classified into three classes: Demospongiae, Calcarea, and Hexactinellida.

Most species of sponges are in the class Demospongiae. Sponges in this class are mostly marine, but the class also contains the few species that do live in fresh water. Because the materials that make up the skeleton and spicules of these sponges are so varied; the overall sizes and shapes of the sponges are also varied. The amoebocytes of the sponges in Demospongiae contain pigment, giving these sponges many different bright colors.

Sponges within the class Calcarea are characterized by spicules made of calcium carbonate. All species in Calcarea have spicules of a similar size and shape. Most species are not colored. Calcarea sponges are usually less than 15 centimeters (6 inches) tall, and live in the shallow ocean waters along coasts.

Glass sponges make up the class Hexactinellida. They are unique because their spicules have six points and a hexagon shape. The spicules fuse together to form elaborate lattice skeletons which make the sponges look as if they are made of glass. Most Hexactinellida live in the Antarctic Ocean and are found in deep waters, from 200 meters (650 feet) down. SEE ALSO Phylogenetic Relationships of Major Groups.

Laura A. Higgins

Bibliography

Anderson, D. T., ed. *Invertebrate Zoology.* Oxford: Oxford University Press, 1998.

Barnes, Robert D. *Invertebrate Zoology*, 5th ed. New York: Saunders College Publishing, 1987.

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Purves, William K., Gordon H. Orians, H. Craig Heller, and David Sadava. *Life: The Science of Biology*, 5th ed. Sunderland, MA: Sinauer Associates Inc. Publishers, 1998.

Predation

Predation is the interaction in which the predator attacks live prey and consumes it. The interaction can be between two or more individuals, and is to the benefit of the predator and at the expense of the prey. The study of predator-prey interactions is broad and includes behaviors of the predator (such as searching, handling, and consuming prey), adaptations of the prey (survival strategies), and phenomena of their coexistence, such as stabilization factors that allow both groups to persist. It should be noted that there are four types of predators: true predators (including cannibals), grazers, parasitoids, and parasites. This entry will focus on true predators.

If a predator were fully efficient, all of its prey would be eaten. The prey would go extinct, and so would the predator. But the predator-prey interactions seen in nature allow both to sustain themselves. The first researchers to model how these interactions operated were A. J. Lotka and V. Volterra, in 1925 and 1926 respectively.

The Lotka-Volterra model assumes that predator reproduction is a function of the amount of prey consumed, so that when predators eat more prey, the predators increase in number through increased reproduction and immigration. There is a circular pattern of predator-prey interactions in this model: (1) when the predator population increases, the prey population decreases; (2) when the prey decrease in number, the predators decrease in number; (3) when the predator population decreases, the prey population increases; and (4) when the prey increase in number, the predator population again increases and the cycle begins anew.

> Many large predators, such as mountain lions, tigers, and wolves, are on the federal list of endangered or threatened species. One of the reasons is that these animals need large areas to hunt; another reason is habitat loss.

When populations are plotted out over time, a pattern of coupled oscillation can be seen in which the apex, or peak, of one population coincides with the low point of the other. The numeral values of the two populations then cross and reverse positions.

A famous example of coupled oscillation between predator and prey populations occurs with the snowshoe hare and the lynx. Population peaks, as determined by numbers of pelts lodged with the Hudson Bay Company, were alternately spaced in time, with that of the lynx closely following that of the showshoe hare. The Lotka-Volterra model easily explains this pattern of predator-prey population sizes.

Although this model is not incorrect, it does oversimplify the scope of predator-prey interactions given that the major assumption, that when predators eat more prey the predator population increases, is often not exactly what is seen in nature. In actuality, when prey increases, a predator can have a numerical response, where predators do in fact increase in number through reproduction or immigration, or a functional response, where each predator eats more prey items.

Three types of functional responses are recognized, each of them showing a different relationship between prey density and amount of prey consumed. The Type I functional response is a direct relationship in which the predator eats all of the prey available up to a certain saturation point, when the predator can eat no more. After the predator reaches that saturation point, the prey density can continue to increase with no effect on how many prey items are being eaten. Some insects employ the strategy of

A grizzly bear finds a red salmon lunch in Brooks Falls, Katmai National Park, Alaska.

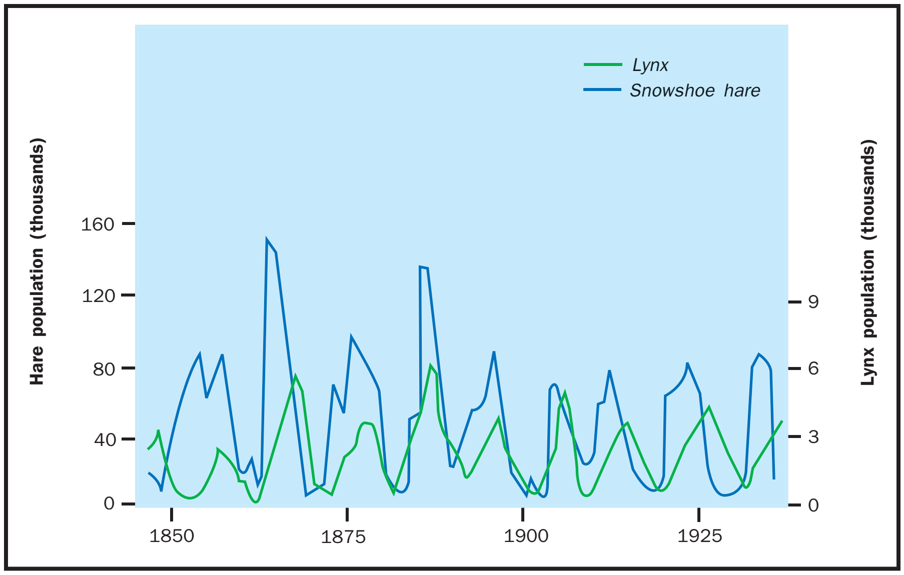
having thousands of offspring that all hatch at once. This suddenly floods the food supply, ensuring that a significant portion will remain after predators eat their fill.

The Type II functional response is more commonly seen because it is more realistic, since it incorporates a factor called handling time. Handling time is the amount of time a predator must devote to each prey item it consumes. It is the time needed for pursuing, subduing, and consuming the prey, and then preparing for further search. In this type of response the relationship between prey density and consumption is not linear because it changes over time. At first, the consumption rate increases, but as prey density continues to increase, there is a decline in the rate at which consumption increases until a maximum level is reached. This gradual deceleration of consumption reflects the factor of handling time.

Lastly, the Type III functional response is the most complex. It is similar to Type II at high prey densities, but includes the additional factor that there is very little or no prey consumption when prey is at low densities. This means that the predator does not eat any of the prey until there is a certain amount available.

One reason for this is that when there are very few prey animals, they can all find ideal hiding places and easily keep themselves out of the reach of predators. When there are more prey, however, some are forced into less ideal refuges, or into foraging places that are out in the open, where they are more visible to predators.

Another reason that prey are often not consumed when they are at low densities relates to search images. A predator gets accustomed to looking in certain types of habitat for certain shapes, colors, or movement patterns in order to hunt at maximum efficiently. Using a search image for the prey items that are most abundant pays off, because the predator will have the most success in hunting that prey. Searching for something that is very rare,



Population cycles in snowshoe hare and lynx.

on the other hand, only wastes time and likely results in less food obtained in a given amount of time.

Related to the idea of search image is the phenomenon of switching. Even though a predator may have a preference for one type of prey, at times when that prey is at low densities and other prey is at high densities, the predator will switch to an alternate prey that is at a high density.

All three of these factors—the ability of prey to hide, a search image for the predator, and prey switching by the predator—combine to result in little or no prey taken when prey densities are particularly low. This allows prey populations to recover. Then, the predators increase their consumption until handling time again becomes a limiting factor. When this happens, the rate of consumption increase slows down and consumption evens out at a maximum.

A cannibal is a special type of predator. The term "cannibal" is applied to an individual that consumes another individual of the same species. Typically, cannibalism appears when there is simply not enough food available; in dense populations that are stressed by overcrowding (even when food is adequate); when an individual is weakened and vulnerable to attack as a consequence of social rank; and when vulnerable individuals, such as eggs and nestlings, are available. Frequently, the larger individuals do the cannibalizing, which can serve the purposes of obtaining a meal and reducing competition for food, mates, or territory in the future. SEE ALSO Food Web; Foraging Strategies; Interspecies Interactions.

Jean K. Krejca

Bibliography

Begon, Michael, John L. Harper, and Colin R. Townsend. *Ecology*, 2nd ed. Cambridge, MA: Blackwell Scientific Publications, 1990.

Lotka, A. J. *Elements of Physical Biology.* Baltimore, MD: Williams & Wilkins, 1925.

Ricklefs, Robert E., and Gary L. Miller. *Ecology*, 4th ed. New York: W. H. Freeman, 2000.

Smith, Robert L. *Elements of Ecology*, 2nd ed. New York: Harper & Row, 1986.

Primates

Primates are one group (order) of mammals that evolved about 65 million years ago (mya). The early primates were probably small tree-dwelling (*arboreal*) animals that hunted for insects at night. Today we recognize at least 167 living species in the order primates. We can classify these species (and the primate fossils we find) into two major groups (suborders): prosimians (at least 38 species) and anthropoids (at least 129 species). Prosimians include lemurs (Lemuriformes), galagos and lorises (Lorisiformes) and tarsiers (Tarsiiformes). Anthropoids include New World monkeys (Platyrrhini; from South America), Old World monkeys (from Africa and Asia), apes and humans (Catarrhini). However, some scientists feel that tarsiers should be classified as anthropoids rather than as prosimians.

Prosimians

The first primates to evolve were prosimians. These early primates split into several subgroups about 55 mya. One lineage (see graph) gave rise to Lorisiformes and Lemuriformes, and the other lineage gave rise to Tarsiiformes and the ancestors of all other primate groups (anthropoids). The first New World monkeys probably evolved about 45 mya, followed by Old world monkeys about 40 mya. The first apes appeared about 25 mya, human ancestors (e.g. *Australopithecus*) about 4 mya, and humans (*Homo*) about 2 mya.

Many modern prosimians still resemble the early primates in appearance and life style. For example galagos, lorises, tarsiers and some lemurs (e.g. from the dwarf lemur family) are all small **arboreal** animals that are active at night (nocturnal), hunting for insects or feeding on gum, tree sap, fruit, flowers or leaves. **Nocturnal** prosimians range in size from 60 g (mouse lemur) to about 2800 g (aye-aye). Only the larger lemurs (about 2–10 kg) have made the transition to being active during the day (diurnal). We assume that their increased size allowed them to make this transition because larger animals are less susceptible to being caught by **diurnal** predators. Diurnal lemurs mostly feed on fruits, flowers or leaves, and some of them may even come down from the trees to travel on the ground (e.g. ring-tailed lemurs and sifakas). The largest prosimians that ever lived were gorilla-sized lemurs on the island of Madagascar. However, when humans colonized the island about 1000 years ago these large lemurs were hunted to extinction. Lemuriformes occur exclusively on the island of Madagascar. Lorisiformes can be found all over Africa and Asia, and Tarsiiformes are restricted to Asia.

arboreal living in trees

nocturnal active at night

diural active through the daytime

Anthropoids

All anthropoids (monkeys, apes and humans) are diurnal with one exception: the owl monkey from South America. Monkeys occur in the Old and New World, but apes are restricted to Africa and Asia. Humans probably originated in Africa, but are now distributed worldwide. Monkeys and apes range in size from about 150g (pigmy marmosets) to about 180 kg (gorillas). They have variable diets including insects, fruits, leaves, meat and grains. Among the Old-World monkeys and apes we find many terrestrial species that have left the trees for the ground. One advantage of **terrestrial** life is that these primates can now use their hands more freely to manipulate objects rather than holding on to branches, and that they can gather in larger social groups.

terrestrial living on land

The front and hind paws of a Western lowland gorilla. The opposable thumbs visible in this image are defining characteristics of primates.

The social life of primates is much more complex than that of other mammals. Among primate species we find a wide range of gregariousness from the small nocturnal primates who spend most of their time looking for food alone, only occasionally meeting others (e.g. mouse lemurs), to primates living in small family groups (e.g. tamarins), and to those that live in large social groups (e.g. baboons) with many individuals of different ages, sex, dominance ranks and relatedness. Individuals within such large groups may compete with each other for food and mating partners, they may collaborate together against others, and may even form friendships.

Primate Evolution

Many of the primate characteristics that we see in primates today (e.g. opposable thumbs, nails instead of claws, forward facing eyes) probably evolved as an adaptation to life in trees. For example primate hands have opposable thumbs that allows them to grasp tree branches, but also allows the handling of tools in apes and humans. The replacement of claws by nails went along with an increased sensitivity of the hands and fingertips and an improved ability to manipulate objects. During primate evolution we also see

a trend from having eyes on the side of the face, as most lemurs do, to having both eyes up front as in monkeys, apes and humans. Moving the eyes up front reduces the visual field on the side of the head, but it increases the overlap of the area seen by both eyes simultaneously, allowing for improved depth perception. Now distances (e.g. between branches) can be better estimated, and vision overall is improved. As the eyes are moved up front we also see a shortening of the snout and a reduction of the sense of smell. As a consequence visual signals are now replacing chemical signals as the main form of social communication.

Dispersal

There are still many open questions about primate evolution and how primates became dispersed to the localities where we find them today. For example we do not know how lemurs reached Madagascar. When prosimians evolved in Africa about 65 mya, Madagascar had already separated from the mainland. One possibility that is being discussed is that a few prosimians may have reached Madagascar by rafting on large trees floating in the ocean, and upon arrival, gave rise to all the lemur species. As an alternative our estimated timeline of primate evolution may be incorrect and prosimians may have evolved much earlier. However, this is highly unlikely and not supported by fossil evidence. A similar problem is posed by the exclusive presence of New World monkeys on the South American continent, which was isolated from Africa and North America when anthropoids evolved. Rafting from North America or from Africa is being discussed, but morphological evidence and the direction of past ocean currents seems to favor Africa as the origin of New World monkeys. And finally, the discovery of new anthropoid fossils from Asia in the 1990s suggests that the first anthropoids may have evolved in Asia rather than in Africa.

In addition to the dispersal questions there are still many puzzling questions about the evolution of the diverse primate social systems. For example researchers are studying which factors may determine whether primates live alone or in groups, or which circumstances may shape the nature of the interactions between individual primates.

Anthropologists are interested in studying non-human primates in the hope to gain insight into the evolution of the complex human social behavior. At present, 50 percent of all non-human primate species are threatened by extinction, and unless their habitats are protected from the ever-expanding human population in the near future, many primates will be lost forever.

Kathrin F. Stanger-Hall

Bibliography

Fleagle, John G. *Primate Adaptation and Evolution.* Academic Press, 1988.

Smuts, Barbara B., Dorothy L. Cheney, Robert M. Seyfarth, Richard W. Wrangham, and Thomas, T. Struhsaker, eds. *Primate Societies.* Chicago: The University of Chicago Press, 1987.

Internet Resources

Beard, Chris. "Vertebrate Paleontology." *Carnegie Museum of Natural History.* <http://www.primate.wisc.edu/pin/factsheets/links.html>.

Primate Ancestors in China. <http://www.cruzio.com/~cscp/beard.html>.

Prokaryota

The prokaryota are one of the two major groups of biological organisms. The other is the **eukaryota**. Prokaryotes consist of two kingdoms: the archaebacteria and the eubacteria. Prokaryotes contribute the greatest **biomass** (amount of living matter) of any biological group and inhabit virtually all known earthly environments.

eukaryota a group of organisms containing a membrane bound-nucleus and membrane-bound organelles

biomass the dry weight of organic matter comprising a group of organisms in a particular habitat

organelles membrane bound structures found within a cell

cytoplasm a fluid in eukaryotes that surrounds the nucleus and organelles

Characteristics of Prokaryotic Cells

Prokaryotes exhibit a comparatively simple cellular organization compared to eukaryotes. For example, they lack membrane-bound **organelles** such as chloroplasts and mitochondria. They also lack a nucleus, and their DNA exists in the form of a single, circular chromosome that floats freely in the **cytoplasm**. Sometimes additional DNA is present in the cell in the form of smaller loops called plasmids. All prokaryotes are characterized by a cell membrane and a cell wall. Prokaryotic cell walls are composed of peptidoglycans, which are composed of amino acids and sugar. While some eukaryotes also possess cell walls, theirs are composed of different compounds.

Prokaryotes are sometimes described by their shape. Cocci are round, baccilli are rod-shaped, and spirochetes are helical. Prokaryotes are largely asexual and reproduce by fission (splitting up). However, some exchange of genetic material between individuals does occur via a process called conjugation.

The prokaryota are an extremely varied group. Some prokaryotes are heterotrophs (which obtain nutrients from other biological organisms), while others are **autotrophs** (which create their own nutrients from inorganic matter and energy sources). Some prokaryotic autotrophs photosynthesize. Others use resources not exploited by any known eukaryotes, such as hydrogen, ammonia, and compounds of sulfur or iron.

autotrophs organisms that make their own food

Major Groups of Prokaryotes

Because of the comparative simplicity of the prokaryotes' morphology (shape and structure), much of the classification within the group relies on features of chemistry, metabolism, and physiology, in addition to shape, motility (ablity to move), and structural features.

archae an ancient linage of prokaryotes that live in extreme environments

The archaebacteria. The archaebacteria, or **archaea**, are prokaryotes that inhabit some of the harshest environments that exist. They are extremely primitive, and retain some of the features of the earliest living cells. They differ from other prokaryotes, and from all living organisms, in the unusual lipids that are found in their cell membranes. Many aspects of their biochemistry are similarly distinctive.

There are three groups of archaebacteria. Species have been classified by their physiological characteristics and ecology(habitat, food resources used, etc.), rather than by their phylogenetic relationships (the sequence of branching events in evolutionary history which have resulted in the production of divergent species), which remain unclear. There is some evidence that archaebacteria may be more closely related to the eukaryotes than to the other group of prokaryotes, the eubacteria.

The methanogens are obligate anaerobes that can only survive in oxygen-free environments. Methanogens use hydrogen gas as an energy source. The symbiotic bacteria that live in the guts of species such as cows and sheep and assist in the digestion of plant material are methanogens. They are so named because methane gas is a by-product of their metabolism.

The second group of archaebacteria, the extreme halophiles, inhabit very salty environments such as the Dead Sea and the Great Salt Lake. Finally, the extreme thermophiles, which represent several distinct lineages of archaebacteria, live in very hot environments, near hot springs or in deep ocean thermal vents. It is believed that the extreme thermophiles were the first living creatures on earth.

The eubacteria. The eubacteria form an extremely diverse group. Some major subgroups of eubacteria are discussed below.

The cyanobacteria are also known as blue-green algae. They perform **photosynthesis**, and many species can fix nitrogen (take in atmospheric nitrogen and incorporate it into the body of the organism) as well. Cyanobacteria are found in aerobic environments in which light and water are available.

photosynthesis process of converting sunlight to food

Some cyanobacteria engage in **mutualistic relationships** with fungi to form lichens. They also form a major component of oceanic plankton. Stromatolites are impressive chalk deposits that result from the binding of calcium-rich sediments by large colonies of cyanobacteria.

mutualistic relationships symbiotic relationships where both organisms benefit

Spirochetes are eubacteria with a unique spiral-shaped morphology. Spirochetes move using structures called undoflagella or axial filaments, which are similar to bacterial flagella but allow spirochetes to move by rotating the way a corkscrew rotates. Most species are free living, and some are **pathogens**; spirochetes are responsible for diseases such as syphilis and Lyme disease.

pathogens disease-causing agents such as bacteria, fungi, and viruses

The enterics are a group of rod-shaped eubacteria that live in the intestinal tracts of other organisms. This group includes the well-known *Escherichia coli* and its relatives. Enterics all ferment glucose. They are part of the normal gut **flora** of humans and have been extensively studied.

flora plants

The myxobacteria are significant for having the most complex life cycles among prokaryotes. Myxobacteria aggregate, or come together, to form multicellular "fruiting bodies" that give rise to spores. They live in the soil.

Vibrios are eubacteria characterized by a curved rod shape. They are found primarily in aquatic habitats. Cholera is caused by a vibrio.

Rickettsias and chlamydiae are two groups of obligate parasites or pathogens. Rickettsias require hosts in order to obtain nutrients, while chlamydiae obtain ATP (adenosine-triphosphate, the organic molecule which forms the basis of energy in all living organisms) from host cells. SEE ALSO EUKARYOTA; KINGDOMS OF LIFE.

Jennifer Yeh

Bibliography

Cano, Raul J. and Jaime S. Colome. *Microbiology.* St. Paul: West Publishing Co., 1986.

Curtis, Helena. *Biology.* New York: Worth Publishers, 1989.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton and Co., 1996.

Singleton, Paul. *Bacteria in Biology, Biotechnology, and Medicine.* New York: J. Wiley and Sons, 1997.

Q

Quaternary

The Cenozoic era, 65 million years ago to the present, is divided into two periods, the Tertiary and the Quaternary. The Tertiary period, 65 to 2 million years ago, encompasses the rebuilding of the animal kingdom at the end of the great Cretaceous extinction. From an unpromising beginning as small, nocturnal opportunists, mammals, along with the surviving birds, radiated into the most numerous and diverse life forms to inhabit Earth.

During the Quaternary, 2 million years ago to the present, dramatic climate changes reduced the overall diversity of animal life, yet saw the rise of another remarkable evolutionary opportunist—the **bipedal hominid**.

bipedal walking on two legs

hominid belonging to the family of primates

The earlier phase of the Quaternary, the Pleistocene epoch (2 million to 10,000 years ago), covers the alternating periods of glacial advance and retreat across the Northern Hemisphere and the corresponding effect on plant and animal life. The current chapter of Earth history, the Holocene epoch, deals with the interglacial period which saw the rise to dominance of *Homo sapiens*, the first mammal to shape its environment as well as be shaped by it.

During the Pleistocene, the continents continued their leisurely drift northward. Antarctica remained in place over the South Pole with a steadily increasing ice cap. The land bridge that formed between North and South America continued to disrupt ocean currents by sending colder water into the tropics. These geographic events, coupled with an overall cooling trend of about 10°F, seem to have tipped the planet into a series of "ice ages" interspersed with more brief, temperate periods. During glaciation, ice sheets formed at the North Pole moved across the Northern Hemisphere, locking up huge amounts of global water. Sea levels dropped by as much as 90 meters (300 feet), connecting previously separated land masses. Europe and Britain became contiguous, as did Siberia and Alaska. The more important effect of the glaciers was the decreasing of worldwide humidity. As the tropics became deserts, the larger mammals of Madagascar and Australia were pushed to extinction. As forests declined into grasslands, animals worldwide were pushed into shrinking refuges and competition with one another. Herds of herbivores that thrived on grasslands were unable to cope when the temperate forests expanded northward during the warmer periods. The grasslands in the colder latitudes closer to the pole were not as lush or varied and were nutritionally poorer. The episodic advance and retreat of habitat may have led to the contemporary patterns of migration in warm-blooded animals.

Continual climate stresses and the mingling of species across what had once been barriers contributed to overall decreased diversity. By the end of the Pleistocene 12,000 years ago, the "megafauna"—mammoths, mastodons, 2.5-metric-ton (3-ton) sloths, and *Aepyornis*, the 400-kilogram (900-pound) bird—had all but disappeared. Almost unnoticed among the giants (mammoths, mastodons, and sloths) of the time was a new evolutionary player. Arboreal primates resembling small tree shrews had flourished 60 million years ago giving rise to several groups. These were the **placental** mammals, which had hands with the ability to grasp, eyes that faced forward, and teeth adapted to an **omnivorous** diet. Hand-to-eye coordination, encouraged by

placental having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

omnivorous eating both plants and animals

Era	Period	Epoch	Million Years Before Present
Cenozoic	Quaternary	Holocene	0.01
		Pleistocene	1.6
	Tertiary	Pliocene	5.3
		Miocene	24
		Oligocene	37
		Eocene	58
		Paleocene	66

Quaternary period and surrounding time periods.

a tree-climbing lifestyle, also forced the development of the "thinking" part of the brain.

As environmental stresses worked on the prosimians, they developed into the brainier anthropoids, and finally hominoids, the apelike family that spread throughout Africa, Europe and Asia 25–10 million years ago. Around 4 million years ago, driven by need or lured by opportunity, certain primates took up a new behavior, walking on their hind legs. Bone fossils show that their originally upright posture alternated with four-legged running and climbing. But gradually, the hominid became more and more bipedal, freeing its hands for carrying and manipulating its environment. Upright walking required dramatic changes in anatomy, and these changes further widened the anatomical gap between this protohuman and its closest relative, the quadripedal ape.

Pelvic changes limited the size of the young at birth, creating a longer period of infant dependency. This in turn encouraged the development of a social organization to protect and rear the young. Other benefits of this cooperation fostered more complex arrangements such as foraging together, using of communal shelters, tool making, the specialization of labor, and sharing resources. Thus began the long journey from the tropical treetops into the remotest regions of the globe, by the mammal which possesses the power to affect all life on Earth.

The history of life can be seen as an unending cycle of environmental pressure → change and decline → **adaptive radiation** → and more pressure. *Homo sapiens*, the first species ever to create its own environmental pressures, now stands at the threshold. Will we adapt or decline? SEE ALSO Geological Time Scale.

adaptive radiation a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

Nancy Weaver

Bibliography

Asimov, Isaac. *Life and Time.* Garden City, NY: Doubleday & Company, 1978.

Fortey, Richard. *Fossils: The Key to the Past.* Cambridge, MA: Harvard University Press, 1991.

———. *Life: A Natural History of the First Four Billion Years of Life on Earth.* New York: Viking Press, 1998.

Friday, Adrian, and David S. Ingram, eds. *The Cambridge Encyclopedia of Life Sciences.* London: Cambridge University, 1985.

Gould, Stephen Jay, ed. *The Book of Life.* New York: W. W. Norton & Company, 1993.

Lambert, David. *The Field Guide to Prehistoric Life.* New York: Facts on File, 1985.

McLoughlan, John C. *Synapsida: A New Look Into the Origin of Mammals.* New York: Viking Press, 1980.

Steele, Rodney, and Anthony Harvey, eds. *The Encyclopedia of Prehistoric Life.* New York: McGraw Hill, 1979.

Wade, Nicholas, ed. *The Science Times Book of Fossils and Evolution.* New York: The Lyons Press, 1998.

R

Reproduction, Asexual and Sexual

Organisms must reproduce and, in the context of evolution, must choose among different methods to do so. There are two major strategies for reproduction—sexual and asexual. Each tactic has its own advantages and disadvantages, and each is appropriate for certain situations. Vertebrates, such as humans, are almost exclusively sexual in their reproduction, many simpler animals are asexual. To decide which reproductive strategy may prove advantageous in a given set of circumstances, it is important to understand how they differ.

Asexual reproduction

Asexual reproduction takes a variety of forms. The simplest one-celled organisms may reproduce by binary fission, in which the cells simply divide in half. This form of reproduction creates a clone of the parent, and has the benefit of usually being very quick and energy efficient. For example, bacteria that reproduce by binary fission can give rise to **progeny** every few hours.

Some organisms, such as *Cryptosporidium parvum*, a **sporozoan** that causes traveler's diarrhea, may utilize multiple fission, in which they split into more than one offspring simultaneously. In multicellular organisms, a similar tactic is called fragmentation. In this process, small pieces break off and grow into new organisms. Still other organisms reproduce by **budding**, in which a smaller copy of the parent grows on the body and eventually splits off to begin life on its own.

All these variations of asexual reproduction have one thing in common, the offspring is a direct clone of the parent. The purpose of reproduction is to propagate one's own genes. Evolutionarily, asexual reproduction is a good deal for the parent. It is quick, simple, and the genes of the parent will not be diluted by those of another individual. In addition, an organism that reproduces asexually can reproduce about twice as fast as one that reproduces sexually. This has shown to be true with the whiptail lizard of the southwestern United States, which can reproduce both sexually and asexually under different conditions.

Sexual reproduction

Sexual reproduction is more much complex than asexual reproduction. It requires the production of sex cells, or **gametes**, which have half the number of **chromosomes** of all other cells in the organism. When the organism needs to make sex cells, it undergoes meiosis, which produces **haploid cells** (one copy of the **genome**) from **diploid cells** (two copies of the genome). A key aspect of meiosis is that the two copies of a single chro-

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

progeny offspring

sporozoans parasitic protozoans

budding a type of asexual reproduction where the offspring grow off the parent

gametes reproductive cells that only have one set of chromosomes

chromosomes structures in the cell that carry genetic information

haploid cells cells with only one set of chromosomes

genome an organism's genetic material

diploid cells cells with two sets of chromosomes

There are a few species of vertebrates that reproduce asexually. The whiptail lizard, which lives in the desert grasslands of the southwestern United States, may reproduce sexually or asexually. Do asexually-reproducing lizards show less genetic variability than sexually-reproducing ones? They do, just like the theory says they should.

mosome can cross over to create a completely new chromosome that contains a new combination of genes. The net effect of crossing-over is that genes on a specific chromosome can change position from one chromosome to the next. This means that genes from both parents may end up next to each other on the same chromosome. Where genes are concerned, switching from chromosome to chromosome is a good way to ensure they will keep active in a given population.

Once the gametes are made in the male and female, they must meet with one another to form offspring. The sperm from the male provides one copy of a genome. The egg from the female provides another copy of a different genome. Thus, the offspring of sexually reproducing organisms has more than one opportunity to switch genes around—crossing-over and the union of the two parents.

Comparing Sexual and Asexual Reproduction

However, note how much energy sexual reproduction takes. The sex cells must be made, and as each parent contributes only half the genome, it propagates only half as many genes from each offspring as does an asexually reproducing organism. Recall that an organism is most interested in propagating its genes; indeed, that is the whole point of reproduction. To reproduce sexually is to reduce the amount of genetic material one reproduces by half, and this reduction does not even take into account the effort sexually reproducing organisms must make to find mates, then impress, select, or defend them. Nevertheless, nearly all higher animals reproduce sexually. Why? The answer to this question is far from settled, but biologists have a few good clues.

The most important thing about sexual reproduction is its ability to switch around successful genes. If it is beneficial to an organism's survival to be both tall and have blue eyes, a short, blue-eyed parent and a tall, brown-eyed parent can get together and stand a good chance of producing offspring with both characteristics. If they reproduced asexually, a short, blue-eyed parent would have to wait around for a height-inducing genetic mutation to change height and eye color. And because mutations, which are basically genetic mistakes, tend to cause bad effects, the mutation rate in most organisms is exceedingly slow. While it would take only a generation for sexually-reproducing parents to beget tall offspring with blue eyes, it might take an asexually-reproducing parent hundreds or thousands of generations!

Asexually reproducing organisms do not readily share genetic material, but they do reproduce much faster. And because asexually reproducing organisms reproduce faster, they do exceptionally well in situations where they have no competition. With sexually-reproducing competition nearby, however, the asexual organisms will quickly be outadapted and outevolved by their neighbors, even though the asexual organisms may have superior numbers due to fast reproduction. Many biologists think that intense competition gives rise to sexual reproduction, because the competition requires rapid innovation and distribution of the most successful genes.

Although these arguments for the existence of sexual reproduction might seem evolutionarily sound, the alleged advantages of sexual reproduction over asexual reproduction are still quite controversial among biologists. Some biologists think that only replicating half of your genes in exchange for sexual reproduction is not an even trade. Others suggest that dilution of groups of genes does not matter. Furthermore, a sexually reproducing organism must expend a great amount of effort to find a mate, in both behavior and new body structures and appendages. Biologists believe that **sexual selection** drives gender size and appearance, plumage, behavior, and many other energetically expensive strategies.

sexual selection selection based on secondary sex characteristics that leads to greater sexual dimorphism or differences between the sexes

Can it be possible that sexual selection, with all its demands, is worth the moderate amount of recombination that results from sexual reproduction? If not, why do all vertebrates, many invertebrates, and most plants sexually reproduce? Many prominent biologists have considered these questions, such Richard Dawkins, J. Maynard Smith, G. C. Williams, and others.

It seems likely that the ability to swap around already successful genes, rather than being forced to sit around and waiting for mutations, is a more successful strategy for complex organisms. And less complex organisms can get by without the larger energy and resource investment that sexual reproduction demands. SEE ALSO EGG; EMBRYONIC DEVELOPMENT; FERTILIZATION; REPRODUCTIVE SYSTEM.

Ian Quigley

Bibliography

Conn, David Bruce. *Atlas of Invertebrate Reproduction and Development.* New York: John Wiley and Sons, 2000.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Hayssen, Virginia, Ari Van Tienhoven, Ans Van Tienhoven, and Sydney Arthur Asdell. *Asdell's Patterns of Mammalian Reproduction: A Compendium of Species-Specific Data.* Ithaca, NY: Comstock Publication Associates, 1993.

Norris, David O., and Richard E. Jones, eds. *Hormones and Reproduction in Fishes, Amphibians, and Reptiles.* New York: Plenum Press, 1987.

Purves, William K., and Gordon H. Orians. *Life: The Science of Biology.* Sunderland, MA: Sinauer Associates Inc., 1987.

Reproductive System *See Endocrine and Reproductive System.*

Reptilia

Most reptiles can be classified into three large groups: the turtles (order Chelonia), the snakes and lizards (order Squamata), and the alligators and crocodiles (order Crocodilia). Most reptiles share a number of general morphological features. In general, reptiles are lung-breathing vertebrates with two pairs of limbs and a horny, scaly skin. Reptiles are **amniotes**, which means that their large, yolky eggs have a protective layer called an **amnion** which prevents them from drying out on land. Rather than laying eggs, some snakes and lizards bear their young live.

amniotes vertebrates which have a fluid-filled sac that surrounds the embryo

amnion the membrane that forms a sac around an embryo

Nonavian reptiles are **poikilothermic** (cold-blooded) creatures, which means that they derive their body heat from external sources (in contrast to homothermic animals that maintain a constant body temperature through internal mechanisms). Contrary to popular belief, the "cold-bloodedness"

poikilothermic an animal that cannot regulate its internal temperature; also called cold-blooded

of reptiles does not mean that they maintain low body temperatures. Reptiles control their body temperature through a process called thermoregulation, and their internal temperature can fluctuate greatly according to their surroundings. Researchers have found that many reptiles exert precise control over body temperature by moving around to different areas within their surrounding habitat.

Chelonia

Turtles are classified into two sister groups, Pleurodira and *Cryptodira.* Pleurodires (side-necked turtles) bring their head and neck against their body by bending the neck to the side. Most cryptodires fully retract the head and neck into the shell, although certain groups such as sea turtles and snapping turtles have lost this ability. All pleurodires are aquatic, while cryptodires include **terrestrial**, aquatic, and marine forms.

terrestrial living on land

Turtles are easily distinguished from other reptiles by the protective shell that encases their body. The turtle shell has two parts, a carapace on top and a plastron under the belly, which incorporate the ribs, vertebrae, and elements of the turtle's **pectoral** (front limb) girdle. The turtle's head, limbs, and tail can protrude from and retract into the shell to varying degrees, depending on the species. The plastron of the box turtle has a hinge that allows the shell to snap shut and provide further protection for the head.

pectoral of, in, or on the chest

Turtles can have many different forms of shells. The bony elements of the shell can be covered with scaly, armored plates, (all land turtles and most aquatic and marine turtles) or leathery skin (soft-shelled turtles and the ocean-dwelling leatherback turtle). Terrestrial turtle shells have relatively high domes; the shells of water-dwelling turtles are flatter and more streamlined. Most extant turtles have shells that are less than 60 centimeters (2 feet) long, although sea turtles can grow up to a shell length of 2.7 meters (9 feet).

All turtles lay eggs. They do not guard their eggs or young while they are developing, but instead leave the eggs buried in loose dirt or sand. The survival rate of eggs and newborn turtles is very low, since turtles will produce large numbers of offspring to compensate for high mortality rather than fewer, stronger offspring that would have greater potential to survive. Some turtles lay multiple groups of eggs (called clutches) during each season, and the clutches of sea turtles may contain up to two hundred eggs. Developing embryos get their nutrients from the yolk in the egg and only become **carnivorous** or omnivorous after they hatch. Most turtles have a varied diet of small insects and worms, crustaceans, nonfibrous plants, or fish. In many turtle species, the sex of the offspring is determined by the temperature at which the eggs are maintained as the young turtles develop.

carnivorous describes animals that eat other animals

Crocodylia

Crocodilians are large, amphibious, and carnivorous reptiles. Their long bodies, powerful jaws, and muscular tail are covered with heavy armor with bony plates. These aggressive predators have conical teeth and short legs with webbed, clawed toes. The largest crocodilian, the Nile crocodile, reaches a length of about 6 meters (20 feet). Many scientists believe that crocodilians are the closest living relatives to birds, but this relationship is still under debate.

There are three major groups in Crocodilya—alligators, crocodiles, and gavials. These three groups are distinguished by characteristics of the teeth and jaw, although all crocodilians are similar with respect to ecology, morphology, and behavior.

Crocodilians are found in swamps, rivers, and lakes of tropical and subtropical habitats in the Northern and Southern Hemispheres. They spend most of their time in the water but are also known to travel long distances over land. They move from place to place in several ways, including sculling, in water (propelling themselves using a side-to-side tale motion), belly sliding (into water), high walking, and galloping. Crocodilians are sit-and-wait predators who float passively in the water while awaiting potential prey. The can knock large mammals into the water with a swing of their powerful tail. With their powerful jaws, some species clamp onto their victim's legs and tear the prey apart by rotating themselves rapidly in the water in an "alligator roll."

Crocodilians lay eggs in nests. After laying her eggs, the mother keeps them warm by covering them with mud and decaying plant material. She guards her eggs until the squeaks of the young signal that the babies are ready to hatch. The mother then knocks the dirt off of the eggs to help the young hatch, but provides no additional care for her young.

Rhynchocephalia

extant still living

Two **extant** species of tuatara (genus *Sphenodon*) belong to this sister group of the squamates. The tuatara is lizardlike in general appearance, but is distinguishable from lizards by a number of characters involving tooth type and arrangement, skull morphology, and genitalia. The tuatara is the only nonavian reptile without a organ used exculsively for sexual intercourse. Like birds, male tuataras transfer sperm to the female while their cloaca (an opening through which feces is expelled, and through which reproduction occurs) are pressed together.

Tuataras are found only in New Zealand, where they live in burrows they construct or those that have been abandoned by other animals. During the daytime they bask in the sun near the entrance to their burrows, but are most active at night. They feed on insects, bird eggs, and young birds. Both species of tuatara are egg layers, and newborn young emerge after a thirteen-month incubation period. Tuataras reach sexual maturation after about twenty years and can live up to the age of fifty. Adult tuataras may reach a total length of up to almost 60 centimeters (two feet).

The human introduction of certain animals to New Zealand has placed many tuatara populations under threat of extinction. Tuataras are slow-moving, and are thus easily captured and eaten by rats, cats, and pigs. An estimated 100,000 tuataras remain on offshore islands near New Zealand. There are no tuataras on the New Zealand mainland. About half of the suriving tuatara live on Stephens Island in Cook Strait, and there have been proposals to relocate some individuals to sanctuaries on other islands so that more of them may be seen in the wild. Tuataras are currently listed as an endangered species by conservation groups, and human interaction with this species is strictly regulated.

Squamata

The squamates are the most diverse group of non-avian reptiles. Squamata consist of lizards (Sauria), snakes (Serpentes) and amphisbaenians (Amphisbaenia). Lizards are divided into two major groups, Iguania and Scleroglossa. These two groups are generally distinguishable by differences in tongue morphology and function. Iguanians have fleshy tongues that are used while capturing prey. The mucous coating on the tongue helps the lizard to pick up small insects, vertebrates, and plant matter, and aids in swallowing. The tongue of the chameleon is a well-known example of this iguanian trait.

Scleroglossans have thin, forked tongues that are used in chemosensation (the process of gathering information about their environment through detecting chemical cues). These lizards use their tongues for "smelling" the air around them and use their jaws for grabbing prey. Snakes and amphisbaenians are both scleroglossans. Iguanians are territorial sit-and-wait predators; scleroglossans are active foragers that generally do not guard territories.

Most of the three thousand species of saurians (lizards, except for snakes and amphisbaenians) have legs, movable eyelids, external ear openings, and long tails. Some species are limbless. Saurians range in size from the 3-centimeter (1.2-inch) long gecko to the 3-meter (10-foot) long Komodo dragon. All saurians are terrestrial, but some species may live in trees and other foliage, under rocks, or in burrows.

Saurians have different ways of reproducing. Most species are **oviparous** (egg-laying), while other species are **viviparous** (bearing live young). Among viviparous lizards, some species rely exclusively on the yolk of the egg to provide nutrients to the developing embryo. In these lizards, the eggs that are retained in the mother's uterus during embryonic development resemble the eggs of oviparous lizards but do not have a hard, **calcified** shell. Instead, there is a thin shell membrane through which water, gas (oxygen and carbon dioxide), and waste materials can pass. In a smaller number of species, the mother transfers nutrients to her young through a **placenta**. The placenta is a region of the mother's uterus characterized by a high density of blood vessels. Through these blood vessels, water, gases, and waste products pass between the blood of the mother and her developing young.

oviparous having offspring that hatch from eggs external to the body

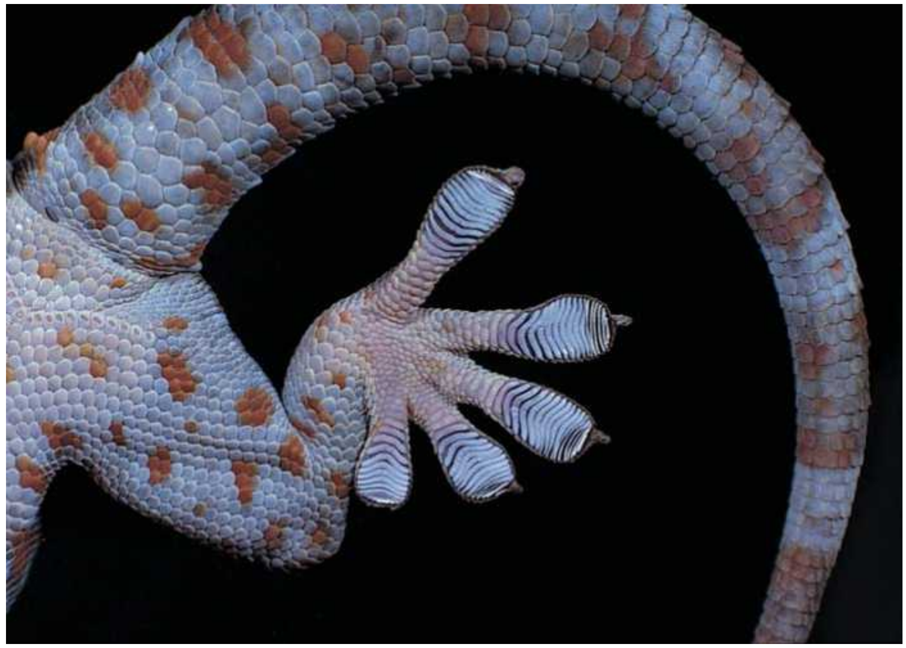
viviparous having young born alive after being nourished by a placenta between the mother and offspring

calcified made hard through deposition of calcium salts

placenta a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

Most saurians are diurnal (active only during the daytime) and regulate their body temperature by basking in the sunlight during the early morning hours and hiding in the shade during hotter periods. Geckos have special physiological characteristics that allow them to pursue a nocturnal (active during the nighttime) lifestyle. For example, the muscles of geckos are able to function under cooler temperatures than other lizards are use to. Saurians spend much of their time feeding, mostly on insects. Larger species also feed on other lizards and on small mammals. Several iguanian species feed exclusively on plants.

Serpents (snakes) are secretive, solitary predators that are found in almost all types of habitat worldwide, except near the North and South Poles. They are limbless, lack eyelids, and have only one lung. Their slim, long body form allows them to search for prey in burrows, nests, and crevices. Many snakes are also excellent tree climbers and swimmers, and several species are fully aquatic. Like saurians, snakes as a group exhibit both egg-laying and live-bearing forms of reproduction.



THe underside of the backfoot of a Tokay Gecko.

Snakes rely mainly on their senses of sight and smell for information about their surroundings. Individuals use chemical signals to communicate to each other, especially during courtship. Some species of boids (such as boa constrictors) and vipers (such as asps and adders) have also evolved heat-sensing **infrared** receptors called pit organs. Studies have shown that many snake species that lack pit organs can also sense infrared radiation, although to a lesser degree.

infrared an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red, heat is carried on infrared waves

Amphisbaenians are elongate, burrowing squamates. With the exception of the genus *Bipes*, which has forelimbs, amphisbaenians are limbless. All species lay eggs. They occupy habitats ranging from tropical rain forests to deserts. SEE ALSO Phylogenetic Relationships of Major Groups.

Judy P. Sheen

Bibliography

Grasse, Pierre-Paul, ed. *Encyclopedia of the Animal World: Reptiles.* New York: LaRousse & Co., 1975.

Pough, F. H., Robin M. Andrews, John E. Cadle, Martha L. Crump, Alan H. Savitzky, and Kentwood D. Wells. *Herpetology.* Upper Saddle River, NJ: Prentice Hall, 1998.

Stebbins, Robert C. *A Field Guide to Western Reptiles and Amphibians.* 2nd ed. Boston: Houghton Mifflin, 1985.

Respiration

Organisms respire in order to obtain oxygen and get rid of carbon dioxide. Oxygen drives cellular metabolism, the process in which glucose from food is converted to usable energy resources in the form of **adenosine triphosphate**, (ATP). Carbon dioxide is a by-product of this reaction. Aquatic species obtain oxygen from water, while **terrestrial** species obtain it from air. These two media, water and air, are often associated with different respiratory strategies. This is partly because the amount of oxygen in air is far greater than that dissolved in water. In addition, air requires much less energy to pump than does water, which is considerably more dense.

adenosine triphoshate an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

terrestrial living on land

Many organisms do not require special respiratory organs because they obtain an adequate supply of oxygen through diffusion across the body surface. This is known as cutaneous gas exchange. Cutaneous gas exchange is often employed by small animals, which have a high ratio of surface area to volume. Some larger animals, such as certain annelid worms, are also able to use cutaneous exchange because of their large surface areas and modest energy demands.

Larger organisms almost invariably possess special respiratory organs. Respiratory specializations can be grouped into three major categories: **gills**, lungs, and **trachea**. All three types of organs evolved to provide extensive surface areas for use in gas exchange.

gills site of gas exchange between the blood of aquatic animals such as fish and the water

trachea the tube in air-breathing vertebrates that extends from the larynx to the bronchi

Gills

Gills describe respiratory structures formed from external extensions of the body. They characterize diverse species, including some annelids, some arthropods such as **horseshoe crabs** and crustaceans, mollusks, certain **echinoderms**, and vertebrates such as fish and larval amphibians. Gills are typically found in aquatic environments, although some terrestrial species, such as terrestrial crustaceans, make use of them as well. Species with very active lifestyles tend to have more highly developed gills, with considerable surface areas for gas exchange. In the fishes, for example, a series of bony **gill arches** supports many primary **gill filaments**, each of which has numerous minute folds referred to as the secondary gill lamellae.

horseshoe crabs a "living" fossil in the class of arthropods

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

gill arches arches of cartilage that support the gills of fishes and some amphibians

gill filaments the site of gas exchange in aquatic animals such as fish and some amphibians

Oxygen is absorbed into the bloodstream as oxygenated water flows over the gills. Some aquatic species rely on natural currents to carry oxygenated water to them. Others expend energy to force water over the gills. Among fishes, ram ventilators swim rapidly with open mouths, forcing water to flow into the mouth, across the gills, and out through the spiracle or **operculum**. Active swimmers, such as sharks and tuna, often employ ram ventilation.

operculum a flap covering an opening

Other fish species use a complex series of mouth and opercular expansions and compressions to pump water over the gills. Many aquatic species, including fishes, are characterized by countercurrent exchange, a system in which oxygenated water and deoxygenated blood flow in opposite directions, maximizing the amount of oxygen **absorption** that occurs.

absorption the movement of water and nutrients

Lungs

Lungs characterize many terrestrial species. Unlike gills, lungs are series of internal branchings that function in respiration. In humans, for example, air flows initially into the trachea. The trachea then splits into two bronchi, which split several more times into smaller and smaller bronchioles. These end at small sacs called **alveoli**, which are closely surrounded by capillary blood vessels.

alveoli thin-walled sacs in the lungs where blood in capillaries and air in the lungs exchange gases

It is in the alveoli that gas exchange actually occurs, with oxygen diffusing across the alveoli into the bloodstream. The alveoli are lined with substances called surfactants, which help to prevent them from collapsing. Humans have approximately 150 million alveoli. As with gills, the surface area available for gas exchange can be quite large.

Lungs characterize a diverse array of terrestrial species, including gastropod mollusks such as snails and slugs, spiders (whose respiratory organs

are called book lungs because they contain a series of lamellae that resemble pages), and most terrestrial vertebrates.

Gas exchange using lungs depends on ventilation, the process through which air is brought from the external environment into the lungs. Ventilation mechanisms vary from taxon to taxon. In amphibian species, air is actively gulped, or forced into the lung by positive pressure. Reptiles, birds, and mammals use negative pressure to ventilate the lungs. These species expand the volume of the **thoracic** cavity where the lungs lie, causing air to be drawn into the lungs.

thoracic related to the chest area

Creating negative pressure in the thoracic cavity is accomplished in a variety of ways. Lizards and snakes use special muscles to expand their rib cages. Turtles extend forelimbs and hindlimbs out of their shells to create negative pressure. In crocodiles, the liver is pulled posteriorly, towards the rear of the animal, in order to expand the thoracic cavity. Mammals employ a combination of contracting their diaphragm, a muscular sheet that lies at the base of the thoracic cavity, and expanding the rib cage.

Birds have evolved unusually efficient respiratory systems, most likely because of the tremendous energy required for flight. The bird respiratory system includes large, well-developed lungs and a series of air sacs connected to the lungs and trachea. Some of the air sacs occupy the hollow spaces in larger bones such as the humerus and femur. The air sacs are involved in ventilating the lungs, and allow for a one-directional flow of air through the respiratory system. This is unique among the terrestrial vertebrates.

The respiratory exchange system of birds is described as crosscurrent exchange. Crosscurrent exchange is less efficient than the countercurrent exchange system of fishes. However, because the concentration of oxygen in air is much greater than in water, this method is extremely effective.

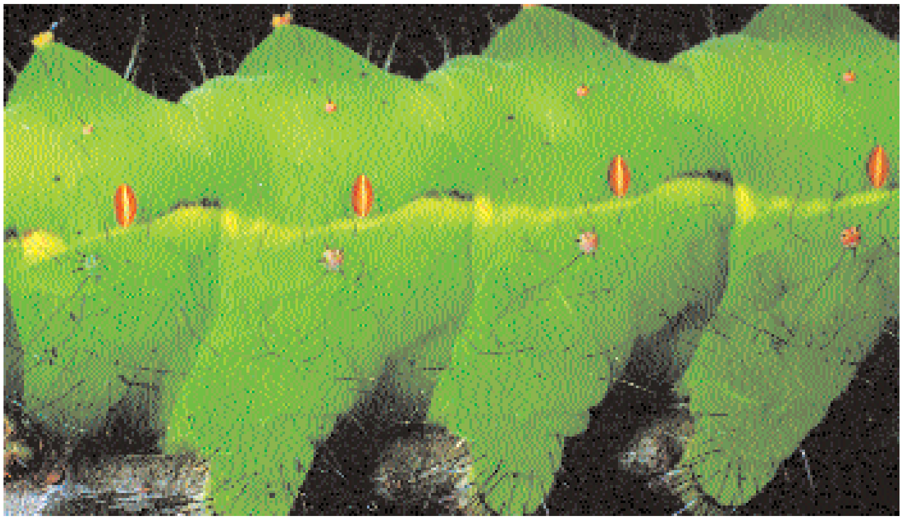
Cutaneous respiration may supplement gas exchange through lungs or gills in many species. It is critical in most amphibians, which are characterized by moist skins consisting of live cells in which oxygen can dissolve and then be taken up and used by the organism. Some amphibians have evolved special adaptations that make gas exchange across the skin more effective. In some aquatic **salamanders**, for example, the skin has become highly folded, an adaptation that increases the surface area available for gas absorption. There is even a large family of salamanders, the family Plethodontidae, in which the lungs have been lost entirely. This group relies almost entirely on cutaneous exchange. Similar developments are seen in other groups, including some species of slugs.

salamander a four-legged amphibian with an elongated body

The Tracheal System

The tracheal system is a respiratory system that is unique to air-breathing arthropods such as millipedes, centipedes, and insects. The tracheal system consists of air-filled tubes that extend into the body from pores on the body surface known as spiracles. These tubules provide oxygen to tissues directly. Centipedes have one spiracle per segment, and millipedes have two per segment. The number of spiracles in insects varies, but there can be as many as ten pairs.

The spiracle is merely an opening to the environment in primitive insect species. However, more advanced groups can close their spiracles, and



The body of a caterpillar magnified to show its spiracles.

some are even outfitted with filtering devices. The ability to close the spiracle is advantageous because it allows for water conservation. Interestingly, the limits of the tracheal gas exchange system are believed to restrict insects to their generally small size. Insects, unlike animals such as vertebrates, do not use their circulatory systems to aid in the transport of oxygen.

Water is lost from all respiratory surfaces in air-breathing organisms. This is particularly serious for species that rely on cutaneous exchange, and explains why most species of amphibians are limited to fairly moist habitats.

Respiration is regulated either by the central nervous system or by more localized mechanisms. Vertebrates have a respiratory pacemaker in the medulla of the brain. In addition, respiratory rates are influenced by internal gas concentrations. Aquatic species usually regulate respiration based on internal oxygen levels, whereas terrestrial species tend to rely on internal carbon dioxide levels. SEE ALSO Digestion.

Jennifer Yeh

Bibliography

Curtis, Helena. *Biology.* New York: Worth Publishers, 1989.

Gould, James L., and William T. Keeton. *Biological Science*, 6th ed. New York: W. W. Norton, 1996.

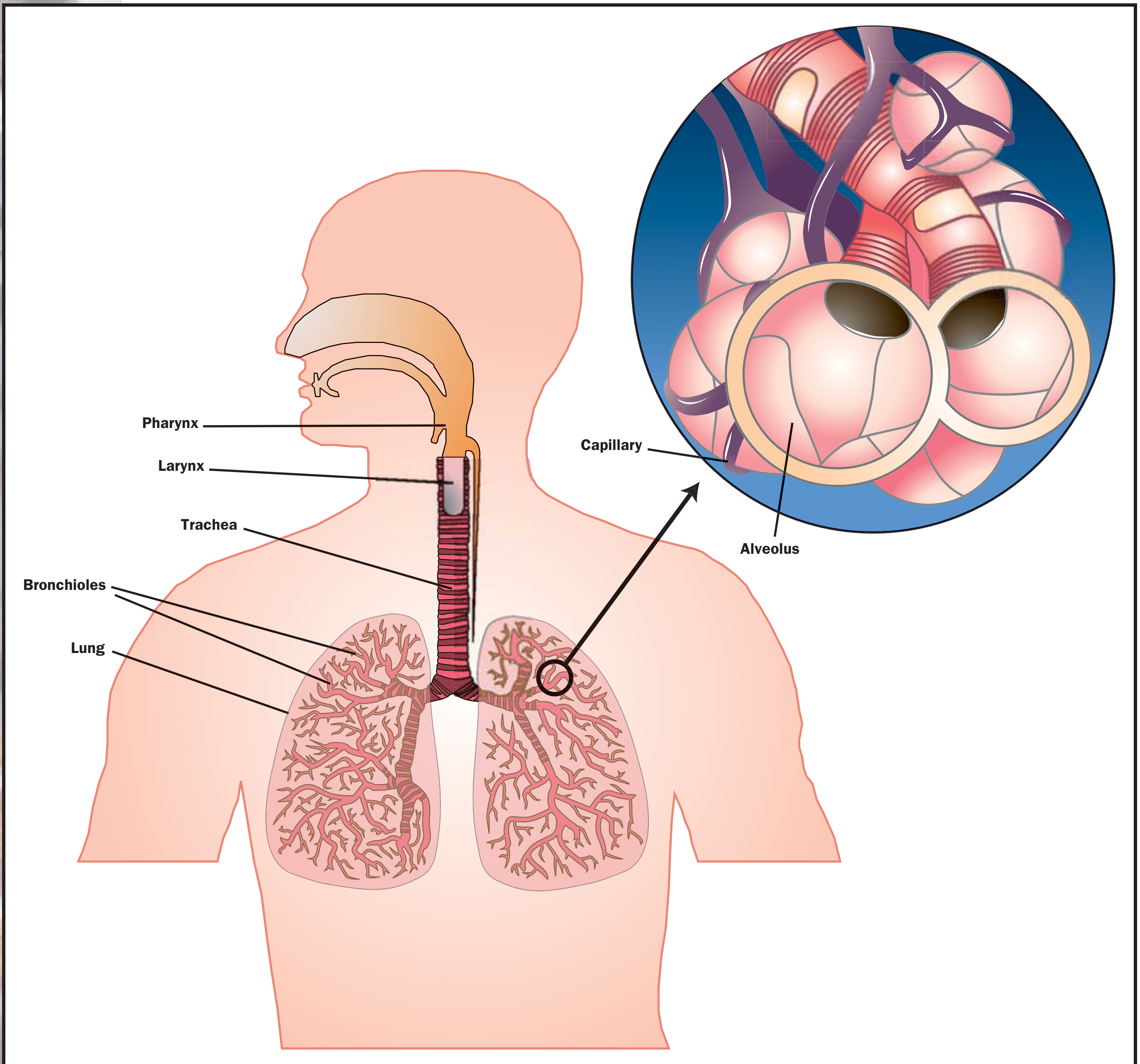
Hickman, Cleveland P., Larry S. Roberts, and Allan Larson. *Animal Diversity.* Dubuque, IA: William C. Brown, 1994.

Hildebrand, Milton, and Viola Hildebrand. *Analysis of Vertebrate Structure*. New York: John Wiley, 1994.

Withers, Philip C. *Comparative Animal Physiology.* Fort Worth, TX: Saunders College Publishing, 1992.

Respiratory System

All animals require oxygen. Oxygen enables living things to metabolize (or burn) nutrients, which releases the energy they need to grow, reproduce, and maintain life processes. Some animals can exist for months on fats or other foods stored in their bodies, and many can live a shorter time without



The human respiratory system. Redrawn from Johnson, 1998.

water. Yet few can survive for long without oxygen because little can be stored in the body. Most animals obtain oxygen from their environment. It is generally believed that life originated in the oceans, where many animals still live, obtaining their oxygen in a dissolved form from the water. In the course of evolution, various animals have become earth dwellers and have developed structures that allow them to breathe air.

Along with supplying oxygen, the respiratory system assists in the removal of carbon dioxide, preventing a dangerous and potentially lethal buildup of this waste product. The respiratory system also helps regulate the balance of acid and bases in tissues, which is a crucial process that enables cells to function. Without the prompt of conscious thought, the respiratory system carries out this life-sustaining activity. If any of the func-

tions of the system are interrupted for more than a few minutes, serious and irreversible damage to body tissues would occur, and possibly result in death.

Respiratory Systems of Various Species

Depending on the animal, the organs and structures of the respiratory system vary in composition and complexity. The respiratory system is composed of the organs that deliver oxygen to the circulatory system for movement or transport to all of the cells in the body. Organs or systems such as body covering, gills, lungs, or trachea allow the movement of gases between the animal and its environment. These structures vary in appearance but function in a similar way by allowing gases to be exchanged.

Animals obtain oxygen in a number of ways: (1) from water or air through a moist surface directly into the body (protozoan); (2) from air or water through the skin to blood vessels (earthworms); (3) from air through gills to a system of air ducts or trachae (insects); (4) from water through moist gill surfaces to blood vessels (fishes, amphibians); (5) from air through moist lung surfaces to blood vessels (reptiles, mammals, humans).

In one-celled **aquatic** animals, such as protozoans, and in sponges, jellyfish, and other aquatic organisms that are a few cell layers thick, oxygen and carbon dioxide diffuse directly between the water and the cell. This process of diffusion works because all cells of the animal are within a few millimeters of an oxygen source.

aquatic living in water

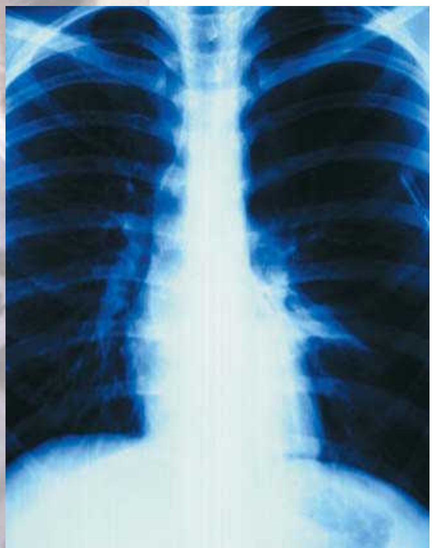
Insects, centipedes, millipedes, and some arachnids have fine tubes or trachea connecting all parts of the body to small openings on the surface of the animal. Movements of the thoracic and abdominal parts and the animal's small size enable oxygen and carbon dioxide to be transported from the trachea to the blood by way of diffusion.

In more complex animals, respiration requires a blood circulatory system and gills, in combination with blood, blood vessels, and a heart. Many aquatic animals have gills, thin-walled filaments that increase the surface area and increase the amount of available oxygen. The oxygen and carbon dioxide exchange occurs between the surrounding water and the blood within the gills. The gills of some larvae and worms are simply exposed to the water, while some aquatic crustaceans, such as crayfish, have special adaptations to force water over their gills. The gills of fishes and tadpoles are located in chambers at the sides of the throat, with water taken into the mouth and forced out over gills.

All land vertebrates, including most amphibians, all reptiles, birds and mammals have lungs that enable these animals to get oxygen from air. A heart and a closed circulatory system work with the lungs to deliver oxygen and to remove carbon dioxide from the cells. A lung is a chamber lined with moist cells that have an abundance of blood capillaries. These membranes take different forms. In amphibians and reptiles they can form a single balloon-like sac. In animals that require large amounts of oxygen, the lungs are a spongy mass composed of millions of tiny air sacs called **alveoli** that supply an enormous surface area for the transfer of gases.

alveoli thin-walled sacs in the lungs where blood in capillaries and air in the lungs exchange gases

In birds a special adaptation allows for the high-energy demands of flight. The lungs have two openings, one for taking in oxygen-filled air, the



An x ray of the human lungs. The finely detailed structure of the lungs is difficult to see in this image.

hemoglobin an iron containing protein found in red blood cells that binds with oxygen

other for expelling the carbon dioxide. Air flows through them rather than in and out as in the other lunged vertebrates.

Respiratory System in Humans

The human respiratory system consists of the nasal cavity, throat (pharynx), vocal area (larynx), windpipe (trachea), bronchi, and lungs. Air is taken in through the mouth and or nose. The nasal passages are covered with mucous membranes that have tiny hairlike projections called cilia. They keep dust and foreign particles from reaching the lungs.

Approximately halfway down the chest the trachea or windpipe branches into two bronchi, one to each lung. Each branch enters a lung, where it divides into increasingly smaller branches known as bronchioles. Each bronchiole joins a cluster of tiny airsacs called alveoli. The pair of human lungs contain nearly 300 million of these clusters and together can hold nearly four quarts of air. After oxygen has crossed the alveolar membrane, oxygen is delivered to the cells by the pigment **hemoglobin**, found in blood.

The lungs in humans are cone-shaped and are located inside the thorax or chest, in the cavity framed by the rib cage. One lung is on either side of the heart. The right lung has three lobes; the left has two lobes. A thin membrane known as pleura covers the lungs, which are porous and spongy. The base of each lung rests on the diaphragm, a strong sheet of muscle that separates the chest and abdominal cavities.

The respiratory center at the base of the brain is a cluster of nerve cells that control breathing by sending impulses to the nerves in the spinal cord. These signals stimulate the diaphragm and muscles between the ribs for automatic inhalation. During inhalation the rib muscles elevate the ribs and the diaphragm moves downward, increasing the chest cavity. Air pressure in the lungs is reduced, and air flows into them. During the exhalation, the rib muscles and diaphragm relax and the chest cavity contracts. The average adult takes about sixteen breaths per minute while awake and about six to eight per minute while sleeping. If breathing stops for any reason, death soon follows, unless breathing movements are artificially restored by mouth to mouth breathing. SEE ALSO Circulatory System; Transport.

Leslie Hutchinson

Bibliography

Hickman, Cleveland, Larry Roberts, and Frances Hickman. *Integrated Principles of Zoology*, 8th ed. St. Louis, MO: Times Mirror/Mosby College Publishing, 1990.

Johnson, George B. *Biology: Visualizing Life*. New York: Holt, Rinehart and Winston, Inc., 1998.

Randall, David, Warren Burggren, and Kathleen French. *Eckert Animal Physiology: Mechanisms and Adaptations*, 4th ed. New York: W. H. Freeman, 1997.

Internet Resources

"Respiratory System." *Britannica Online*. 1994–2000. Encyclopedia Britannica. <http://www.eb.com/>.

Roundworms *See Nematoda.*

Rotifera

The 1,500 to 2,000 species in the phylum Rotifera, like other members of the kingdom Animalia, are multicellular, heterotrophic (dependent on other organisms for nutrients), and lack cell walls. But rotifers possess a unique combination of traits that distinguish them from other animals, including **bilateral symmetry** and a **pseudocoelom**, a fluid-filled body cavity between two different layers of embryonic tissue. The pseudocoelom serves as a sort of circulatory system and provides space for a complete digestive tract and organs. It is also found in the closely related phylum Nematoda, a very common group of roundworm species. Unlike nematodes, which tend to live in moist soil, rotifers generally inhabit fresh water, although some species can be found in salt water or wet soil. Rotifers (Latin for "wheel bearers") have an unusual mode of transportation: a crown of beating cilia surrounds their mouth, propelling the animal head-first through the water. Rotifers eat protists, bits of vegetation, and microscopic animals (such as young larvae), which they suck into their mouths with the vortex generated by their cilia. Their jaws are hard and their pharynx is muscular, allowing them to grind up their food.

bilateral symmetry characteristic of an animal that can be separated into two identical mirror image halves

pseudocoelom a body cavity that is not entirely surrounded by mesoderm

Another unusual rotifer trait is parthenogenesis, an asexual mode of reproduction in which females produce unfertilized eggs which are essentially clones of the mother. Some parthenogenetic species are completely female, while others produce degenerate, or poorly developed, males whose sole purpose is to fertilize eggs under stressful environmental conditions. Fertilized eggs are more resistant to drying out than unfertilized eggs. When conditions are favorable again, females return to producing unfertilized eggs. Because parthenogenesis is rare, rotifers provide valuable clues to biologists trying to understand the evolution of sexual reproduction, which remains one of the great unsolved mysteries of evolution.

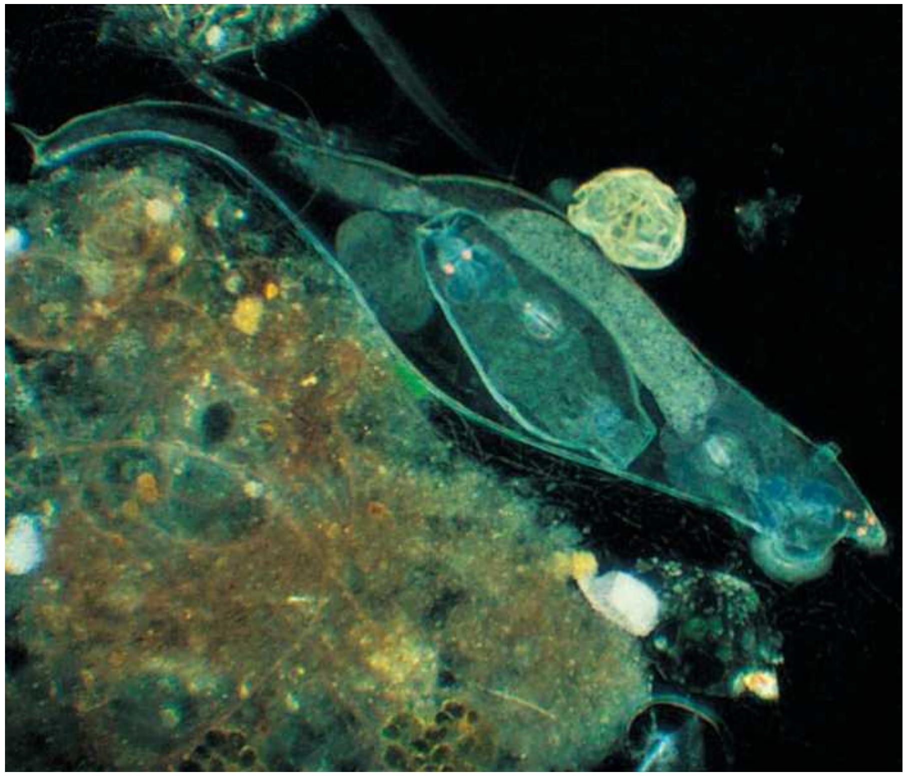
Most rotifers are between 0.1 to 0.5 millimeters (0.004 to 0.02 inches) long, and generally contain only a few hundred cells. Another unusual characteristic of the phylum is that the number of cell divisions during development is fixed. This means that the animal is unable to grow new cells in response to damage. One might view this inflexibility as a drawback, but the fact that most of the rotifer's closest relatives do not share this trait suggests that the rotifer's recent ancestors were capable of **regeneration**. This means that rotifers could have inherited the ability to regenerate, but did not. Perhaps the ability to regenerate has costs as well as benefits, and the costs outweighed the benefits for the ancestor of the rotifers. Such costs are that regeneration requires energy, cell division, and can result in cancer-causing mutations.

regeneration regrowing body parts that are lost due to injury

Both **asexual reproduction** and deterministic cell division are examples of traits that might be considered "primitive" because they are simpler or tend to appear in older taxa. Yet, by examining a phylum like Rotifera and understanding its evolutionary history, we realize that there are situations in which apparently "primitive" traits replace "advanced" ones. A complex

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

A freshwater rotifer with an embryo inside.



trait is not necessarily better than a simpler one. Each has its place in the diversity of life. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Brian West

Bibliography

Campbell, Neil A. *Biology*, 2nd ed. Redwood City, CA: The Benjamin/Cummings Publishing Company, Inc., 1990.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishers, 1989.

Scales, Feathers, and Hair

integument a natural outer covering

exoskeleton a hard outer protective covering common in invertebrates such as insects

The term "**integument**" is applied to any outer covering of an animal. Basically, it means the skin, although many scientists describe the **exoskeleton** of arthropods as an integument. An exoskeleton is a coating of hard protein type substances that entierly cover the outside of the animal. It provides a place for muscle attachment. The vertebrate skeleton is internal and muscles attach from the outside. This permits larger growth of the animal. Vertebrate animals have developed some very interesting excrescences, or projections of the skin, some of which are well-known and easily oberved by most people. They are scales, feathers, and hair. Although these characteristics are common among the most vertebrates, they are not all that common in the animal world as a whole.

The primary function of the excrescences is protection and insulation. Claws, hooves, and nails are other types of excrescences, but do not provide the animal with the complete body protection it gets from the three main body coverings. All, however, are made from special proteins. The primary protein used by vertebrates is keratin. It occurs as two forms: alpha (more pliable) and beta (more stiff) keratin. The way in which the keratin is constructed at the molecular level is what determines the structural differences among the various excrescences.

Scales

Scales occur on fishes and reptiles. Fish scales are made from more than just keratin. They are often derived from bone in the deeper layers of the skin (the middle section of tissues called the mesoderm), which are named the dermal layer. Some have a **placoid scale** that is formed from bone and covered with enamel, the same covering as the outer portion of a human tooth. Such scales are rough, spiny projections that give the surface of the fish a sandpaper-like feel.

placoid scale a scale composed of three layers and a pulp cavity

A primitive type of scale is the **ganoid scale**. While this type of scale was common to fishes that lived hundreds of millions of years ago, today it is primarily found in a fish named the gar. Scales of this type are similar to placoid scales, but have an extra coating of a very strong substance called ganoin. It is even stronger than enamel and these gar-type scales are very common in the fossil record. They are believed to have provided a great deal of protection against rocks and abrasive surfaces that fishes may have rubbed against. It is also possible that they provided some protection against predators, since the scales make it very hard to bite through the skin of fishes. Many scientists believe that the ganoid scale is the precursor or original type scale that led to tooth evolution.

ganoid scale hard, bony, and enamel covered scales

The **ctenoid scale** is found in most modern fishes and is much lighter than the placoid or ganoid scale. Growth rings are an interesting feature of a ctenoid scale. Under a microscope, small circular folds are apparent. There is some debate about the timing of the growth rings. Some researchers once believed they were annual rings, but this has been disproved. The growth rings appear with various timings among varieties of fishes and there are still many questions about what the growth rings may indicate about the life of fishes.

ctenoid scale a scale with projections on the edge like the teeth on a comb

In both fishes and reptiles, the scales cover the entire body. The construction of reptile scales, however, is different. Both lizards and snakes have scales over their entire bodies. Many species are identified by the pattern the scales make on the head and body. Reptiles have evolved a unique layer in the skin from their **aquatic** ancestors. In order for reptiles to live free from water a waxy layer, the stratum corneum, evolved to keep the animal from drying out on land. These waxy layers lie between the layers that produce the keratin for the scales. The scales are overlapping layers of skin with an inner and outer coating. A unique adaptation is a basal hinge region from which the scales can be somewhat flexible and fold back without falling off.

aquatic living in water

The stratum corneum, or cornified layer, contains beta keratin and in some species both beta and alpha keratin. This provides strength to the scale, which enables reptiles to climb on rocks and slither along various surfaces such as gravel and sand. As the animal grows, every so often **epidermis** (the outer covering) is sloughed off during a process called shedding. A new epidermis forms and is, in turn, shed as the animal continues to grow.

epidermis the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

There is a wide variety of scale structures among reptile groups, including turtles and crocodiles who are sometimes excluded by researchers as true reptiles. Colors are achieved by a wide variety of pigments that are incorporated into the scale or that lie in layers of the skin.

This photomicrograph shows the shaft, barbs and barbules of a hummingbird feather.

Feathers

Feathers are interesting excrescences whose origins are not completely understood. It was once believed that only birds had feathers, but later research revealed a striking relationship between dinosaurs and birds. This debate has been recently reduced with the finding of new and important fossils in China. Scientists now see a much closer relationship, if not actual descent, between birds and dinosaurs. Dinosaur fossils discovered in China near the end of the twentieth century revealed a skeleton which is clearly that of a dinosaur but which has impressions of feathers all over the body. The most fascinating discoveries began in the mid 1990s and is ongoing. It is easy to observe the relationship between birds and dinosaurs and their contemporary reptile cousins by looking at a bird. A bird has scales over its legs and have many characters, including skull and skeleton, that are very reptilian. They are highly modified scales composed of beta keratin.

A feather is a scale in which a long center shaft, the rachis, is the dominant feature. On either side of the shaft, the keratin is divided into tiny barbs that, under a microscope, look like the close-knit leaves of a fern. The barbs have tiny hooks, or hamuli, on them, which help the barbs attach to one another and keep them close to each other. These interlocked barbs are called the vane of a feather.

contour feathers feathers that cover a bird's body and give shape to the wings or tail

There are three basic types of feathers. The **contour feathers** (tail and flight feathers) are long and used as an aerodynamic device for flight. The plumules (down feathers) are for insulation to keep the bird warm. Their barbs or barbules (smaller versions of barbs) are not closely knit and so the plumules appear fluffy. The feather is built somewhat like a fern frond. There are primary barbs that come of a sturdy shaft. The smaller barbules emerge from the barbs and help hold the feather in shape by interlocking the barbs. This design is crucial for keeping the feather sturdy during flight.The hair feathers (filoplumes) are not as fluffy as the down, but are still used for insulation.

pterylae feather tracks

Bird feathers are composed of beta keratin. They occur in tracts along the bird's skin called **pterylae**. These tracts are easily seen on plucked chickens or turkeys used for food. It surprises many people to learn that the entire bird is not covered with feathers.

Hair

Hair is one of the most familiar excrescences, since humans are endowed with varying amounts of it. It is a characteristic of mammals. Hair or fur is made from beta keratin and grows from follicles located all over the epidermis. Its primary function is to provide insulation for the animal to keep it warm. However, there are several kinds of hair that provide sensory functions. Whiskers, or vibrissae, are located at places near a mammal's head. The roots of the vibrissae are connected to sensory nerves that are sensitive to movement and so help the animal to detect its environment.

The structure of hair is different from that of scales and feathers. A hair is basically a cone of keratin that is derived from keratinized cells in the dermis, or middle layers of skin. The hair is generated and formed in a pit in the skin called the follicle. The hair has an inner and outer sheath. Near the base of each hair attached to the follicle is a small muscle, called an erector pilli. When stimulated, this muscle contracts and pulls the hair straight up. In humans this condition is called goose bumps. They come as result of the tightening of the skin which helps prevent heat loss. It serves as a warning gesture in cats and dogs and other mammals.

As in most animals with scales and feathers, the loss of hair is cyclic. The heavy winter coats of many animals are shed in spring and replaced by lighter summer ones. Shedding may occur again in fall when a warmer coat is needed.

Whatever the excrescence, the variety and color of scales, feathers, and hair make watching animals a pleasant activity. The variety of patterns and structures continually provide a wonderful display of life on earth. SEE ALSO Keratin.

Brook Ellen Hall

Bibliography

Hildebrand, Milton. *Analysis of Vertebrate Structure.* New York: John Wiley, 1998.

Moyle, Peter, and Joseph Cech Jr. *Fishes: An Introduction to Ichthyology.* Englewood Cliffs, NJ: Prentice Hall, 1992.

Sloan, Christopher. *Feathered Dinosaurs.* Washington, D.C.: National Geographic Society, 1999.

Internet Resources

Encyclopedia Britannica. <http://members.eb.com>.

Hair: Animal Diversity Page. Museum of Zoology at the University of Michigan. <http://animaldiversity.ummz.umich.edu/anat/hair.html>.

Scientific Illustrator

How do toads unfurl their tongues? What goes on inside a car's engine? How do hummingbirds hover? What happens when atomic particles collide? Scientific illustrators have the fascinating job of turning such ideas and theories into clever colorful charts, diagrams, and three-dimensional models. Artists with a keen eye for detail and a penchant for science and technology work with engineers, scientists, and doctors to make information that is difficult to convey with words comprehensible at a glance. Their assignments may range from illustrating the spores of a fungus to depicting the surface of Mars or building a model of an atom to making a model of a prosthetic limb. Scientific illustrators work with computer graphics, plastics, and modeling clay as well as traditional techniques such as charcoal, pens, and brushes.

Some scientific illustrators are self taught. One of the most famous was the English naturalist and author, Beatrix Potter. Potter never attended school, yet spent her entire life studying the world around her in finer and finer detail, rendering her observations—especially those of fungi—in exquisite drawings which were presented to the Royal Academy of Sciences.

Students who wish to become scientific illustrators must have a strong background in the graphic fine arts, with an additional emphasis on biology, engineering, architecture, or design. Some illustrators work for specific magazines or publishing houses, but most are freelance and work from home. To be successful, scientific illustrators must be able to run a small business.

The field of medical illustration is more specialized, concentrating on human anatomy and physiology. Medical illustrators produce drawings for textbooks and models for anatomical displays, and may also be called upon to present visual testimony in court cases. To become certified, medical illustrators must complete a special master's program which is currently offered only to a handful of students each year at six schools in North America. Prerequisites for entrance to these programs are a bachelor's degree with majors and minors in art and biological science. The coursework includes vertebrate anatomy, embryology, physiology, chemistry, and histology.

Nancy Weaver

Bibliography

U.S. Dept. of Labor. *Occupational Outlook Handbook.* Washington D.C.: Bureau of Labor Statistics, 2000.

Segmented Worms ***See Annilida.***

Selective Breeding

Selective breeding is evolution by human selection. As nineteenth-century British naturalist Charles Darwin noted in *Variation of Animals and Plants under Domestication*, selective breeding may be methodical or unconscious. Methodical selection is oriented toward a predetermined standard, whereas unconscious selection is the result of biases in the preservation of valuable individuals. Methodical selection requires great care in discriminating among organisms and is capable of rapid change in specific traits, such as milk production or silk color. Unconscious selection, more common in ancient times, resulted in grains and seeds such as wheat, barley, oats, peas, and beans, and in animal traits such as speed and intelligence.

Historical Overview

Selective breeding began about 10,000 years ago, after the end of the last Ice Age. Hunter-gatherers began to keep flocks and herds and to cultivate cereals and other plants. This process of domestication was probably stimulated by a combination of human population pressure and environmental stress caused by a rapid change in climate. **Global warming** at the end of the Ice Age created drought in areas where rainfall had previously provided sufficient water, forcing people to congregate around reliable water sources. The increased population density favored the cultivation of plant and animal species for use during times when they were not naturally plentiful.

global warming a slow and steady increase in the global temperature

Selective Breeding vs. Natural Selection

Like natural selection, selective breeding requires genetic variation on which to act. If the variation in a trait is strictly environmentally induced, then the

An Aberdeen angus breed is shown at the 1993 Royal Highland Show in Scotland. Professional breeders would have carefully chosen the parents of these show animals in order to increase their chances of winning "best of breed."

selected variants will not be inherited by the next generation. Selective breeding also requires controlled mating. Thus, animals that are social and easily manipulated, such as **bovids**, sheep, and dogs, were easier targets for selective breeding than territorial species, such as cats and other carnivores. Cultures without a strong concept of property rights, such as those of pre-Columbian South America, were less likely to domesticate species because of their difficulty segregating different breeds. A short generation time also facilitates selective breeding by speeding up the response to selection. For example, most plants with multiple breeds (races) are annuals or biennials.

bovids members of the family bovidae which are hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

Selective breeding differs fundamentally from natural selection in that it favors **alleles** (forms of a gene) that do not contribute favorably to survival in the wild. Such alleles are usually **recessive**, for otherwise they would not persist in wild populations. Selective breeding is essentially a process of increasing the frequency of rare, recessive alleles to the point where they usually appear in homozygous form. Once the wild-type alleles are eliminated from the population, the process of domestication has become irreversible and the domestic species has become dependent on humans for its survival.

alleles two or more alternate forms of a gene

recessive hidden trait that is masked by a dominant trait

There is abundant evidence of the effectiveness of selective breeding. In general, there is more genetic variation among breeds of the same species for valuable traits than for others. For example, tubers are diverse among potatoes, bulbs are diverse among onions, fruits are diverse among melons. The implication is that selective breeding for valuable traits has created the diversity.

Domestication

The earliest archaeological evidence of selective breeding has been found in the Near East, where plants and animals were domesticated 10,000 years ago. China followed suit 2,000 years later, and sub-Saharan Africa, central Mexico, the central Andes, and eastern North America began selective breeding around 4,000 years ago. Historical evidence includes rules given for influencing sheep color in chapter thirty of Genesis, ancient Greek philosopher Plato's note that Glaucus selected dogs for the chase, Alexander the Great (356–323 B.C.E.) selecting Indian cattle, Roman poet Virgil's (70–19 B.C.E.) description of selecting the largest plant seeds, and the Roman emperor Charlemagne's selection of stallions in the ninth century. The Incas of Peru rounded up wild animals and selected the young and the strong for release, killing the rest. This strategy mimicked the action of natural selection, whereas elsewhere artificial selection used the most valuable individuals.

alluvial composed of sediments from flowing water such as silt, sand, mud, and gravel

Selective breeding was invented independently in several different parts of the world, but its first appearance was in the Fertile Crescent, an **alluvial** plain between the Tigris and Euphrates Rivers. Ten thousand years ago, hunter-gatherers in a western part of the Crescent known as the Levantine Corridor began to cultivate three cereal crops: einkorn wheat, emmer wheat, and barley. Each was descended from a different wild species. A thousand years later, hunters in the eastern region of Zagros began to herd goats. Within 500 years after that, cereal cultivation and goat herding had spread to the center of the Crescent and combined with sheep and pig herding to form a diverse agricultural economy.

The process of domestication resembles a common mechanism of natural speciation. First, a barrier is created to separate a species into distinct reproductive groups within its geographical range. Over many generations the reproductively isolated groups begin to diverge as a result of selection, whether artificial or natural. All of a species' adaptations to artificial selection, both deliberate and incidental, are referred to as its "adaptive syndrome of domestication." Domesticated species eventually lose the ability to survive in the wild as part of their adaptive **syndromes**.

syndromes groups of signs or symptoms that, occurring together, form a pattern

The path to domestication followed a stereotypical sequence of events. The first step in the domestication of a seed plant was the disturbance of the earth near settlements. This disturbed habitat facilitated the spread of pioneer plants that were adapted to natural disturbance. It also provided a colonization opportunity for the plants with seeds gathered, and dropped, by humans. The second step was the deliberate planting of seeds that were gathered from favored plants in the previous generation. Favored species tended to be pioneers adapted to growing in dense stands. One byproduct of this process was the selection of greater harvest yields. Since seeds that were collected were the only ones that reproduced, selection for increased seed production was strong. Another hallmark of domesticated plants was rapid sprouting, since competition between seedlings can be strong. The seeds themselves lost the ability to lie dormant and become larger. All of these traits were accidental byproducts of the storage and planting of seeds, rather than the results of methodical selection.

The domestication of animals also produced stereotypical traits. Animal species that were hardy, useful to humans, easy to breed in captivity, and friendly toward humans and each other tended to be successful targets for selective breeding. Of particular importance was flexibility of feeding habits, which facilitated human management. Solitary species with **idiosyncratic**

idiosyncratic a trait or manner peculiar to an organism feeding behaviors were unlikely to reproduce successfully in captivity in spite of early agriculturalists' best efforts. Domestic animals were probably already an important source of food before they were domesticated. Just as plants became domesticated as a result of controlled reproduction, animals were reproductively isolated as herds and flocks. There is, however, only one hallmark of selective breeding in animals: small body size. The remainder of the adaptive syndrome of domestication is unique to each species. SEE ALSO Domestic Animals; Evolution; Farming; Genetics; Genetic Variation in a Population; Natural Selection.

Brian R. West

Bibliography

Clutton-Brock, Juliet. *Domesticated Animals from Early Times.* Austin: University of Texas Press, 1981.

Darwin, Charles. *The Variation of Animals and Plants under Domestication.* Washington Square: New York University Press, 1988.

Sense Organs

The nervous system is responsible for sensing the external and internal environments of an organism, and for inducing muscle movement. Human sensation is achieved through the stimulation of specialized neurons, organized into five different modalities—touch, balance, taste, smell, hearing, and vision. The touch modality includes pressure, vibration, temperature, pain, and itch. Some animals are also able to sense magnetism and electric fields. Modality, timing, intensity, and location of the stimulus are the four features that allow the brain to identify a unique sensation.

Sensation Receptors

The neurons specialized to detect sensation are also called receptors because they are designed to receive information from the environment. Each receptor responds only to a stimulus that falls within a defined region, called its receptive field. The size of the stimulus can affect the number of receptors that respond, and the strength of the stimulus can affect how much they respond. For example, when a cat sits on your lap, a large population of receptors responds to the cat's weight, warmth, claws, and the vibrations from its purring.

Transduction refers to the transfer of environmental energy into a biological signal signifying that energy. Sensory receptors either transduce their respective stimuli directly, in the form of an **action potential**—the electrochemical communication between neurons—or they chemically communicate the transduction to a **neuron**. Neurons collect information at their **dendrites**, a long, branched process that grows out of the cell body. Information travels through the cell body, and then reaches the **axon**, another long process designed to transfer information by apposing, or synapsing on, another neuron's dendrites. In some receptors, the axon is branched, and is specialized for both initializing and transmitting action potentials.

action potential a rapid change in the electric charge of the cell membrane

neuron a nerve cell

dendrites branched extensions of a nerve cell that transmits impulses to the cell body

axons cytoplasmic extensions of a neuron that transmit impulses away from the cell body

Touch receptors. Touch receptors are a type of mechanoreceptor because they are activated by mechanical perturbation of the cell membrane. The axon is located in either shallow or deep skin, and may be encapsulated by specialized membranes that amplify pressure. When the appropriate type of

This snake uses its tongue to smell the surrounding environment.

pressure is applied to the skin, these membranes pinch the axon, causing it to fire. The action potential travels from the point of origin to the neuron's cell body, which is located in the **dorsal** root ganglion. From there, it continues through another branch of the axon into the spinal cord, even as far as the brainstem.

dorsal the back surface of an animal with bilateral symmetry

A very similar system allows **proprioceptors** to convey information concerning the position of the limbs and body, and the degree of tension in muscles. The axon of the nerve cell is located either in the muscle, tendon, or joint, and firing is instigated by pinching, as with touch receptors.

proprioceptors sense organ that receives signals from within the body

Nociceptors convey information about pain and include temperature, mechanical, and **polymodal** receptor types. Temperature nociceptors are activated only by extremely high or low temperatures. Mechanical nociceptors are activated by extremely strong pressure against the skin. Polymodal nociceptors are activated by high temperature, pressure, or chemicals released from damaged cells. Most nociceptors are free nerve endings unassociated with specialized membranes.

polymodal having many different modes or ways

Vision receptors. Campaniform organs are insect proprioceptors that play a role in feedback control of body position, as well as normal walking motor programs that allow the coordinated movement of all six legs.

Vision receptors are called **photoreceptors** because the stimuli that activate them are photons of light. The two types of photoreceptors are called rods and cones. Rods only sense the intensity of light, while cones can sense both intensity and color. While cones function best in bright light, rods function better in dim light. Furthermore, rods are located diffusely over the **retina** at the back of the eye, but cones are located in the central line of vision in a region of the retina called the fovea. For this reason, dim objects in the darkness can be viewed better from peripheral vision than from direct focus. There are three kinds of cones in the vertebrate eye—one responsive to wavelengths of light corresponding to the color blue, one responsive to red wavelengths, and one responsive to green wavelengths. These three colors form the entire range of colors that humans can perceive.

photoreceptors specialized cells that detect the presence or absence of light

retina a layer of rods and cones that line the inner surface of the eye

Visual information is carried along the optic nerve and passes through several relay points before reaching the primary visual area of the cerebral

cortex, located at the back of the brain. From there it splits into two routes. The dorsal pathway processes depth and motion while the ventral pathway processes color and form.

Insects have **compound eyes** organized in hundreds or thousands of practically identical units called ommatidia, each of which has its own lens system and its own tiny retina. This gives the eye a faceted appearance. The insect's retinula cell is a sensory neuron that contains photopigments similar to rods and cones. Overall, compound eyes resolve images about one sixtieth as well as vertebrate eyes. This is because the image is fractionated into so many ommatidia lenses and is difficult to reconstruct again in the brain. However, insects can have a greater range of vision than vertebrates, one that encompasses nearly the entire sphere of space around their bodies, due to the relatively large size of their eyes.

compound eyes multi-faceted eyes that are made up of thousands of simple eyes

Hearing receptors. Hearing receptors, or hair cells, are mechanoreceptors located within a bony spiral structure called the cochlea. Sounds are interpreted by the brain from patterns of air pressure caused by the vibration of objects. Sounds can also travel through water or solid objects. In mammals, the pressure in the air is transformed into mechanical pressure by three ear bones called the **malleus**, **incus**, and **stapes**, located in the middle ear.

malleus the outermost of the three inner ear bones

incus one of three small bones in the inner ear

stapes the innermost of the three bones found in the inner ear

Pressure waves that strike the tympanum, a thin membrane separating the middle from the outer ear, force it to push inward. The malleus is attached to the incus and the incus to the stapes, so that the mechanical activity of the tympanum is transferred to a coiled structure of the inner ear called the cochlea. Because this is a fluid-filled structure, the pushing and pulling of the stapes generates waves in the fluid. A semi-flexible membrane called the basilar membrane is located within the fluid, and also conducts the waves of pressure. The wave-like motion of the basilar membrane causes a series of hearing receptors grounded in the basilar membrane to be pushed up against another membrane just above it, the tectorial membrane.

Hair-like extensions, stereocilia, at the apex of the hair cell push and bend against a tectorial membrane, when the basilar membrane reaches the peak of its wave phase. This instigates a change in the electrochemical properties of the cell. The basilar membrane is formed so that only a particular region of hair cells is pushed up to the peak of the wave form for any one frequency, or tone, of sound. The frequency that a particular hair cell responds to is its receptive field. Hair cells are closely coupled to the auditory nerve, and transmit their auditory information to neurons from this nerve, which then travels up through the brain.

Insect hearing receptors are typically located on the legs, and sometimes on the body, of the insect. In crickets, the ear is located on the tibia of the foreleg. The eardrum of crickets is called a tympanum, and consists of an oval membrane on one side of the leg, and a smaller round tympanum on the other surface. Inside the tympanum is a large air sac formed by the leg trachea, which is the insect respiratory organ. Transduction mechanisms in the cricket ear are not well understood, but the vibration of the tympanum is known to stimulate the activity of auditory neurons behind the membrane.

Balance receptors. Vertebrate balance receptors are located in a specialized organ in the inner ear called the vestibular organ. This structure is located directly adjacent to the cochlea, and is composed of a triplet of semicircular canals, each of which is oriented in a different plane—the X, Y, or Z axis. Movement of liquid in these tubes caused by rotation of the head or body are measured by vestibular hair cells. The stereocilia of these cells are embedded in a gelatinous material called the otolithic membrane.

Gravity and body movements cause the otolithic membrane to slide, which cause the stereocilia to bend in a particular direction. This leads to electrochemical changes in the hair cell, causes an action potential in the associated nerve ending. Information from the vestibular system allows eye and head movements to fix on a particular target, and to stabilize a moving image. It also allows organisms to balance—for example, when a cat walks atop a fence.

olfactory the sense of smell

chemoreceptors a receptor that responds to a specific type of chemical molecule

Smell receptors. Smell receptors, or **olfactory** sensory neurons, are **chemoreceptors**, meaning that the binding of molecules causes these neurons to fire. Olfactory neurons extend a single dendrite to the surface of the skin in the nose, where it expands—along with dendrites from other neurons—to form a large knob. Thin hair-like projections extend from this knob into the thin layer of mucus within the nose. These projections contain a diverse array of receptors for odorants, so that all olfactory neurons are able to respond to a particular scent. The number that actually do respond is relative to the concentration of the scent molecules in the air.

progeny offspring

Taste receptors. Taste-detecting, or gustatory, organs are also chemoreceptors and are located in functional groupings called taste buds on the tongue, palate, pharynx, epiglottis, and the upper third of the esophagus. Taste cells have a very short life span, which is why each unit contains a population of stem cells that continuously divides, producing **progeny** cells to replace the dying taste cells. The remainder of the cell types in the taste bud has hair-like projections called microvilli that extend into a pore at the top of the taste bud. When taste molecules bind or interact with the microvilli, the taste cell undergoes an electrochemical change that is conveyed to an associated neuron; however, taste cells are not neurons. Four basic taste sensations can be distinguished by humans: bitter, salty, sour, and sweet. SEE ALSO Growth and Differentiation of the Nervous System; Nervous System.

Rebecca M. Steinberg

Bibliography

Ehret, Gunter, R. Romand, et al. *The Central Auditory System*. New York: Oxford University Press, 1997.

Finger, Thomas E., D. Restrepo, Wayne L. Silver, et al. *The Neurobiology of Taste and Smell*. New York and London: Wiley-Interscience, 2000.

Hubel, David H. *Eye, Brain and Vision*. New York: Scientific American Library, 1995.

Kruger, Lawrence, ed. *Pain and Touch*. San Diego: Academic Press, 1996.

Singh, Naresh R., Nicholas James Strausfeld, et al. *Neurobiology of Sensory Systems*. New York: Plenum Press, 1989.

Whitlow, W. L., Arthur N. Popper, and Richard R. Fay. *Hearing by Whales and Dolphins*. New York: Springer, 2000.

Serial Homology

As organisms evolve, their existing structures or body parts are frequently modified to suit their needs. For example, an invertebrate with a working limb design may end up changing it and incorporating it somewhere else in its **body plan**. The practice of modifying a specific structure more than once and using it somewhere else is known as **serial homology**.

body plan the overall organization of an animals body

serial homology a rhythmic repetition

As evolution is necessarily a stepwise process, certain complex structures, such as legs or wings, cannot spring into being instantly. They must slowly evolve over time, and each new and slightly different version must be more useful to its owner than the last. Replicating previously existing parts and building on them is a common strategy in organismal evolution. As such, serial homology is a widespread evolutionary tactic that can be observed in a large number of animals.

Explaining Strange Mutations

Comparative biologists first had an inkling that copies of body parts were altered and used again when they started noticing odd mutants in their collections. At the end of the nineteenth century, comparative biologist William Bateson found some specimens in his collection that were odd-looking: he had **arthropods** with limbs in odd places, such as legs popping out of an animal's head. He also noticed certain ribs or vertebra swapped in other animals. However, these examples were rare and frequently unique. It wasn't until 1915 that Calvin Bridges, while breeding fruit flies *(Drosophila)*, came across a mutant that he could consistently breed where the rear flight appendage, or the haltere, resembled a wing.

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

This wing resemblance was no accident. The *Drosophila* wing and haltere are serially **homologous**. They were both modified from the same basic structure, and it should come as little surprise that interrupting the proper development pathway of one of them might cause it to resemble another. In terms of genetics, the two appendages are quite closely related; indeed, nearly identical. But at one location on the body, only a haltere will grow. At another, only a wing will grow. What mechanism makes this decision possible, the decision to grow a certain appendage on a certain part of the body? In the case of the wing and the haltere, the answer is **Hox genes**.

homologous similar but not identical

Hox genes also known as selector genes because their expression leads embryonic cells through specific morphologic developments

Hox Genes

Hox genes are extremely common and evolutionarily very, very old. They are first **described** as belonging to a common ancestor of **bilateria** and **cnidaria** (in the neighborhood of 700 million years old). It is the Hox genes' job to locate different structures inside the organism's body plan. The particular gene in charge of making sure the haltere develops properly, and not into a wing or something else, is called *Ubx*.

described a detailed description of a species that scientists can refer to identify that species from other similar species

bilateria animals with bilateral symmetry

cnidaria a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

What Bridges found was a partial mutation in *Ubx*. The halteres in his flies had wing bristles. *Ubx* controls a variety of other genes integral to haltere formation as well as genes important in the suppression of wing formation. *Ubx* discourages *spalt-related*, a gene that makes veins for the wings. It also stops genes that control wing epithelium formation, and other mechanisms and structures.

If there is a certain problem with the *Ubx* gene, a fly will grow halteres that have wing-like characteristics. While complete removal of a Hox gene generally results in death during early development, a certain triple mutation in *Ubx* can cause a second pair of fully-formed wings to develop where the halteres are supposed to be. Different mutations in Hox genes have produced flies with legs where antennae are supposed to be, and other odd body modifications.

Hox Genes in Fruit Flies

In *Drosophila*, eight Hox genes, organized into two gene complexes, orient the body plan. By investigating where and when Hox genes were expressed, developmental biologists discovered that various genes were restricted to various body segments. Some of them overlap one another: *abd-A* and *abd-B* share a portion near the end of the abdomen, for example. The Hox genes in particular body segments affect the development of structures inside those segments. For example, the shape of the first pair of adult legs is influenced by the *Scr* gene, the second pair by the *Antp* gene, and the third pair by the *Ubx* gene.

While the Hox genes dictate the identity of a certain developing segment, they are not required for structures inside that segment to form. In *Drosophila*, the mouthparts and legs are serially homologous to the antennae. Thus, in the absence of these controlling Hox genes, the segments will still develop all their structures, but differently. Where the legs or mouthparts should be, antennae will develop instead. Such substitution of one part for another that is serially homologous is known as homeotic substitution. As William Bateson discovered with his collection, such substitution happens occasionally in nature to serially homologous structures.

So, as it is a useful evolutionary tactic to copy existing structures and modify them, the Hox genes evolved to keep tabs on what body segment is where so that the proper structural modifications can take place during development. While Hox genes are integral to differentiating the different segments of *Drosophila*, it is important to remember that they also delineate different areas of early developmental tissue (ectoderm, endoderm, and mesoderm) and specify location in a variety of fields for a staggering number of organisms.

There is a remarkable similarity in Hox gene sequences between *Drosophila* and vertebrates, such as mice, frogs, zebrafish, and humans. Alterations of Hox gene expression in *Drosophila* can prevent expression or growth of certain limbs or organs, and similar results have been found in birds, amphibians, and fish. This demonstrates that Hox genes function similarly over a wide variety of organisms, and that serial homology is a true evolutionary tactic when it comes to generating novel structures on one's body plan.

Hox Genes and Body Designs

Different organisms use serial homology to different extents. Vertebrates have modified vertebrae and ribs in a large number of ways; the basic vertebra has been reiterated and altered into different backbone types: sacral, lumbar, **thoracic**, and cervical. However, perhaps one of the best examples

thoracic the chest area

of serial homology can be found in the body design of the common crayfish.

All appendages of crayfish, with the possible exception of the first antennae, are called biramous, which is to say they are derived from double-branched structures. The three components that make up these branches are known as the protopod (the base), the exopod (lateral; or on the side) and the endopod (in the middle). Crayfish have quite a large number of appendages in their body plans. The biramous structure plan is incorporated in crayfish head appendages, legs, swimmerets, mandibles, and many others.

Evolutionarily, it is easy to see how the earliest design might have been copied and modified several times, producing a highly specialized and versatile body plan. And as all the new structures are based on one older one, variations in Hox (or other developmental) genes will affect only a small number of structures, rather than all of them. Serial homology is a method for creating new, more specialized body plans, and it is observed in species throughout the living world. SEE ALSO Morphology.

Ian Quigley

Bibliography

Carroll, Sean B., Jennifer K. Grenier, Scott D. Weatherbee. *From DNA to Diversity.* Malden, MA: Blackwell Science, 2001.

Davidson, Eric H. *Genomic Regulatory Systems.* San Diego, CA: Academic Press, 2001.

Hickman, Cleveland P. Jr., Larry S. Roberts, and Allan Larson. *Integrated Principles of Zoology*, 10th ed. Dubuque, IA: Wm. C. Brown Publishers, 1997.

Service Animal Trainer

The Americans with Disabilities Act describes a service animal as any dog or other animal individually trained to provide assistance to a disabled human. Service animals perform some of the functions and responsibilities of a human without disabilities. For example, seeing eye dogs lead the blind through their environment, and hearing dogs alert their hearing-impaired owners to relevant sounds. Other examples include dogs that direct wheelchairs, fetch and carry items for mobility-impaired people, provide balance for unsteady people, monitor their owners for signs of a seizure, or provide therapeutic companionship.

Police dogs are service animals trained to recognize the scent of illegal substances such as drugs or gunpowder. They are also employed in locating missing persons, tracking down fugitives, and controlling jail riots. Search and rescue dogs are utilized on ski slopes, glacier parks, and mountains to seek out people who are injured or lost. They can be trained to rescue drowning people, pull a sled, deliver medications, or provide warmth for someone with hypothermia. Training teaches these dogs to be reliably calm and obedient in extreme situations.

Although not required, a background in animal behavior would benefit all animal trainers. Through a certification training program, or by apprenticing with a skilled trainer, anyone can acquire the qualifications necessary to train service dogs for impaired humans. The training program familiarizes students with concepts of classical conditioning, positive

reinforcement, and operant conditioning, all of which involve reward, punishment, and emotional support for the animal.

Conversely, each state or country defines the requirements for becoming a police dog trainer. Most programs require a minimum amount of time as a police canine handler, completion of an instructor development program, written recommendation from other police canine trainers, additional coursework, and successful prior training of several service animals. Classes that offer certification the training of search and rescue dogs are open to anyone. The skill takes many years to master. In each of these cases, a strong relationship needs to form between the handler and the canine companion.

Rebecca M. Steinberg

Bibliography

American Rescue Dog Association. *Search and Rescue Dogs Training Methods.* New York: Howell Book House; Toronto: Maxwell Macmillan Canada, 1991.

Duncan, Susan, and Malcolm Wells. *Joey Moses.* Seattle, WA: Storytellers Ink, 1997.

Robicheaux, Jack, and John A. R. Jons. *Basic Narcotic Detection Dog Training.* Houston, TX: J. A. R. Jons, 1996.

Sexual Dimorphism

Sexual dimorphism is the presence of nongenital physical differences between males and females of the same species. These differences may be in coloration, body size, or physical structures, and can be quite striking. Male and female mallard ducks (*Anas platyrhynchus*) are so different in appearance that they were originally classified as different species. Mule deer bucks have antlers while females do not, male peacocks display an elaborate tail not found in females, and male elephant seals may weigh 2.5 tons (2.25 metric tons) more than their mates. All these differences are examples of sexual dimorphism.

The word "dimorphic" means "having two forms." Species in which males and females appear identical are called sexually monomorphic. Sexual dimorphism generally results from different reproductive roles and selective pressures for males and females. Scientists have proposed several hypotheses to explain the existence of sexual dimorphism, including niche **differentiation**, sexual selection through intrasexual competition, and sexual selection through female choice.

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

Niche differentiation

The niche differentiation hypothesis states that the differences between males and females of a species allow them to exploit different food resources and thus reduce competition for food. For example, male raptors (hawks, falcons, eagles, and owls) are considerably smaller than females. This difference is especially pronounced in raptors that prey on birds, such as the Cooper's hawk (*Accipiter cooperii*). The small male Cooper's hawks are better than their larger mates at catching small, fast birds. The male catches these often-abundant small birds to feed to his mate as she incubates the eggs and later while the chicks are young. Once the young hawks are bigger, the female hunts for larger birds in the area to feed the growing chicks.

Intrasexual Competition

In 1871 Charles Darwin suggested that larger, more aggressive males would be more successful in competing for females. Intrasexual competition results in males that are larger, stronger, or equipped with different physical traits than females because they must compete with other males to win access to mates. American elk (*Cervus elaphus*) bulls have large antlers and use them aggressively to fight for harems of females. A harem is a group of adult females defended by one male from other males in the area. This dominant male mates with most if not all females in the group. Bulls that have large antlers and outweigh their opponents are able to dominate their opponents and pass on their genes for size to their offspring. Elk cows are not involved in such battles and have no need for antlers or such massive bulk.

Finally, the female choice hypothesis states that females of dimorphic species prefer to mate with males that are colorful, large, or ornamented. If this is the case, the flashier, larger, or more-ornamented males are more likely to sire offspring and pass on their genes than their dull, small, plain competitors. Why females might prefer to mate with elaborate males is a matter of debate. It may be that the traits advertise the males' ability to find food or avoid predators.

A male mandrill rests on his paws at the Ft. Worth, Texas, zoo. Male mandrills exhibit coloring consistent with the theory of sexual dimorphism.

Sexual Selection

By mating with obviously successful males, females increase the chances that their offspring will inherit their father's traits and also be successful. It may also be that some sexually selected traits, such as the peacock's unwieldy tail, advertise the male's ability to escape predators in spite of a severe handicap. Longer tails make it harder for the males to run or fly away, so males that have particularly long tails and yet manage to escape predators must be particularly strong and fast. Competition between males, and female choice among males are both forms of sexual selection. This means that they cause differences in mating success of individuals and therefore result in adaptations for obtaining mates.

In species that are sexually dimorphic, the male is usually the bigger, more brightly colored, or more elaborately ornamented sex. However, there are several cases where this pattern is reversed, such as in raptors and toads. The female is often the larger sex in polyandrous birds such as phalaropes, where brightly colored females compete to attract male mates. This unexpected situation, sometimes called reverse sexual dimorphism, led the American ornithologist and painter John James Audubon (1785–1851) to incorrectly label the male and female in all his phalarope paintings. The plumage patterns of phalaropes make sense in light of sexual selection, but also highlights the importance of selection for dull plumage. Male phalaropes incubate the eggs and take care of the young with no help from the female. Their cryptic (meaning blending into the surroundings) brown plumage makes them difficult to see on the nest and helps them avoid predators. In general, the sex that cares for the young is under strong selection for dull coloration.

The hypotheses discussed here are not mutually exclusive, and different species may be more or less affected by various selective pressures. Why some species are sexually dimorphic and others are not is an active area of research in evolutionary biology.

Emily DuVal

Bibliography

Darwin, Charles. *The Descent of Man, and Selection in Relation to Sex.* London: John Murray, Albermarle Street, 1871.

Ehrlich, Paul R., David S. Dobkin, and Darryl Wheye, eds. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds.* New York: Simon and Shuster, Inc., 1988.

Owens, Ian P. F., and Ian R. Hartley. "Sexual Dimorphism in Birds: Why Are There So Many Different Forms of Dimorphism?" *Proceedings of the Royal Society of London*, series B. 265 (1998):397–407.

Pough, F. Harvey, Christine M. Janis, and John B. Heiser. *Vertebrate Life*, 5th ed. Upper Saddle River, NJ: Prentice Hall, 1999.

Zahavi, Amotz, and Avishag Zahavi. *The Handicap Principle: A Missing Piece of Darwin's Puzzle.* New York: Oxford University Press, 1997.

Sexual Selection

Males and females of many species exhibit significant differences in addition to the difference in reproductive organs. The distinction of gender through secondary sex characteristics is known as sexual dimorphism. This is most often expressed as a difference in size, with the males usually larger, but also involves differences such as plumage in male birds, manes on male lions, and antlers on male deer. In most cases, the male is the showier sex of the species.

What It Is and How It Works

Sexual selection is the evolutionary process that arises from competition among members of one sex (the competitive sex) for access to members of the other sex (the limiting sex). According to the theories of Charles Darwin, sexual selection should be distinguished from the process of natural selection because the traits that evolve via sexual selection often appear to have a negative effect on the survival rate of their bearers. There are two basic forms of competition for mates that affect the type of traits that evolve. One is intrasexual selection, which includes overt competition among the members of the competitive sex to gain control or monopoly over the limiting sex. This leads to selection of traits such as weapons, large body size, aggression, strength, and endurance. Intersexual selection is when the limiting sex can exercise a choice of mates, leading to elaboration of structures, displays, **vocalizations**, and odors in the competitive sex.

vocalizations sounds used for communications

Sending and receiving signals is a significant step toward mating as the type and intensity of the signal will determine whether or not a mate is obtained. One process of signal evolution that is involved in the search for a mate is called sensory exploitation. According to this model, signal receivers often have inherent, or built-in, preferences that can be exploited by a manipulative signaler to create new signals. For instance, suppose female birds searched preferentially for red seeds while foraging. Because the only time they encounter red is in seeds, it would be advantageous to evolve a general preference for red objects. A mutant male that adds red to its plumage may

This male prairie chicken displays his colors, indicating he is ready to breed.

then be able to exploit this preference for the color red as long as it can be expressed in the context of mate choice. A new signal can then evolve that had no historical link to mate choice but only to an irrelevant context such as foraging.

It is important to note that there is no new information conveyed to the females by the red males. In fact, there may be predatory risks if red males are easier to spot and thus more likely to be killed. Costs to females may be an adaptation to avoid exploitation such as better discriminating abilities or the decoupling, that is, the separation of behavioral strategies, for foraging and decisions about mating. However, females may be able to find males of the same species, termed conspecific males, more easily if the males bear a red patch. Furthermore, red males may provide additional information not provided by normal males. If the intensity of redness is a good indicator of the males' health, then a preference for red males over nonred ones could be a way for females better to identify a good mate. Whether the signal is costly or beneficial, sensory exploitation by itself is highly unstable. Instead, it is followed by **coevolution** between sender and receiver.

coevolution a situation in which two or more species evolve in response to each other

Male Attraction Signals

Females are more often the choosy sex and males the competitive, advertising sex (though in some animals the roles are reversed). Two significant models for the evolution of mate-attraction signals are the *runaway selection model* and the *good genes model*. In both of these there is a simultaneous evolution of a female preference for a particular male trait and evolution of that male trait.

Runaway selection model. This model best defines polygynous species (one in which a number of mates are taken). Initially, there must be some genetic variability associated with variability in physical characteristics of a male trait such as the brightness of a color spot. Males with the preferred trait will obtain more mates, and because the females will be those who tend to prefer that trait, the genes for the female preference will become linked with the male trait in their offspring. Females with the preference also benefit because their sons will have that trait and so will win more mates, thereby spreading the genes of the female. Under the right conditions, a runaway evolutionary process can occur with the male trait becoming larger and the female preference for it becoming stronger. This process stops when the male trait becomes so large that it imposes a cost on the male that outweighs the benefits. The traits that evolve through this model are termed arbitrary traits, because they can take any type of conspicuous form and not provide any information to the female about the male's fitness.

Although this process requires a certain set of circumstances to get under way, there are several different situations that could bring about the initial trait and the preference for it. One possibility is sensory exploitation, as discussed above. Another factor could be that the male trait is initially favored by natural selection and a female preference for this trait subsequently evolves. A third possibility is that the females evolve a preference for the trait because it helps distinguish conspecific males from those of a closely related species, thereby preventing genetic mixing between different species, a process termed interspecific hybridization.

Good genes model. This model actually proposes that costly and conspicuous male traits become the trait of choice by females because they indicate some aspect of male quality. Females will benefit from mating with these males because the offspring will have higher survivorship or viability. The male traits are called indicator traits, and the costs to males are deemed necessary costs when in pursuit of a mate. Coevolution of the male indicator trait, intrinsic male viability, and female preference for the trait is the basis for the genetic model of this process. One example of how this may work is the *classic handicap model*, in which males acquire a trait such as a heavy set of antlers, which obviously imposes a survivorship cost. Low-quality males cannot support the cost of this trait, and so it is seen as a handicap, whereas high-quality males survive and their genes dominate. However, the handicap is balanced out by the higher net fitness of males without this trait and its cost. Another theory is the *condition-dependent indicator model*, in which males vary the expression of the preferred trait, such as the speed at which the call is performed (termed call rate) so as to optimize their mating success and survival. High-quality males can afford to expend more energy on expression than can low-quality males and so trait magnitude is a good indicator of male quality. Last, in the revealing indicator model all males attempt to develop the trait to the same magnitude and pay the same cost, but the condition of the trait is lower in low-quality males. For instance, call frequency (the number of times a call is repeated) or feather condition are good examples of such traits.

Signalling for a Mate

Many aspects are taken into account when an animal signals for and chooses a mate. Anatomical traits play a role in the attraction of a potential mate. Non-weapon body structures such as color patches, elongated tails, and fins and feather plumes are termed ornaments. Many ornaments appear to be

good indicators of the quality of the male. They often come into play when the male performs visual displays to attract the attention of a female. Vigorous displays are indicative of a male's high energy, and thus that male is likely to win out over the less vigorous male.

Auditory signals. In birds, insects, mammals, and fish, these are also obvious targets of female choice. In all of these groups, the females tend to prefer males with greater calling rates, sound intensity, and call duration. These features actually increase the stimulation value of the signal, so it is possible that the preference arose from the sensory bias of the female receivers and that the traits themselves are just arbitrary. These call characteristics are all energetically expensive, and it seems that females prefer the most costly calling. For example, female grey tree frogs prefer calls that have a long duration and are repeated at a slow rate over a call that is brief and at a high rate though it has the same acoustic "on" time, meaning the calls are heard for the same amount of time. Studies have shown that the long duration calls require a lot more energy than the shorter calls. Such findings suggest that display vigor is an accurate indicator of male quality. It has also been found that costly call characteristics are correlated with age, size, dominance, or parasite load. In addition, they provide females with good gene benefits such as faster growing and more viable offspring. Finally, in some species, call rate is a good index of benefits the females can expect to receive, such as large sperm or territory rich in resources.

Vocal signals. Another type of call is the **copulation** call. These are usually vocal signals and may be given by the male, female, or both sexes. In most cases it is difficult to determine the function of the signal and the intended receiver. However, copulation signals are unlikely to be incidental as they are highly structured and individually distinctive. In monogamous species, female copulation signals may be for synchronization of orgasm with the male, as there is usually no other possible intended receiver in the vicinity at that time. In socially mating species, the intended receiver could be external to the copulating pair. The female signals could be intended for other females and to increase dominance status in the group. The signals could also serve as a recruiting call for other male mates and incite competition among them so that the female can choose the dominant male as father of her offspring.

copulation the act of sexual reproduction

Male copulation signals could serve to transmit information about the male's mating success to other females. It has been found that males who make these calls are more likely to get attacked by other males, but they are also more likely to obtain more matings compared to males that 'do not call. Alternatively, the intended recipient of male copulatory signals could be other males. For example, postcopulatory male rats repeatedly **emit** vocalizations that are similar to the ultrasonic whistles signaling an alarm situation or a defensive threat. The male rats often appear lethargic and inactive at this time but will aggressively attack any other male that tries to approach the mated female. The signal then seems to be indicating mate-guarding intentions.

emit to throw or give off

The nuptial gift. This is a slightly different tactic in the search for a mate. Males of some insect and bird species will offer prey items as nuptial gifts during courtship. The females may base their decision on the size, or quality of these items, as well as the rate at which these items are provided. Females that are egg-producing would clearly benefit from receiving food as a nuptial gift. If provisioning rate is correlated with offspring feeding rate in paternal care species, the behavior is an obvious indicator with direct benefits. Another consideration is that if the cost to the male increases with gift magnitude, then it could be an indicator of heritable fitness. However, there is a risk of "false advertisement." In the marsh hawk, provision of the nuptial gifts is a good indicator of the male's nesting provisional ability. But the males sometimes use this signal deceptively in order to attract females into polygynous matings, a disadvantageous position for the female hawk.

In some species there is a sex-role reversal in terms of competing for mates. The sex-role reversal results from evolution of male parental investment, although not all paternal care species display complete reversal of courtship roles. A determining factor is the extent to which the male cares for the offspring. If the males can care for the offspring of several females simultaneously, the sex ratio is still skewed in favor of males. In those circumstances, males are still the competitive gender and will perform aggressive or persuasive courtship behaviors. However, if the males can care for the offspring of only one female, then males become a limiting resource for females. The females will then compete for males and develop aggressive behaviors, ornaments, and mate-attraction displays most often associated with the male gender. SEE ALSO Reproduction, Asexual and Sexual; Sexual Dimorphism.

Danielle Schnur

Bibliography

Andersson, M. *Sexual Selection.* Princeton, NJ: Princeton University Press, 1994.

Bradbury, Jack W., and Sandra L. Vehrencamp. *Principles of Animal Communication.* Sunderland, MA: Sinauer, 1998.

Campbell, Neil A. *Biology*, 3rd ed. Berkeley, CA: Benjamin/Cummings Publishing Company, 1993.

Parker, G. A. *Mate Choice.* Cambridge, U.K.: Cambridge University Press, 1983.

Sharks *See Chondricthyes.*

Shells

Every year, thousands of shells wash up on beaches around the world. Have you ever found a shell and wondered where it came from or what its function once was?

These shells come from a large phylum of animals known as mollusks which includes members such as snails, clams, oysters, scallops, squid, and octopuses. One of the prominent characteristics of most mollusks is a hard exterior shell, although some mollusks, including the squid and the sea hare, produce internal shells.

The bodies of mollusks are very soft. Their shells protect them from predators. The body of the mollusk is formed of a combined structure called a "head-foot" that is used for locomotion. If threatened, shelled mollusks can retreat the "head-foot" quickly inside their shells.

A thin, fleshy fold of tissue called the **mantle** covers the internal organs of most mollusks. The mantle, which is made up of specialized cells, secretes the substance that creates the shell. The shell is formed almost entirely of calcium carbonate crystals, which is the chemical base of rocks like limestone. The shell starts as a semi-liquid substance that hardens very rapidly as soon as it is exposed to water or air.

The shell begins to form as tiny crystals of calcium carbonate are exuded onto a **matrix** of **conchiolin**, a brownish, horn-like material composed of proteins and **polysaccharides** produced by the animal. This surface serves as a microscopic latticework for new crystals. Additional calcium carbonate crystals are laid down in thin layers as either **calcite** or **aragonite**.

Shells vary in structure and hardness depending upon their crystallization type. Six-sided calcium carbonate crystals may be prism-like, becoming calcite, or they may be very flat and thin, becoming aragonite.

Both calcite and aragonite are forms of calcium carbonate. Aragonite is heavier than calcite, and it has a mother-of-pearl appearance. The shells of freshwater clams and land snails are typically made of aragonite. In saltwater genera such as Nerita, layers of calcite and aragonite may alternate during shell formation. Whether shells are made of calcite or aragonite, as additional layers are added, the shells grow in thickness.

Many mollusks also have special glands called chromogenic glands located on the margin of the mantle. These glands secrete colored pigments that stain the calcium carbonate, which would otherwise create a white shell. When the glands are in a continuous series and are steadily active, the developing shell will be a solid color. If the glands secrete continuously but are some distance from each other, spiral lines will appear on the shell. The color will show as dotted lines, if the glands work intermittently. In some cases, groups of adjacent glands secrete different pigments, creating multicolored shell designs of infinite variety.

Shelled mollusks are linked directly to their shells; they ordinarily cannot live separately from the shell. When a mollusk dies and the shell is no longer attached to a living creature, other aquatic animals (i.e. crustaceans such as crabs) sometimes use the shell as temporary shelter, in the water or on the shore. Throughout human history, shells have been valued as decorative objects, tools, and mediums of economic exchange. They continue to be popular collectibles around the world. SEE ALSO Morphology.

Stephanie A. Lanoue

mantle the tissue in mollusks that drapes over the internal organs and may secrete the shell

matrix the nonliving component of connective tissue

conchiolin a protein that is the organic basis of mollusk shells

polysaccharides carbohydrates that break down into two or more single sugars

calcite a mineral form of calcium carbonate

aragonite a mineral form of calcium carbonate

Bibliography

Saul, Mary. *Shells.* New York: Doubleday and Company, Inc., 1974.

Solem, Alan. *The Shell Makers.* New York: John Wiley and Sons, 1974.

Tucker, Robert. *Kingdom of the Shell.* New York: Crown Publisher, Inc., 1982.

Silent Spring

In 1955 Rachel Carson was at the peak of her profession as a popular writer of science books about the sea. *Under the Sea Wind* (published in 1941), *The Sea Around Us* (1951), and *The Edge of the Sea* (1955) were all best-sellers, and they catapulted her into celebrity as one of the best loved and most sought after American authors. By 1956, she was planning a book in which she intended to explore the human race's relationship with nature. Fearing that human beings were severing their connection to the web of life, she began the painstaking research that would form her next work, *Silent Spring*, a book that would change her life and the world.

Carson's deepest held beliefs were in the delicate interconnectedness of nature and the sanctity of life. Her work as a biologist for the U.S. Fish and Wildlife Service during World War II (1939–1945) had involved studying documents concerning the horrendous chemical and human-made devastations that were occurring. After the war, many of the chemicals developed for the military were unleashed on neighborhoods and farms in a war against nature. By 1960, there were some 200 untested chemicals used in pesticide formulas. That same year, 638 million pounds of poisons were broadcast in the United States alone. The chemical pesticide business was a $250 million industry enthusiastically supported by the U.S. Department of Agriculture (USDA) and other agencies. Government researchers had documented the dangers of uncontrolled pesticide use, but their warnings were ignored or destroyed, with many of the scientists encouraged to find other jobs. A chance note from an ornithologist friend concerning a die-off of baby birds after a DDT spraying of a nearby marsh spurred Carson to act. As she began reading hundreds of scientific papers and contacting biologists, chemists, agriculture experts, and doctors around the world, her alarm and her determination grew. "The more I learned about the use of pesticides the more appalled I became. I realized that here was the material for a book. What I discovered was that everything which meant the most to me as a naturalist was being threatened and that nothing I could do would be more important" (Jezer 1988, p. 79).

After four years of research, *Silent Spring* began appearing in a serialized condensed version in *The New Yorker* on June 16, 1962. It included an appendix of more than fifty pages of scientific references. Response was immediate and overwhelming. Praise and concern in the form of thousands of letters and telegrams poured into the magazine from citizens, scientists, and even the new U.S. president, John F. Kennedy. The response from the American Medical Association, the USDA, and the chemical companies was even more vocal, however. They targeted a quarter of a million dollars for a brutally negative publicity campaign, impugning Carson's science and her morals. One member of a government pest control board scoffed that Carson had no business worrying about genetics as she was a "spinster." The Velsicol Chemical Corporation sent her publisher a threatening letter insisting that Carson was part of a communist conspiracy to undermine the economy of Western nations. Houghton Mifflin was undeterred and the book was published on schedule, on September 27, 1962. As the book soared on the best-seller list, the attacks intensified in print and on television. Her opponents must have realized—as was indeed the case—that she was questioning not only the indiscriminate use of poisons but also the basic irresponsibility of an industrialized, technological society toward the natural world. She refused to accept the premise that damage to nature was the inevitable cost of progress.

President Kennedy initiated a Science Advisory Committee to study the dangers and benefits of pesticides. After eight months of study, their report concluded that "Until the publication of *Silent Spring* by Rachel Carson, people were generally unaware of the toxicity of pesticides." A U.S. Senate committee was formed to study environmental hazards. Secretary of the Interior Stewart Udall acknowledged, "She made us realize that we had allowed our fascination with chemicals to override our wisdom in their use." Most importantly she touched a chord in the population of the United States and the dozens of countries worldwide where her book was translated. Grassroots conservation and environmental organizations sprang up demanding political action. By the end of 1962 more than forty bills regulating pesticides had been introduced in legislatures across the United States. By 1964, the U.S. Congress had amended federal laws to shift the burden of demonstrating the safety of new chemicals to the manufacturers, requiring the proof of safety before the chemicals could be released. As her ideas gained momentum, Carson was showered with honors and awards, including the Audubon Medal and honors from the American Academy of Arts and Letters, the National Wildlife Federation, the Animal Welfare Institute, and the American Geographical Society. Carson continued to warn that "modern science has given human beings the capacity to destroy in a few years life forms that have taken eons to evolve. Humans are challenged to use this new power intelligently and cautiously. Conservation is a cause that has no end" (Jezer 1988, p. 99).

On April 14, 1964, Carson died of breast cancer. Before she wrote *Silent Spring* few people were aware of the ecological principle that all of life is interrelated. Because of her courage, determination and eloquence, these ideas have become widespread. Millions of human beings have begun to take responsibility for humanity's place in the natural world. They agree with Carson that "man is a part of nature and his war against nature is a war against himself. The human race now faces the challenge of proving our maturity and our mastery, not of nature, but of ourselves" (Jezer 1988, p. 105). SEE ALSO CARSON, RACHEL; DDT; ENVIRONMENTAL DEGRADATION; HABITAT; HABITAT LOSS; PESTICIDE.

Nancy Weaver

Bibliography

Carson, Rachel. *Silent Spring.* Boston: Houghton Mifflin, 1962.

Harlan, Judith. *Sounding the Alarm.* Minneapolis: Dillon Press, 1989.

Jezer, Marty. *Rachel Carson.* New York: Chelsea House, 1988.

Silurian

The Silurian period of the Paleozoic era, 440–410 million years ago, follows the Ordovician period of the Paleozoic, "the age of ancient life." The Silurian was named by the R. I. Murchison in 1835 in honor of the Silure

The silurian period and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

tribe of Celts who had inhabited the Welsh borderlands where he first studied these rocks.

A long, warm, stable period followed the ice age and mass extinctions of the Ordovician, when over half of all previous life forms became extinct. Silurian fauna built upon the evolutionary patterns that had preceded it. No major new groups of invertebrates appeared, although a great radiation in number and form of existing invertebrates occurred. It has been said that the evolution of life cannot be separated from the evolution of the planet. In the Silurian, geologic trends greatly influenced animal development. As the two great supercontinents, Laurasia in the Northern Hemisphere and Gondwanaland in the Southern Hemisphere, once again drifted toward one another on their tectonic plates, mountains were heaved up to form distinct ecosystems where species could evolve uninfluenced by one another. And as the glaciers began to melt, warm, shallow seas flooded much of Laurasia, providing ideal conditions for a variety of **benthic** (bottom-dwelling) species. These included a rich variety of sea lilies, lampshells, trilobites, graptolites, and mollusks. The crinoidal sea lilies and graptolites are particularly interesting. They are both echinoderms: small, soft-bodied wormlike creatures that lack a normal head but have a well-developed nervous system located in a rudimentary **notochord** ("backchord"), the precursor of a backbone. The presence of a notochord makes these once-abundant sea-floor scavengers the ancestors of the chordates, animals with backbones.

benthic living at the bottom of a water environment

notochord a rod of cartilage that runs down the back of Chordates

A recurrent theme occurs in the origin of new marine species. They first tend to appear in very shallow waters along the shore, then disperse into deeper habitats. The shoreline is a harsh area of constant tides, storms with silt flows, and temperature fluctuations. These conditions favor species that are resilient and adaptive. Gradually the offspring expand into deeper water. The new forms of all the existing invertebrates followed this pattern: the **brachiopods**, sponges, bryozoans, **arthropods**, and echinoderms, as well as the vertebrate fishes. In the deeper waters, mobile predators appeared in unprecedented sizes. The free-swimming nautiloids, which grew up to 3 meters (10 feet) long and the eurypterids, sea-scorpion arthropods at 2-meters (6-feet) long, fed on the vast numbers of early jawed fishes that now appeared. The great reefs destroyed by the ice age were rebuilt, coral by individual coral.

brachiopods a phylum of marine bivalve mollusks

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

The most noteworthy event of the Silurian (from the human point of view) took place on land. The first minuscule plants began to creep across the previously barren land masses, followed by tiny scorpions and millipedes. The whiskery, or pleated, tracks of arthropods appear in the Silurian rocks of western Australia, and for a brief while these arthropods dominated Earth. The formerly rare agnathans (jawless fishes), became plentiful and began to explore up the **brackish estuaries** and into the freshwater rivers and upstream pools where they flourished. SEE ALSO Geological Time Scale.

Nancy Weaver

brackish describes a mix of salt water and fresh water

estuaries areas of brackish water where a river meets the ocean

Bibliography

Asimov, Isaac. *Life and Time.* Garden City, NY: Doubleday & Company, 1978.

Fortey, Richard. *Fossils: The Key to the Past.* Cambridge, MA: Harvard University Press, 1991.

———. *Life: A Natural History of the First Four Billion Years of Life on Earth.* New York: Viking Press, 1998.

Friday, Adrian and David S. Ingram, eds. *The Cambridge Encyclopedia of Life Sciences.* London: Cambridge University, 1985.

Gould, Stephen Jay, ed. *The Book of Life.* New York: W. W. Norton & Company, 1993.

Lambert, David. *The Field Guide to Prehistoric Life.* New York: Facts on File, 1985.

McLoughlan, John C. *Synapsida: A New Look Into the Origin of Mammals.* New York: Viking Press, 1980.

Steele, Rodney and Anthony Harvey, eds. *The Encyclopedia of Prehistoric Life.* New York: McGraw Hill, 1979.

Wade, Nicholas, ed. *The Science Times Book of Fossils and Evolution.* New York: The Lyons Press, 1998.

Simpson, George Gaylord

American Paleontologist and Biologist
1902–1984

George Gaylord Simpson was born to middle-class parents in Chicago, Illinois, on June 16, 1902. The family soon moved to Colorado, where he became fascinated by the dramatic geology and vertebrate fossils of the West. Graduate work at Yale University culminated in a Ph.D. in Geology in 1926 with a thesis on Mesozoic mammals. Simpson married psychologist Anne Roe and later collaborated with her on several books and conferences about behavior and evolution.

George Gaylord Simpson's work has helped generations of biology students to better understand the types of animals that lived through the Mesozoic, Paleocene, and Eocene time periods.

In 1927 Simpson began his thirty-two-year association with the American Museum of Natural History, of which he became curator in 1942. During those years he led expeditions to Mongolia, Patagonia, and Montana and taught at Columbia University. His work in organizing all the known fossil vertebrates of the Mesozoic, Paleocene, and Eocene was summarized in a series of textbooks including: *Tempo and Mode of Evolution* (1944), *The Meaning of Evolution* (1949), and *The Major Features of Evolution* (1952). His most significant achievement may be the application of population genetics to the analysis of the migration of extinct mammals between continents.

From 1959 to 1970 Simpson was professor of vertebrate paleontology at the Museum of Comparative Zoology at Harvard University. In 1967, at the age of sixty-five, he moved to Tucson to become professor of geosciences at the University of Arizona.

Simpson's lifelong enthusiasm for and contributions to his chosen field were recognized by numerous honorary degrees and medals worldwide. He was elected to the National Academy of Sciences in 1941 and the National Academy of Arts and Sciences in 1948. He was cofounder and first presi-

The skeleton of a turkey.

dent of both the Society of Vertebrate Paleontologists and the Society for the Study of Evolution. George Gaylord Simpson died October 6, 1984.

Nancy Weaver

Bibliography

Greene, Jay, ed. *Modern Scientists and Engineers*, vol. 3. New York: McGraw-Hill, 1980.

Porter, Ray, ed. *The Biographical Dictionary of Scientists.* New York: Oxford University Press, 1994.

Simpson, George Gaylord. *Attending Marvels: A Patagonian Journal.* New York: Time-Life Books, 1965.

Skeletons

Skeletons provide the framework for the bodies of most multicellular animals. They lend structural support to soft tissues and give muscles something to attach to and pull against. Without skeletons, most animal bodies would resemble a limp bag of gelatin.

Skeletons come in a number of forms, each suited for a particular set of lifestyles and environments. Skeletons can be rigid, semirigid, or soft. They can also be external or internal. Vertebrates have internal skeletons, called bony skeletons, which consist mainly of calcified **bone tissue**. Most invertebrates, such as insects, spiders, and crustaceans, have outer skeletons called exoskeletons. Some aquatic animals, such as octopuses, sea anemones, and tunicates, and a number of small, land-dwelling invertebrates such as earthworms and velvetworms, have soft supporting structures called **hydrostatic skeletons**.

bone tissue dense, hardened cells that makes up bones

hydrostatic skeletons pressurized, fluid-filled skeletons

Bony Skeleton

Vertebrata (vertebrates) is an animal group that includes fishes, amphibians, reptiles, and mammals. The vertebrate skeleton is an internal collection of relatively rigid structures joined by more flexible regions. The hard components of the skeleton are made up of bone, **cartilage**, or a combination of these two **connective tissues**.

Vertebrates are closely related to a number of less-familiar aquatic organisms, such as tunicates, sea squirts, and **lancelets** (Amphioxus). These animals have a skeleton composed entirely of a **cartilaginous** rod called a notochord. The notochord is somewhat flexible and runs along the back of the animal.

In all vertebrates, the framework first laid down during development is cartilaginous. As development proceeds, most of the cartilage is replaced by calcified bone through the action of bone precursor cells called **osteoblasts**. This process is called **ossification**. During ossification, some bones fuse together, reducing the total number of bony elements. At birth, human infants have over 300 bones. As adults, they have 206.

The bony skeleton of vertebrates consists of an **axial skeleton** and an **appendicular skeleton**. The axial skeleton is made up of the skull, spinal column, and ribs. This skeleton provides the general framework from which the appendicular skeleton hangs. The appendicular skeleton consists of the pelvic girdle, pectoral girdle, and the appendages (arms and legs).

cartilage a flexible connective tissue

connective tissues cells that make up bones, blood, ligaments, and tendon

lancelets a type of primitive vertebrate

cartilaginous made of cartilage

osteoblasts potential bone-forming cells found in cartilage

ossification the deposition of calcium salts to form hardened tissue such as bone

axial skeleton the part of the skeleton that makes up the head and trunk

appendicular skeleton the part of the skeleton with the arms, legs, and hips

Bony skeletons have a number of advantages over other types of skeletons. Because bony skeletons are living tissue, they can grow along with the rest of the body as an individual ages. As a result, animals with bony skeletons do not replace their skeletons as they grow older. Bone itself is a dynamic tissue that adjusts to the demands imposed by its environment and by its owner. Bone not only repairs itself when broken, but thickens in response to external stresses.

Bony skeletons are denser and stronger than exoskeletons and hydrostatic skeletons, and are able to support animals of a large size. By assuming a more upright posture, large animals can support a tremendous amount of weight on their skeletons. Internal skeletons are also less **cumbersome** in large animals than external skeletons would be. As an animal increases in size, its surface expands to an area that would be too large to be reasonably accommodated by an exoskeleton. All large, land-dwelling animals have bony skeletons.

cumbersome awkward

Bony skeletons can respond to increasing weight-bearing demands by adjusting bone density and by distributing the weight through changes in posture. However, the bones of some animals have actually become lighter to accomodate other functions. Bird bones, which are hollow structures, constitute a mere 4 percent of the animal's body weight, compared to 6 percent in the mammals.

A major disadvantage to the bony skeleton, relative to an exoskeleton, stems from its internal location. Although certain elements of the bony skeleton, such as the skull and rib cage, provide protection to the soft organs they encase, the skeleton offers no protection to the other soft tissues of the body. External protection is therefore left to other structures, such as the skin and its associated hair, fur, and nails.

Exoskeleton

Exoskeletons are found in most invertebrates and assume a variety of forms. Some exoskeletons are made of calcium or silica, as seen in protozoa called foraminiferans. Exoskeletons can also be elastic, such as those worn by sponges, or hard and stony, like those secreted by coral. In contrast, mollusks (clams and snails) house themselves in hard shells comprised mainly of calcium carbonate.

When compared to bony skeletons, exoskeletons have two advantages. First, they provide a hard, protective layer against the environment and potential predators. And second, they protect their wearer against drying out, which is a great threat to land-dwelling species. It is important to avoid **dessication** because water molecules play an important role in many of life's critical physiological processes, including those related to digestion and circulation.

dessication drying out

chitin a complex carbohydrate found in the exoskeleton of some animals

Insect, spider, and shellfish (lobster and shrimp) exoskeletons contain a compound called **chitin**, a white horny substance. These **arthropods** have segmented exoskeletons that bend only at the joints. The exoskeleton covers the entire surface of an arthropod's body, including the eyes. The thickness of the exoskeleton varies depending on the nature and function of the body part it covers. For example, the exoskeleton is thinner at the joints,

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

which require a degree of flexibility in order to bend. The chemical composition of the exoskeleton also differs depending on location and function.

Insects have three principle body segments—the head, thorax, and abodomen—and six segmented legs. Each segment is curved and hinged to its neighbor. Spiders have a thorax and abdomen and eight legs. Their head is fused to their thorax. Other arthropods, including scorpions, centipedes, and shrimp, may have more body segments than an insect and more legs than a spider.

molted the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

Exoskeletons have two major disadvantages when compared to bony skeletons. Because they are composed of a blend of rigid, inorganic substances, they cannot expand as their owner grows. Arthropods must therefore shed their exoskeletons periodically through a process called molting. A newly **molted** animal is vulnerable to attack by predators before its new shell hardens. The shell hardens through a process similar to the tanning of leather.

The second disadvantage of exoskeletons is that physical contraints limit the size attainable by animals that have them. As the animal gets larger, the size of the exoskeleton required to cover its surface area would render the covering heavy and cumbersome.

Hydrostatic Skeletons

hydrostatic skeleton a pressurized, fluid-filled skeleton

Hydrostatic skeletons are found mostly in aquatic organisms such as octopusses, jellyfishes, sea anemones, and tunicates. Although earthworms and velvetworms have hydrostatic skeletons as well. Bony skeletons and exoskeletons are made of relatively rigid substances, but hydrostatic skeletons contain no hard parts at all.

These soft, supporting structures have two components, a fluid-filled body cavity and a muscular body wall. Animals with hydrostatic skeletons move using the combined actions of these two features. They use the muscles of the body wall to squeeze fluid into other regions of the body cavity, allowing them to change shape. These shape changes allow the animal to extend parts of its body in the direction it wants to move and withdraw other parts from areas it is leaving.

One benefit that hydrostatic skeletons give to some soft-bodied organisms is an ability to take in important materials such as oxygen, water, and waste products through the skin. This eliminates the need for a separate transport system. It is beneficial for these animals not to have a separate transport system because transfer of these materials is a passive process, which means that energy does not need to be expended to take in oxygen, rid the body of waste products, and maintain the balance of water between the body and the environment. In addition, these skeletons are relatively light compared to bony skeletons and exoskeletons.This is beneficial because not as much muscle mass is required to move it. Hydrostatic skeletons work well in aquatic environments, but they would not be useful on land. They give little protection against drying out, and larger animals would be too flimsy to stand up on their own. SEE ALSO Bones; Cartilage; Chitin; Keratin.

Judy P. Sheen

Social Animals

Sociability is a trait that applies to the ecology and behavior of a species and not to individual organisms. Social species are genetically inclined to group together and follow a particular set of rules defining interactions between individuals. Humans can be considered a social species because we tend to live in communities instead of segregating ourselves as individuals and dispersing to unoccupied territory. In many species, a family unit, meaning parents and their immediate dependent young, groups together and follows particular guidelines of interaction. However, this does not qualify as a society. A society must be composed of more individuals than are contained in a family unit. Even in typically antisocial species, individuals may temporarily unite to bear and raise young before re-dispersing.

Sociability in animals must be either permanent or semi-permanent, unlike family units. The species must also divide social responsibilities among individuals within the group. For example, one group of individuals, whether determined by age, gender, or body shape, must consistently perform a particular function. This requirement disqualifies animals that are merely nonaggressive with one another, but that do not partake in the formality of social structure.

Definition

A rigorous definition of an animal society is: a group of animals belonging to the same species, and consisting of individuals beyond those in a family unit, who perform specific tasks, spend distinctly more time together, and interact much more within the group than with members of the same species outside of that group. A social animal is defined as any animal species that typically forms into societies.

Many ecologists are concerned with social behaviors, which are any behaviors specifically directed towards other members of the society. These can include cooperative, selfish, hurtful, or helpful behaviors. The sum of these behaviors determines the character of the society, such as its size and location, and the responsibilities of different societal members. For example, walruses live in coastal arctic regions, within herds containing up to several hundred individuals. Males within a herd are known to attack one another over disputes pertaining to female choice, territory, or food; however, entire herds have been known to come to the defense of a single member when placed in danger. Plants, fungi, and single-celled organisms are not considered social because their interactions are strictly dictated by physical and chemical needs. Thus they cannot behave, and without social behaviors a society is impossible.

Why Species Form Societies

The tendency of a species to form into societies is considered to be caused by the influence of **natural selection**. During the process of evolution, individual animals of a particular species that formed into societies were more likely to survive than those animals that remained isolated from one another. This pressure to be social could be genetic in origin, meaning that high levels of kinship cause extended families to protect one another. It could also be an environmental pressure—a particularly harsh environment

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

may force animals to depend on each other for greater support. A certain species that is observed to be social today may no longer be under selective pressure to form societies, but retains the trait of sociability for genetic reasons.

Some species may be social in certain environments and solitary in others. This can be linked to food abundance. For example, if food is readily available, individuals can group together for greater protection from predators. If food is scarce, they will remain as individuals so as to avoid the responsibility of supporting weaker individuals. This illustrates how societies can be both cooperative and competitive.

They are cooperative because the animals within a society must share their space and resources in order to ensure the survival of as many members as possible. However, they are competitive because each individual animal within a society is primarily concerned with its own survival. In the case of ample food, a strong animal may enlist the help of weaker animals. The stronger animal benefits from the extra labor and shares the surplus with the weaker animals who may not have survived on their own. This is cooperative behavior.

If the same society is deprived of food, however, the stronger animal no longer benefits from sharing its scarce supplies. It separates from the weaker animals, which are now forced to fend for themselves. This is competitive behavior. In less extreme situations, members of a healthy, normal society express both types of behavior at different times.

Degrees of Sociability

Different species of animals may be social in greater or lesser degrees. The degree of sociability is loosely determined by the likelihood of forming a society, the degree of variation in societal size, the specificity of division of labor, the interdependence of members for survival, and possible **phenotypic** specializations, difference of body shape, related to societal rank. A non-social species may form into societies in extreme or abnormal situations. This is a common occurrence for captive **populations** of territorial animals that normally have large ranges in which they remain isolated. In zoos and research laboratories, these animals are artificially forced to live in close proximity to one another. They may display signs of cooperation that herald societal behavior, but this is most likely forced interaction that would not occur in the wild.

phenotypic physical and physiological traits of an animal

populations groups of individuals of one species that live in the same geographic area

The Sizes of Societies

The relative sizes of societies within the same species is a clue to understanding their degree of complexity. If members of the same species located in similar environments always form societies of approximately the same number of individuals, then that species may have complex societal laws dictating group size. Often, maximum group size is determined by local predation on the social species, when regional predators are better able to locate large groups than small groups of prey.

Some species maintain equivalent societal populations even in the absence of heavy predation, and these can be considered more socially complex. Highly complex societies divide tasks among societal members in a

very precise manner. For example, some individuals may be responsible for hunting, some for reproducing, some for maintaining the society's living space, and some for raising the young. The clearer the distinction between the duties of societal members, the more complex that society is. In the most complex societies, individuals of a particular caste or rank almost never switch roles within their society. An animal may exchange roles only in situations where a particular caste that performs a particular function is severely depleted in numbers and needs to be augmented by new members.

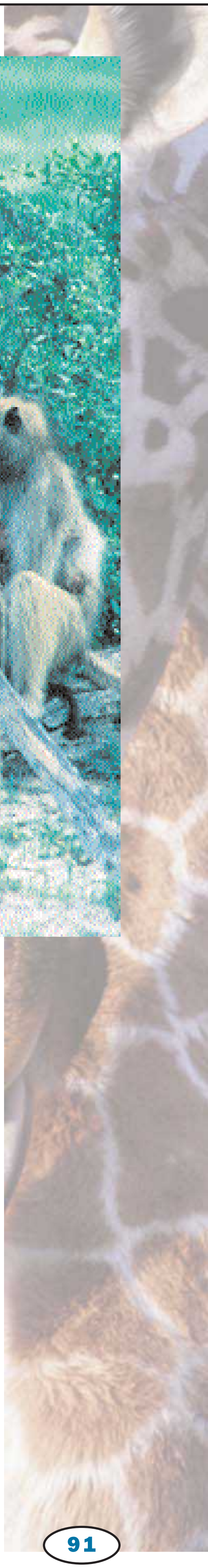
These Chacma Baboons (*Papio ursinus*) from Zimbabwe form a highly social family group.

In less complex societies, animals may have shifting duties and responsibilities. In such a society, a female may reproduce one year, but care for young the following year, and hunt the next year. The roles of individuals within the society continually shift based on the needs of the individual versus the needs of the group.

Effects of Sociability

Occasionally, in species with a very high degree of task specificity, the **phenotype**, or set of body characteristics, of individuals is determined by their

phenotype the physical and physiological traits of an animal



caste. This principle supercedes gender differences in body type. An animal's societal role may be so distinct that its body grows into a form that can best perform that role. Often, the role is easily determined by the appearance of the animal. This is a very rare phenomenon for vertebrates, although it is relatively common in insects such as honeybees and termites.

phenotypic variation differences in physical and physiological traits within a population

pheromones small, volatile chemicals that act as signals between animals that influence physiology or behavior

hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

This **phenotypic variation** is often based on internal **hormones**, or external **pheromones**. Pheromones are hormones released into the environment that can alter the development, behavior, and appearance of individual animals. Pheromones have species-specific effects, meaning that they typically affect only animals within the same species. Type of food consumed, environmental conditions, and population ratios between the castes can affect the caste phenotype of individuals either directly or indirectly by altering the exposure of individuals to particular pheromones.

Sociability is a trait of many organisms, but two particular animals provide models of highly complex animal societies. Termites and naked mole rats come from entirely divergent evolutionary origins, yet they share a similar social organization. This raises the question for ecologists of why this social strategy is so effective that it arose multiple times in multiple branches of the evolutionary tree. Understanding the social interactions of these animals can contribute to the theoretical explanation of this organizational pattern.

eusocial animals that show a true social organization

The highest degree of sociability in animals is given its own classification term, **eusocial**. Eusocial animals must exhibit a reproductive division of labor, which means that many sterile individuals work to support those individuals capable of breeding. Furthermore, they must be organized into a system of discrete castes distinguishable by differences in skeletal or body characteristics, and these castes must contribute to care of the young. Finally, the generations must overlap in time, meaning that the young do not have time to mature before another group of young is produced. Termites and naked mole rats both conform to this definition.

Termites

Termites live in carefully constructed structures entirely shut off from the light, usually within dead trees or wood products. Their social structure is relatively flexible compared to that of ants: In an ant colony, the sizes and body forms of individuals are fixed and constant at maturity, but termites change the shapes of their bodies depending on their role in the colony, even as adults.

Termite colonies may contain from several hundred to several million individuals. New colonies are founded annually during a short season when an existing colony produces sexual winged members that leave the nest by the thousands in a marriage flight. After about two and a half hours, the termites drop to the ground and purposefully break off their wings. The male and female dig a tunnel into a damp log for approximately two days and then mate within two weeks. Termites undergo incomplete development, which means that they resemble miniature, immature adults at hatching, and never pass through a grub stage of development. When the brood is old enough, they assume complete responsibility for feeding and caring for their parents, which are now called the royal couple, or the king and queen. Both the king and queen grow much larger than other caste members, and the queen's abdomen swells with eggs until she becomes up to 20,000 times the size of other colony members.

Termites continuously exchange food and clean one another, probably to ensure cleanliness, but these behaviors also serve to cement the social interaction of the colony. Pheromones secreted by the royal couple and spread through saliva and food-sharing inhibit the development of more sexual forms in the colony, but the mechanisms underlying **differentiation** of other castes are unclear. They seem to develop when needed by the colony.

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

Termites are divided into more castes than most social insects, and the castes are far more varied. The basic division of labor includes the reproductive royal couple and sterile soldiers and workers. There are two possible types of soldiers, although any given species contains only one type. The mandibulate uses its large pincers to attack enemies, while the nasute excretes a sticky, poisonous substance from its elongated snout to immobilize enemies.

Soldiers only serve to defend the nest from enemies, and cannot feed themselves or perform any other function in the colony. Workers perform all of the construction tasks of the colony as well as feeding and cleaning the royal couple, eggs, and soldiers. Substitute sexual forms develop from juveniles when one or both of the royal couple dies. They battle amongst themselves until only one reproductively capable couple remains, and these two will develop into the new king and queen.

As decomposers, termites are highly important members of their ecological communities. Termites feed on dead plant cell wall material, with their most prevalent form of food being wood. Termites themselves do not digest the cellulose; rather, the protozoans and bacteria that live symbiotically in the termites' gut break down the tough wood fibers. In some communities, termites can be responsible for recycling up to one third of the annual production of dead wood, thereby making many needed nutrients available to their environment.

Like termites, every species of ant, most species of bees, and many species of wasp live in similarly-structured social colonies, with one reproductive pair and many sterile castes. This strategy has evolved independently many times in insects, which means that it must confer some general evolutionary advantage to the species. Perhaps by sequestering the only viable pair in the heart of a well-defended fortress, these insects are better able to ensure the safety of mating and survival.

Naked Mole Rat

One species of vertebrate, the naked mole rat, has also adapted a colonial social structure. Naked mole rats are more closely related to voles than to either moles or rats. They mainly inhabit Somalia, Ethiopia, and Kenya, in sandy soil burrows that extend from near-surface level to several meters below the ground. These are the only known cold-blooded vertebrates. Their body temperatures are always equivalent to ambient temperature except when they are highly active.

These animals also differ from other mammals in that they live in a complex social environment. There is one breeding female per colony, and she can be considered the equivalent of a queen in the termite colony. She is longer-bodied and heavier than other members. Unlike the termite example, there is no single king to mate with the lead female; instead, any male in the colony is free to mate with the lead female, but there is little aggression or competition between these males. This female gives birth to one to six pups per litter, and approximately two litters per year, and these animals have a life span of twenty to forty years.

> Naked mole rats consume their own feces and that of other mole rats. They also roll their bodies in the feces to ensure that no nutrients are lost through fecal matter that has not been entirely digested, and to mark colony members with an identical signature scent.

Castes in the naked mole rats are partially determined by age and partially by body size. The leading female maintains her dominance in the colony through shoving and threatening non-breeders. All castes except for the breeding female engage in building, digging, and transporting food and soil, but the amount of work they perform is clearly delineated by their caste. Small-bodied juveniles are frequent workers, meaning that they carry the bulk of work activity of the colony. Slow-growing individuals remain frequent workers their entire lives, although larger, faster-growing individuals move into the infrequent workers caste, and eventually into the nonworkers caste.

The infrequent workers and nonworkers are most often colony-defenders. When the breeding female dies or is killed, the younger, smaller-bodied female caste members set upon one another. Their bodies begin to produce greater degrees of female hormones, and they fight until one dominant female remains alive. At this point, the colony recognizes their new breeding female, and colony life reestablishes itself.

Being social seems to confer many advantages to social animals, such as increased defense of breeding individuals, increased likelihood of survival, and increased stability of food stores and habitat. However, many animals are not social. An example is sloth bears, which hunt termites for food and come together only for the sake of reproduction. Explaining the reasons for the sloth bear's asocial behavior is not entirely possible without knowing its distinct evolutionary history. However, the bear's large body size and scarce food source may be reasons why colonial living is inappropriate for this species. SEE ALSO Behavior; Dominance Hierarchy; Sociality.

Rebecca M. Steinberg

Bibliography

Bennett, Nigel C., and Chris G. Faulkes. *African Mole-Rats: Ecology and Eusociality*, Cambridge and New York: Cambridge University Press, 2000.

Bonner, John Tyler. *The Evolution of Culture in Animals*. Princeton, NJ: Princeton University Press, 1980.

Caro, Timothy M. *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species*. Chicago: University of Chicago Press, 1994.

Gadagkar, Raghavendra. *Survival Strategies: Cooperation and Conflict in Animal Societies*. Cambridge, MA: Harvard University Press, 1997.

Ito, Yoshiaki. *Behaviour and Social Evolution of Wasps: The Communal Aggregation Hypothesis*. Oxford and New York: Oxford University Press, 1993.

Wilson, Edward Osborne. *Sociobiology: The New Synthesis*, 25th anniversary ed. Cambridge, MA: Belknap Press of Harvard University Press, 2000.

Sociality

Sociality is a genetically determined social behavior that dictates the social structure of particular groups of animals. Manifestations of sociality include living in close proximity, dividing tasks and responsibilities, and traveling together. Insects express sociality more frequently and to greater extremes than do most other animals, and as a result these animals have formed the archetype of all social animals.

Hives are the preferred "living arrangements" for eusocial bees. Various castes of bees will live harmoniously within the close living quarters of their hive.

Social insects live in every terrestrial **ecosystem** and form an important part of many food webs. **Eusocial** (extremely social) animals live in collective societal units referred to as hives or colonies. As adults eusocial animals serve their society in narrowly defined capacities know as "castes." Some examples of a caste are the worker, soldier, nurse, or reproductively capable king or queen.

ecosystem a self-sustaining collection of organisms and their environment

eusocial animals that show a true social organization

In highly social animals all animals excepting the reproductive pair are sterile. In some animals the juvenile's role is predetermined, and it matures into the appropriate body size and shape. However, in other animals the caste of the mature adult is not decided until the animal has matured. In the latter case the individual's body size and abilities, and sometimes its age, will subsequently determine its caste position. There is evidence that some dinosaurs had complex social structures that caused them to herd and nest together. Although only one genus of vertebrate (the naked mole rat), is eusocial, many mammals, birds, reptiles, amphibians, and fish show social behaviors to a lesser degree.

Several theories have arisen to explain the evolution and conferred benefits of eusociality. One of these is "kin selection", suggested by W. D. Hamilton in his 1964 paper, "The Genetical Theory of Social Behavior." This theory suggests that social animals are often genetically very similar to each other. If one accepts that the evolutionary goal of a species is to en-

genomes the sum of all genes in a set of chromosomes

sure the survival of its DNA, then in animals with identical **genomes**, the survival and reproduction of individuals lose importance.

For example, if animal A and animal B have very different DNA, then each will desire to pass on its hereditary code to offspring because each code is unique. However, if A and B have very similar genomes, only one of them needs to reproduce for both of their genetic codes to be carried on to future generations. If the entire colony shares similar DNA, only two members of the colony are required to reproduce so as to pass on their genetic codes. This frees the remaining colony members from reproductive drive and allows them time and incentive to protect, feed, and house the reproductive couple. Thus the kinship of the animals ties them together.

The theory of kin selection is related to the idea of "inclusive fitness," which relates how a trait can pass from generation to generation directly, from parent to offspring, or indirectly through the help provided by individuals who possess the same trait as the parent. Wasps, bees, and ants have a genetic system in which all individuals are at least 50 percent identical, and this genetic similarity makes them a good candidate for kin selection and thus sociality. SEE ALSO Behavior; Dominance Hierarchy; Social Animals.

Rebecca M. Steinberg

Bibliography

Bourke, Andrew F. G., and Nigel R. Franks. *Social Evolution in Ants.* Princeton, NJ: Princeton University Press, 1995.

Frank, Steven A. *Foundations of Social Evolution.* Princeton, NJ: Princeton University Press, 1998.

Hamilton, W. D. "The Genetical Evolution of Social Behavior." *Journal of Theoretical Biology* 7 (1964): 1–52.

Sociobiology

In 1975 Harvard University biologist Edward O. Wilson wrote a controversial book called *Sociobiology: The New Synthesis* in which he proposed to undertake "the systematic study of the biological basis of all social behavior" (Meachan 1998, pp. 110–113). Following a lifelong fascination with ants and their social structures, Wilson was interested in determining the degree to which genetic evolution influences cultural evolution. He applied the principles of evolution to the analysis of **behavioral** questions such as altruism, competition, cooperation, parasitism, dominance, **population** control, sex differences, and division of labor among social animals.

behavioral relating to actions or a series of actions as a response to stimuli

population a group of individuals of one species that live in the same geographic area

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

genetics the branch of biology that studies heredity

The theory of **natural selection** formulated by nineteenth-century British naturalist Charles Darwin would seem to indicate that the most successful animals would be those who act in their own self-interest. Yet clearly, social animals—societies of cooperating organisms—exist and often put the welfare of the group above their own. Wilson attempted to explain this using **genetics** and population models. He proposed that any organism—from the simplest to the most complex—exists as DNA's way of making more DNA. Therefore, a mother sacrificing herself for the sake of two or more offspring would overall benefit her DNA, as would the actions of a herd animal sacrificing itself for the sake of multiple related members.

Wilson attempted to apply sociobiology to human beings, saying that "We eat, sleep, build shelters, make love, fight and rear our young because, through the process of natural selection interacting with social influences, we developed genetic predispositions to behave in ways that ensured our survival as a species." This idea was violently rejected by fellow sociologists. It was taken to mean that everything humans did was predetermined genetically, although Wilson himself explained: "It is wrong to say that if a behavior is adaptive—that is evolutionarily advantageous—it cannot be conscious." He believed that while there is a biological basis for behavior such as nepotism, altruism, and status seeking, individuals within species are capable of immense variation. And further, he held that different species reacting to different environmental pressures tend toward particular forms of societies. Ant colonies, in other words, behave differently than elephant herds, and human groups behave like neither.

The questions raised by sociobiology have been incorporated into the larger field of behavioral **ecology**. These questions include: Which social arrangements best accommodate the general features of which species? What particular environmental conditions trigger different tendencies?Meanwhile, despite a superficial impression that nature is filled with constant competition, closer examination shows that cooperative behavior occurs throughout **ecosystems** and is far more stable and beneficial to all the species involved. SEE ALSO BEHAVIOR; DOMINANCE HIERARCHY; SOCIAL ANIMALS; SOCIALITY.

ecology the study of how organisms interact with their environment

ecosystems self-sustaining collections of organisms and their environments

Nancy Weaver

Bibliography

Concise Dictionary of Scientific Biography. New York: Scribner. 2000.

Meachan, Dyan. "Please Pass the Ants." *Forbes* 164, no. 6 (1998): pp. 110–113.

Sponges *See Porifera.*

Spontaneous Generation

From the seventeenth century, through the Middle Ages, and until the late nineteenth century, it was generally accepted that some organisms originated directly from nonliving matter. Such "spontaneous generation" appeared to start in decaying food, urine, and manure because worms or maggots could be seen hatching there after a few days. It was also believed that animals that lived in mud, such as frogs and salamanders, were generated by the mud in which they lived. Additionally, there were the widely held misconceptions that rats were spontaneously generated in piles of garbage or created from magical recipes. One seventeenth-century recipe even called for the creation of mice from sweaty underwear and wheat husks placed together in a jar for twenty-one days. Although such a concept may seem ludicrous today, it was congruous with other cultural and religious beliefs of the time.

Francesco Redi, an Italian physician, naturalist, and poet, first challenged the idea of spontaneous generation in 1668. At that time, it was widely held that maggots arose spontaneously in rotting meat. Redi did not believe this.

He hypothesized that maggots developed from eggs laid by flies. To test his hypothesis, he set out meat in a variety of jars, some open to the air, some sealed completely, and some covered with gauze. As Redi had expected, maggots appeared only in the jars in which the flies could reach the meat and lay their eggs.

Unfortunately, many people who were told or read about these experiments did not believe the results, so if they still wanted to believe in spontaneous generation, they did. Even Redi continued to believe that it occurred under some circumstances and cited the example of grubs developing in oak trees. The invention of the microscope during this time only seemed to further fuel this belief, as microscopy revealed a whole new world of microorganisms that appeared to arise spontaneously.

The debate over spontaneous generation continued for centuries. In the mid-eighteenth century, two other well-documented experiments—one by John Needham, an English naturalist, and the other by Lazzaro Spallanzani, an Italian physiologist—were attempted but were considered by proponents of spontaneous generation to be unpersuasive.

The idea of spontaneous generation was finally laid to rest in 1859 by the French chemist, Louis Pasteur. The French Academy of Sciences sponsored a competition for the greatest experiment that could either prove or disprove spontaneous generation. Pasteur devised a winning experiment where he boiled broth in a flask, heated the neck of the flask in a flame until it became pliable, and bent it into the shape of an "S." With this configuration, air could enter the flask, but airborne microorganisms could not, they would settle by gravity in the neck of the flask. As Pasteur had expected, no microorganisms grew. However, when he tilted the flask so that airborne particles could enter, the broth rapidly became cloudy with life. Pasteur had both refuted the theory of spontaneous generation and demonstrated that microorganisms are everywhere, including the air. SEE ALSO Biological Evolution.

Stephanie A. Lanoue

Bibliography

Krebs, Robert. *Scientific Development and Misconceptions Throughout the Ages.* Westport, CT: Greenwood Press, 1999.

Random House Dictionary of Scientists. New York: Random House, 1997.

Starfishes

See Echinodermata.

Stevens, Nettie Maria

American biologist
1861–1912

Nettie Maria Stevens was a prominent biologist who discovered that the sex of an organism was determined by a specific chromosome. Although her research career spanned less than a decade (1903–1912), she published forty papers and became one of the first American women to achieve recognition for her contributions to scientific research.

Stevens was born July 7, 1861 in Cavendish, Vermont. She graduated from the Westford Academy in 1880 and enrolled at the Westfield Normal School, a educator college founded to cerify teachers, in 1881. She received the highest scores on the college's entrance exams of any student in her class. Clearly an outstanding student, she earned the four-year teacher certification in just two years.

In 1883, Stevens graduated from Westfield Normal School with the highest academic scores in her class. After graduation she took a job as a librarian at a high school in Lebanon, New Hampshire. In 1896, at the age of 35, she transferred to Stanford University in California, where she earned a B.A. degree in General Biology in 1899 and an M.A. in **physiology** in 1900. She began her doctoral studies at Bryn Mawr which included a year of study (1901–1902) at the Zoological Station in Naples, Italy, and at the Zoological Institute of the University of Würzburg, Germany.

Stevens received a Ph.D. in Morphology from Bryn Mawr in 1903 and remained at the college as a research fellow in biology the following year. She was an associate in experimental morphology at Bryn Mawr from 1905 until her death from breast cancer on May 4, 1912, in Baltimore, Maryland at the age of 51.

Stevens' earliest field of research was the morphology and **taxonomy** of ciliate **protozoa**. One of her major papers in that field was written in 1904 with zoologist and geneticist Thomas Hunt Morgan, who won the Nobel Prize in 1933 for his work. Stevens' investigations into regeneration led her to a study of **differentiation** in embryos and then to a study of **chromosomes**. Steven's research showed that very young embryonic cells could not fully regenerate. In 1905 Stevens published a paper in which she announced her landmark finding that the chromosomes known as X and Y were responsible for the determination of the sex of an individual.

Stephanie A. Lanoue

Nettie Maria Stevens was one of the first American women to have her scientific achievements recognized.

physiology study of the normal function of living things or their parts

taxonomy the science of classifying living organisms

protozoa a phylum of single-celled eukaryotes

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

chromosomes structures in the cell that carry genetic information

Bibliography

Morgan, Thomas Hunt. "The Scientific Work of Miss N. M. Stevens." *Science* 36, no. 928 (1912):21–23.

Ogilvie, Marilyn Bailey, and Clifford J. Choquette. "Nettie Maria Stevens (1861–1912): Her Life and Contributions to Cytogenetics," *Proceedings of the American Philosophical Society*, 125, no. 4 (1981):10–12.

Shearer, Benjamin F., and Barbara S. Shearer. *Notable Women in Life Sciences.* Westport, CT: Greenwood Press, 1996.

Surface-to-Volume Ratio *See Body Size and Scaling.*

Sustainable Agriculture

Thanks to a complex international system of production, processing, shipping, and marketing, people today can eat a vast selection of out-of-season and out-of-region fruits and vegetables year round. In addition, modern farming practices have provided an abundant, not just a varied, food supply. However, the availability of abundant and varied food relies on energy-intensive, nonrenewable resources such as fossil fuels, and many practices associated with agribusiness have had a detrimental impact on the environment.

Agribusiness

Agribusiness looks at farms as factories to be run as profitably and efficiently as possible. "How much, how fast" replaces the old values of carrying capacity (how much the land can yield without being depleted) and a season of lying fallow. Monocropping (fields used for only one crop, the same crop year after year, commonly wheat, soybeans or cotton) and increased field size do away with **biodiversity** and hedgerows, and thus with fertility, pollinators, and resistance to insects and disease.

biodiversity the variety of organisms found in an ecosystem

Effects of fertilizers. Millions of tons of chemical fertilizers applied to fields destroy microorganisms that are vital to the health of the soil. The intensive use of herbicides and **pesticides** kills pollinating insects that are essential for crop production. Manure and crop residues, once valuable sources of soil nutrition, are no longer tilled in and have become polluting waste products themselves, to be burned or dumped. Underground aquifers (natural water reservoirs) that took thousands of years to fill are pumped dry to irrigate fields in semi-arid regions.

pesticides substances that control the spread of harmful or destructive organisms

Additionally, ground water is full of dissolved mineral salts. As the water evaporates it leaves a salt concentration buildup that is poisoning the soil. Intensive plowing opens up hundreds of thousands of acres of topsoil to erosion by wind and rain, filling the air with dust or silting up waterways.

Loss of biodiversity. As more and more wild land is converted to growing one particular crop on a massive scale, genetic biodiversity diminishes. Rain forests are bulldozed to provide pastures for cheap beef. Massive feedlot operations are susceptible to catastrophic diseases, and they pollute drinking water supplies with their tons of confined manure.

Economic consequences. Agribusiness also affects the economy. Family farmers are increasingly replaced by corporate managers, and the price of farm equipment and capital outlay soars. Profits from production may go to a large company based far away from the actual farm and never enter the local economy. In addition, large-scale food production and distribution have become vulnerable to the vagaries of international politics and the stock market, and any breakdown in the network places everyone at risk. The price of oil, interest rates, trucking fees, politics and the weather all affect the availability and price of food. In countries where there is economic or military chaos, even though there might be plenty of food on farms or at food aid centers, the breakdown in the complex distribution system results in famine.

Sustainable Agriculture

Sustainable agriculture is the practice of working in concert with nature to replenish the soil in order to assure a secure, affordable food supply without depleting natural resources or disrupting the cycles of life. Proponents of sustainable agriculture suggest we can reverse the damage done by agribusiness. They believe that a dependable long-term food supply must rely on the protection of resources—seeds, food species, soil, breeding stock,

A farmer spreads fertilizer on his fields in northeastern Pennsylvania.

and the water supply, as well as the farmer who knows and cares for a particular piece of land and the community with which the farmer is interdependent. Sustainable agriculture promotes regional and local small-scale farms that rely on the interplay of crops and livestock to replenish the soil and control erosion. The aim of a healthy farm is to produce as many kinds of plants and animals as it reasonably can. Ordered diversity is the practice of maintaining many kinds of plants and animals together to complement one another.

Cover cropping. The practice of planting a noncommercial crop on fields to increase fertility, conserve soil moisture, keep topsoil from eroding or blowing away and encourage soil microrganisms is called cover cropping. Soil fertility, which is the major capital of any farm, can be largely maintained within the farm itself by this method and by plowing back in manure and other organic wastes. Food grown for local consumption is more fresh, can be harvested when ripe, and uses less energy to get to market. Farm stands and local farmers' markets provide more money for the farmer and higher quality, lower-price food for the consumer.

Diversity of methods. Sustainable agriculture embraces diversity of method and scale, looking for what is appropriate to a given location. One example is urban homesteading, in which thousands of vacant inner-city lots can be used to grow neighborhood gardens. Renewable energy sources, such as passive-solar greenhouses or windmills, are encouraged. Sustainable agriculture advocates organic solutions to pest control such as crop rotation, the introduction and maintenance of beneficial insects, and intercropping (growing more than one kind of crop on the same land in the same growing season). All these methods discourage insect infestations, thus reducing the amount of pesticides in the environment.

Agriculture cannot survive for long at the expense of the natural systems that support it. And a culture cannot survive at the expense of its agriculture. SEE ALSO Farming.

Nancy Weaver

Bibliography

Berry, Wendell. *The Unsettling of America: Culture and Agriculture*. San Francisco: Sierra Club Books, 1977.

Organic Farming Research Foundation. *Winter 2001 Information Bulletin*, no. 9. Erica Walz, ed. Santa Cruz, CA: Organic Farming Research Foundation, 2001.

Systematist

Systematics is the field of biology that deals with the diversity of life. It is the study of organisms living today and in the past, and of the relationships among these organisms. Systematics includes the areas of taxonomy and phylogenetics. Taxonomy is the naming, describing, and classification of all living organisms and fossils. Phylogenetics is the study of evolutionary relationships among organisms. It is also the study of the physical and environmental settings in which evolutionary changes occurred.

biogeography the study of the distribution of animals over an area

Systematics is also an essential part of other fields such as **biogeography** (the mapping of where species occur), ecology (the study of the habitats and environmental factors that control where species occur), conservation biology, and the management of biological resources.

Systematists collect plants and animals, study them, and group them according to patterns of variation. Systematists study plants and animals in nature, laboratories, and museums. Some study the scientific basis of classifications so they can better understand evolution. Others study ever-changing aspects of nature, such as the processes that lead to new species or the ways that species interact. Other systematists study the human impact on the environment and on other species. Some systematists screen plants for compounds that can be used for drugs. Others are involved in controlling pests and diseases among plant and animal crops. Many systematists have teaching careers. They may work in colleges and universities. They teach classes, teach students how to conduct research, and conduct their own research in their particular area of interest. An important part of the research is writing up the results for publication.

ecology study of how organisms interact with their environment

Systematists are employed mostly by universities, museums, federal and state agencies, zoos, private industries, and botanical gardens. Universities with large plant or animal collections often hire systematists as curators to maintain the collections and conduct research on them. Federal and state agencies employ systematists in many fields including public health, agriculture, wildlife management, and forestry. Industries that employ systematists include agricultural processors, pharmaceutical companies, oil companies, and commercial suppliers of plants and animals. Most jobs in government and industry center on taxonomy and **ecology**, rather than evolution issues.

At the high-school level, persons interested in becoming systematists should study math, chemistry, physics, biology, geology, English, writing, and computer studies. Although there are career opportunities for systematists with bachelor's degrees, most professionals have either a master's or doctoral (Ph.D.) degree. Undergraduate degrees can be obtained in biology, **botany**, or zoology. Graduate students focus specifically on systematics. They study taxonomy, **population** biology, genetics, evolution, ecology, biogeography, chemistry, computers, and statistics. SEE ALSO MORPHOLOGY.

botany the scientific study of plants

population a group of individuals of one species that live in the same geographic area

Denise Prendergast

Bibliography

Keeton, William T., James L. Gould, and Carol Grant Gould. *Biological Science.* 5th ed. New York: W.W. Norton & Company, Inc., 1993.

Internet Resources

American Society of Plant Taxonomists: <http://www.csdl.tamu.edu/FLORA/aspt/asptcar1.htm>.

Society for Integrative and Comparative Biology: <http://www.sicb.org/>.

Tapeworms *See Cestoda.*

Taxonomist

Taxonomy is the naming, describing, and classification of all living organisms and fossils. It is an important part of systematics, the field of biology that deals with the diversity of life. There are three main schools of taxonomy:

- Phenetic taxonomy—which classifies organisms based on overall form and structure or genetic similarity, also called numerical taxonomy;
- Cladistic taxonomy—which classifies organisms strictly based on branching points, focuses on shared, relatively recent (not of ancient origin) characteristics that are common to the species being studied, also called **phylogenetic** taxonomy; and
- Evolutionary taxonomy—which classifies organisms based on a combination of branching and divergence, also called traditional taxonomy.

phylogenetic relating to the evolutionary history of species or group of related species

Taxonomists collect plants and animals, study them, and group them according to patterns of variation. Taxonomists study plants and animals in nature, laboratories, and museums. Several million species of animals and over 325,000 species of plants are presently known. It is estimated that between several million and 30 million species await discovery. Animal species are included in the International Code of Zoological Nomenclature, a document that also contains the rules for assigning scientific names to animals.

Some taxonomists study the scientific basis of classifications so they can better understand evolution. Others study the ever-changing aspects of nature, such as the processes that lead to new species or the ways that species interact. Other taxonomists study the human impacts on the environment and on other species. Some taxonomists screen plants for compounds that can be used for drugs. Others are involved in controlling pests and diseases among plant and animal crops. Many taxonomists have teaching careers. They may work in colleges and universities. They teach classes, teach students how to conduct research, and conduct their own research in their particular area of interest. An important part of the research is writing up the results for publication.

Taxonomists are generally employed by universities, museums, federal and state agencies, zoos, private industries, and botanical gardens. Universities with large plant or animal collections often hire taxonomists as curators to maintain the collections and conduct research on them. Federal and state agencies employ taxonomists in many fields including public health, agriculture, wildlife management, and forestry. Industries that employ taxonomists include agricultural processors, pharmaceutical companies, oil companies, and commercial suppliers of plants and animals.

At the high-school level, persons interested in becoming taxonomists should study mathematics, chemistry, physics, biology, geology, English, writing, and computer studies. Although there are career opportunities for taxonomists with bachelor's degrees, most professionals have either a master's or doctoral (Ph.D.) degree. Undergraduate degrees can be obtained in biology, botany, or zoology. Graduate students focus specifically on taxonomy. They study population biology, **genetics**, evolution, ecology, biogeography, chemistry, computers, and statistics. SEE ALSO Taxonomy.

genetics the branch of biology that studies heredity

Denise Prendergast

Bibliography

Keeton, William T., James L. Gould, and Carol Grant Gould. *Biological Science.* 5th ed. New York: W.W. Norton & Company, Inc., 1993.

Internet Resources

American Society of Plant Taxonomists: <http://www.csdl.tamu.edu/FLORA/aspt/asptcar1.htm>.

Society for Integrative and Comparative Biology: <http://www.sicb.org/>.

Taxonomy

Taxonomy is the practice of classifying and naming biological organisms and groups of biological organisms. Modern taxonomy originated in the eighteenth century with the work of a Swedish botanist, Carolus Linnaeus, who developed an organized hierarchical classification system that could be applied to all biological organisms. This system is still referred to as Linnaean taxonomy. Under the Linnaean system, all organisms are classified hierarchically into a series of groups from most inclusive to least inclusive. Each species belongs successively to a kingdom, a phylum, a class, an order, a family, a genus, and a species. Sometimes additional categories are used, such as subphylum, superorder, superfamily, subfamily, etc.

One important aspect of taxonomy is the description and naming of biological species. Since the time of Linnaeus, species have been named using what is called binomial nomenclature, in which each species has a two-word name that includes a genus name and a species name. Species names are universal, that is, the same names are used by scientists worldwide. In addition, no two species can have the same name. If more than one name has been applied to a given species, the oldest name generally takes precedence. There are a few rules that govern the choice of species names. The entire binomial name must be in Latin or must be Latinized, with the genus name capitalized and the species name in lowercase. The binomial species name is always italicized or underlined in print.

As an example of taxonomic classification, the domesticated dog belongs to the kingdom Animalia (multicellular animals), the phylum Chordata (multicellular animals possessing a nerve cord), the subphylum Vertebrata (having a backbone), the class Mammalia (mammals), the order Carnivora (which includes carnivores such as dogs, cats, weasels, and hyenas), the family Canidae (including dogs, wolves, foxes), the genus *Canis*, and the species *familiaris*. The binomial species name for the domesticated dog is therefore *Canis familiaris*, where *Canis* designates the genus, and *familiaris* designates the species.

In Linnaeus's time, classification was based primarily on similarities between species, particularly anatomical similarities. Modern classification systems remain hierarchical, but use evolutionary relationships, rather than similarity among organisms, as the basis of classification. In order to achieve this, taxonomists try to describe supraspecific **taxa** that are **monophyletic**—that is, they attempt to create supraspecific taxa that include all the species that are descended from a common ancestor. Monophyletic groups are also known as **clades**. Many currently recognized groups are not monophyletic. For example, the group Reptilia, as it is traditionally conceived, is not monophyletic. Traditionally, Reptilia has included only turtles, lizards, snakes, and crocodiles. However, an analysis of the evolutionary relationships among different vertebrate groups reveals that the common ancestor of the traditionally recognized reptiles also gave rise to birds. Therefore, to make the group Reptilia monophyletic, birds should be included as reptiles.

taxa named taxonomic units at any given level

monophyletic a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

clades a branching diagram that shows evolutionary relationships of organisms

The study of evolutionary relationships among organisms, which makes up the field of systematics, is a necessary first step in the creation of a modern taxonomy. As scientists study evolutionary relationships among organisms, they make changes in taxonomy in order to eliminate nonmonophyletic groups. Consequently, taxonomy is constantly changing as new knowledge is gained. SEE ALSO Classification Systems; Carolus Linnaeus; Phylogenetic Relationships of Major Groups.

Jennifer Yeh

Bibliography

Futuyma, Douglas J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, 1998.

Ridley, Mark. *Evolution.* Boston: Blackwell Scientific, 1993.

Territoriality

A pattern of animal behavior, territoriality implies a fixed area (or territory) from which intruders are excluded by the owner through a combination of advertising, threatening, and attacking behaviors. It is important to distinguish between a territory and a **home range**, because the appearance of an

home range the area where an animal lives and eats

These elk rutting bulls fight in a field in Yellowstone National Park.

outsider will elicit different reactions from the animal that lives in, or frequents, the area. Unlike an animal's marked territory, its home range is an area in which the individual roams about but the individual rarely defends it against other animals. There are some species, such as the breeding song sparrow, whose territory and home range are one and the same. In the majority of species, however, the territory tends to be smaller than the home range or the two areas overlap so that only part of the home range is defended as territory.

A question most often asked regarding the defense of a territory is: Why do owners usually win? In weighing the benefits versus the costs of defense, the owner is more likely to escalate the battle than the intruder because the owner has already invested in the area of conflict. The land is worth more to the owner not only because of familiarity with the area but also because the individual may be fighting to maintain exclusive access to the resources found on the territory. These resources may include one or more of the following: food, water, nest sites, and potential/current mates.

There are some costs of defense that the owner must assess as well. There may be time loss from other activities, such as foraging for food or mating. There is also an energy cost in defending an area. The signaling activities can be energetically expensive be they through continual chattering (e.g., squirrels), proclamations through singing (e.g., songbirds), or leaving scent marks at different points in and around the territory (e.g., bears). Further energy is expended in patrolling the perimeters and chasing off any animal that is getting too close to the boundaries or has crossed over into the territory. Finally, there is the risk of injury in battle with any intruder as well as a risk of predation as the owner focuses more on guarding and is therefore less guarded against attack.

There are three categories of territories: breeding, feeding, and all-purpose. The breeding territory is relatively small. It usually contains only a nesting or mating site. This type of territory is most characteristic of colonially nesting species that cluster nests at limited safe sites, such as in lekking or chorusing species where the males aggregate to attract females. The feeding territory tends to be larger than the breeding territory because it must contain sufficient food to support the owner of the territory and any mate or offspring that may also be residing there. Defense of the feeding territory is greatest during the nonbreeding season, because the individual's attention is more focused on the territory. The owner also becomes more vigilant during times when food is scarce. The cost of defense is worthwhile to the owner as it ensures the individual exclusive access of the area's resources. Finally, the all-purpose territory is generally the largest as it includes aspects of both breeding and feeding territories.

For all three of these types of territories, there are usually adjacent territories contiguous with an individual's proscribed area. The owner of a particular territory may have as few as two and as many as six neighbors with whom it shares common boundaries. The network of these contiguous territories is known collectively as a "neighborhood."

Territorial defense is generally employed only against animals of the same species, because animals of a different species will often inhabit a different **niche** within the same territory. In this manner, different species can coexist in the same area and not impinge on each other's food resources. Furthermore, there is no threat of the other animal stealing the owner's mate.

niche how an organism uses the biotic and abiotic resources of its environment

With the hierarchies that are found within communities, the territorial system comes into play as the stronger, more aggressive animal generally wins the better territory and maintains it against others. These systems have effects not only on an individual basis but also at the **population** level as well. If resources were allocated "fairly" to each member of a community or a species, then there actually may not be enough to sustain any one individual. (If resources become scarce because of a fire or drought, the individual may expand its territory in order to find sustenance.) This kind of division of territories, and thereby resources, would lead to population crashes. While it may be difficult to establish one's own territory, that kind of competition is necessary in order for the species to survive. SEE ALSO Foraging Strategies; Home Range.

population a group of individuals of one species that live in the same geographic area

Danielle Schnur

Bibliography

Alcock, John. *Animal Behavior: An Evolutionary Approach*, 4th ed. Sunderland, MA: Sinauer, 1989.

Bradbury, Jack W., and Sandra L. Vehrencamp. *Principles of Animal Communication.* Sunderland, MA: Sinauer, 1998.

Campbell, Neil A. *Biology*, 3rd ed. Berkeley, CA: Benjamin/Cummings, 1993.

Tertiary

The Tertiary era, from 65 to 2 million years ago, consists of six epochs: the Paleocene, Eocene, Oligocene, Miocene, and Pliocene, which represent

chapters in the story of the mammal's rise to dominance of land and oceans. The Tertiary follows the great Cretaceous extinction in which the dinosaurs, who had dominated the terrestrial food chain for hundreds of millions of years, inexplicably vanished, leaving only a few reptiles and mammal-like creatures as survivors.

The ancestors of the mammals, the therapsids, had been evolving into a broad range of ecological niches since the Permian–Triassic periods, some 260 million years ago. During the Mesozoic reign of dinosaurs, these mammals had dwindled almost into nonexistence, a few rat-sized species eking out a **nocturnal** insectivorous living, staying out of the way of predators.

nocturnal active at night

This long period of trying to avoid being eaten may actually have produced the very features that later allowed mammals to spread across the entire planet. Smaller animals had a greater need for maneuverability, selecting for skeletal changes toward speed and flexibility of joints and spine. Smaller mammals need proportionately greater energy to maintain a constant body temperature, thereby selecting for more efficient teeth and jaws as well as digestive systems. And what may have seemed like their greatest drawback, the birth of helpless young who need a period of parental care, actually produced offspring who were uniquely flexible in their behavior patterns and able to be taught by their parents.

In the Tertiary with the dinosaurs gone, mammals along with birds underwent a cycle of massive evolutionary expansion into the greatest range of shapes and sizes to ever populate Earth.

The story of evolution parallels that of geography. During the Permian period (250 million years ago) the supercontinent of Pangaea allowed for migration of plants and animals across the whole of Earth. When Pangaea, driven by the forces of **plate tectonics**, began to break up into separate continents, each chunk of land took with it a random cargo of the original inhabitants. Separation breeds diversity and all of the earliest archetypes (orginal ancestors of a group of animals), grazers, browsers, carnivores, **insectivores**, and canopy dwellers were free to evolve in wildly different ways.

plate tectonics the theory that the Earth's surface is divided into plates that move

insectivores animals who eats insects

In the first epoch of the Tertiary, the Paleocene (65–55 million years ago), mammals still consisted of survivors from the Cretaceous, including the **monotremes**, primitive egg-laying mammals.

monotremes egg-laying mammals such as the platypus and echidna

Condylarths, the ancestors of the **ungulates**, or hoofed animals, were widely present in the Paleocene. This group included carnivores and **scavengers**, as well as more common **herbivores**. Some rodent-like early primates also appeared in the Northern Hemisphere during this epoch.

ungulates animals with hooves

scavengers animals that feed on the remains of animals that it did not kill

herbivores animals who eat plants only

In the Paleocene seas, sharks became the most abundant fishes, while **gastropods** and **bivalves** replaced the once-dominant ammonites.

gastropods mollusks that are commonly known as snails

bivalves mollusks that have two shells

By the Eocene, also known as the "dawn of early life" (55–39 million years ago), Pangaea had begun to break apart. Australia had split off, carrying a load of marsupials, mammals who give birth to immature young who then crawl into a pouch (marsupium) in which they suckle and grow. Freed from competition with placental mammals, the marsupials diversified into every ecological niche across the whole of the Australian continent. Limestones in northern Queensland reveal a tropical rainforest of marsupials for every niche.

Era	Period	Epoch	Million Years Before Present
Cenozoic	Quaternary	Holocene	0.01
		Pleistocene	1.6
	Tertiary	Pliocene	5.3
		Miocene	24
		Oligocene	37
		Eocene	58
		Paleocene	66

The Tertiary period and surrounding time periods.

Eocene seas chronicle the momentous return of the first mammals to the oceans they had emerged from several hundred million years earlier. The legs of the first whales began to change to flippers and increase in size, thanks to the new weightless environment.

In the Oligocene (39–22 million years ago), the Antarctic ice cap was beginning to form, provoking a marked cooling effect and a pattern of seasonal fluctuations. These changes apparently favored **homeothermic**, or warm-blooded animals, because the turtles, lizards, and crocodiles of the time did not undergo the explosion of evolution (cycles of immense activity and then decline in evolution) that the mammals underwent.

homeothermic describes animals able to maintain their body temperatures

By the Miocene (22–5 million years ago), a dryer, warmer **climate** again produced changes in vegetation which rippled through the world of herbivores and predators. Teeth patterns of Miocene fossils suggest that the vast **deciduous** forests and their leaf-browsing inhabitants were being replaced by vast grasslands and grazing animals. These early **ruminants** (cud-chewing animals) included several types of deer and the first horses. Predation tends to shape evolution, and the new open plains encouraged longer, swifter legs in horses or burrowing capabilities in smaller animals closer to the ground. Condylarths and creodonts, the flesh-eating ungulates, had begun to decline, replaced by other orders of carnivores that were faster, and had sharper teeth and claws.

climate long-term weather patterns for a particular region

deciduous having leaves that fall off at the end of the growing season

ruminants plant eating animals with a multi-compartment stomach such as cows and sheep

By the Pliocene, (5–2 million years ago) the continents had shifted into more or less their present-day locations. The **isthmus** of Panama had arisen to reconnect North and South America, allowing animals that had developed independently for millions of years to mingle. The two-way traffic across the isthmus sent the ponderous sloths and glyptodonts (giant armadillos) north. Highly evolved predators (such as sabre-toothed cats) traveled south, leaving numerous extinctions of South American marsupials in their wake. The isthmus also separated the ocean into two, Atlantic and Pacific, causing **differentiations** in marine species. SEE ALSO Geologic Time Scale.

isthmus a narrow strip of land

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

Nancy Weaver

Bibliography

Asimov, Isaac. *Life and Time.* Garden City, NY: Doubleday & Company, 1978.

Fortey, Richard. *Fossils: The Key to the Past.* Cambridge, MA: Harvard University Press, 1991.

———. *Life: A Natural History of the First Four Billion Years of Life on Earth.* New York: Viking Press, 1998.

Friday, Adrian, and David S. Ingram, eds. *The Cambridge Encyclopedia of Life Sciences.* London: Cambridge University, 1985.

Gould, Stephen Jay, ed. *The Book of Life.* New York: W. W. Norton & Company, 1993.

Lambert, David. *The Field Guide to Prehistoric Life.* New York: Facts on File, 1985.

McLoughlan, John C. *Synapsida: A New Look Into the Origin of Mammals.* New York: Viking Press, 1980.

Steele, Rodney, and Anthony Harvey, eds. *The Encyclopedia of Prehistoric Life.* New York: McGraw Hill, 1979.

Wade, Nicholas, ed. *The Science Times Book of Fossils and Evolution.* New York: The Lyons Press, 1998.

Tetrapods—From Water to Land

vertebrates animals with a backbone

fossil record a collection of all known fossils

Tetrapods—including the modern forms of amphibians, reptiles, birds, and mammals—are loosely defined as **vertebrates** with four feet, or limbs. Many species we see today, like the snakes or whales, may not appear to be tetrapods, but their lack of well-developed limbs is a secondary adaptation to their habitat. This means that they originally had four limbs, but lost them as they adapted to a certain style of living. In the **fossil record** scientists often see intermediate forms which has reduced limbs. In modern skeletons of these animals you can often see vestiges of appendages that indicate that they are, indeed, tetrapods.

Life on Land

buoyancy the tendency of a body to float when submerged in a liquid

fertilization the fusion of male and female gametes

The appearance of tetrapods on land signaled one of the most hazardous and important evolutionary events in the history of animals. Life began in water. The body systems of early organisms were adapted to a mode of life in which water provided **buoyancy** against gravity. Desiccation, or drying out, was not a problem for animals whose bodies were constantly bathed in fluid. Movement from place to place usually required little energy and often involved simply floating along with the current. Reproduction was easier when sperm and eggs could be released into the water for **fertilization**. So the transition from living in the ocean to living on land required that ancestral vertebrates (who gave rise to the tetrapods) have physical traits that would helped them make this shift.

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

Tetrapods were not the first animals to make the move to land. Around 400 million years ago, primitive **arthropods** quickly followed the invasion of the first land plants, such as the mosses and liverworts, the first organisms to establish a foothold in the drier, but still moist, habitats, such as shorelines streams, and marshes. Both plants and insects continued to evolve and invade increasingly arid and varied habitats. They provided an important and diverse potential food base for the future land vertebrates.

Fins and Legs

aquatic living in water

Paleontologists believe that only 50 million years after the first plants left their **aquatic** environments, two conditions existed that paved the way for the first tetrapods. First, competition for food in the oceans was extremely fierce. Second, a group of bony fishes called the lobe-finned (or sarcopterygian) fishes had developed the physical characteristics necessary for the transition from water to land.

In particular, one group of lobed-fin fishes, the Rhipidistians, had a general **body plan** that was very similar to and can be traced back to early amphibians. Rhipidistians had pairs of front and back fins with sturdy bones, instead of **cartilaginous** rods, for resting their bulky bodies on the sea floor. These special fins were strengthened by a particular arrangement of the bones that resembled the structure of tetrapods in many ways. Large single, heavy bones in the fins were located nearest to the body and attached to a central girdle, like the pelvis.

body plan the overall organization of an animals body

cartilaginous made of cartilage

When the land animals began to use the fins for standing and walking, the girdle bones had to become stronger to support the body on the legs. These bones eventually became the femur (upper leg bone) and humerus (upper arm bone) of the tetrapods. Pairs of bones (the radius and ulna of the arm, and the tibia and fibula of the leg) were attached to the femur and humerus, followed by a series of smaller bones that correlate to the fingers of tetrapods.

However, the Rhipidistian fishes had many more fingers and finger bones. The loss and reduction of the numbers of bones of these animals is one of the way scientists can trace the more modern animals from the older ones. Modern living members of this group of extraordinary fishes include the coelacanths (considered to be living fossils) and the lungfishes. Lungfishes do not have gills, but have primitive **lungs** that enable them to remain out of water for extended periods of time. The mouth and skull structures of lungfishes are very similar to those of ancestral amphibians.

lungs sac-like, spongy organs where gas exchange takes place

Tetrapods in the Fossil Record

The fossil record of tetrapods is not complete. There are many gaps that prevent scientists from clearly understanding the relationship between ancestral amphibians and modern ones. In addition, the transitional form of animals representing the shift from amphibian to reptiles is still poorly understood. However, places like China, Europe, Mongolia, North America, and South America constantly provide new fossil information about the history of tetrapods, and tetrapod fossils have even been discovered in Greenland and Antarctica.

What is well-known about the history of tetrapods starts about 400 million years ago when the first terrestrial (no longer dependent on water for a complete life cycle) vertebrates appeared. By the beginning of the Triassic period many unusual amphibians ruled the land. A group of large and slow-moving creatures, the labyrinthodonts, and the smaller newtlike and salamander-like lepospondyls, dominated the swamps and humid environments of Earth.

Labyrinthodonts were named because the structure of their teeth whose outer and inner surfaces reminded researchers of a labyrinth, or maze. The teeth of lepospondyls were very simple and cone-shaped as compared to the labrinthodonts. The labyrinthodonts were some of the largest amphibians to have ever lived. Some genera, like the *Euryops*, were about 2 meters (six feet) long.

Euryops is considered one of many possible ancestors of modern amphibians The great diversity of these types of tetrapods has been vastly reduced. Only the salamanders and frogs are still living, but are found over most of the world. Amphibians still have the primitive fishlike trait of laying eggs in water and have never lost their dependency on water-rich environments. As their skin does not retain moisture, they must live near a wet habitat to keep from drying out. They are good examples of the tetrapods' link to watery beginnings.

On the Land and in the Sea

amniotic describes a vertebrate that has a fluid-filled sac that surrounds the embryo

The development of the **amniotic** egg and the growth of scales that prevented water loss allowed tetrapods to move into newer, more arid environments. An evolutionary explosion then occurred that produced the early ancestors of the turtles, crocodiles, lizards, snakes, dinosaurs, and even mammals. Many other tetrapods, like the pterosaurs, also emerged. In the marine environment, several tetrapods returned to the sea. Fierce marine reptiles like the mosasaurs and plesiosaurs found an abundant food source in the huge stocks of fishes in the oceans. These animals, although aquatic, were structurally tetrapods. They retained the tetrapod body plan of a thick, upper-arm bone connected to a girdle (hip and chest bones), two smaller bones, and a series of small bones for fingers. However, instead of appearing like an arm or a leg the bones were covered by tissue that formed a flipper.

Around 65 million years ago at the close of the Cretaceous period, a massive extinction killed many life forms including the large tetrapods (dinosaurs) and other animal and plant species. However, many life forms did not die out. Mammals, reptiles, and birds survived, and eventually became the most abundant tetrapods on Earth.

Modern Tetrapods

The most familiar modern group of tetrapods is the mammals, which includes humans. These furred animals began their evolutionary history back with the beginnings of the dinosaurs. Early mammals were small, about the size of a rat. After the large Cretaceous extinction, mammals survived to become some of the largest tetrapods on Earth, including elephants and whales. Just as the marine reptiles had done, whales returned to the sea, developing fins as a secondary adaptation.

habitat loss the destruction of habitats through natural or artificial means

Tetrapods today can be found in nearly every environment. Unfortunately, as the world continues to change, the numbers of many types of tetrapods are declining. With increasing **habitat loss** and pollution many tetrapods are in danger of extinction. The loss of so many species of birds, reptiles, and mammals, such as the panda, is a serious threat to the continued survival of the tetrapods. SEE ALSO Living Fossils; Phylogenetic Relationships of Major Groups.

Brook Ellen Hall

Bibliography

Carroll, R. "Vertebrate Paleontology and Evolution." New York: W. H. Freeman and Company, 1988.

Lillegraven, J. A., Z. Kielan-Jaworowska, and W. Clemens. "Mesozoic Mammals; The First Two-Thirds of Mammal History." Berkeley: University of California Press, 1979.

Macdonald, D. "The Encyclopedia of Mammals," New York: Facts on File Publications, 1987.

Threatened Species

Biodiversity—the vast numbers of species of plants and animals interacting on Earth—provides people with food, building materials, fibers, and medicines. Insects pollinate crops, wild plant **genes** reinvigorate domestic ones, forests provide breathable air, microorganisms create soil, and **aquatic** microorganisms cleanse and purify water. Without the millions of known and unknown species operating interdependently, life on Earth would be impossible for human beings. Yet life-forms are dying off at an unprecedented rate. Biologists estimate that there were 1 million fewer species in 2000 than in 1900.

genes segments of DNA located on chromosomes that direct protein production

aquatic living in water

The U.S. Endangered Species Act of 1973 defines an endangered species as one that is on the brink of extinction. A threatened species is defined as one with a good chance of becoming endangered in the foreseeable future. What pushes a healthy animal species into the threatened category? Almost all of the answers involve human beings. Either through misuse, thoughtlessness, or overconsumption of Earth's resources, humans are the source of the current mass extinction.

population a group of individuals of one species that live in the same geographic area

acid rain rain that is more acidic than non-polluted rain

pesticides substances that control the spread of harmful or destructive organisms

As human **populations** soar, more and more of the world's natural habitats are being destroyed. Forests are cleared for logging, shopping centers, and housing developments. Wetlands are drained for farms and factories. Valleys and rivers are flooded for hydroelectric power and recreation. Oil spills at sea threaten marine life. **Acid rain** from factories and automobile exhaust, **pesticides** scattered indiscriminately and chemical pollution of air and water further stress animal species. Legally protected animals are poached in wildlife preserves for their body parts, and ranchers and hunters exterminate grizzlies, wolves, large cats, and prairie dogs alike for trophies or because they consider them to be a nuisance.

One of the species headed for endangered status is the Pribilof seal. About 30,000 a year die entangled in plastic fishing lines and six-pack aluminum can holders. Most species require a critical number of members in order to successfully breed. The Key deer and Florida panther are diminishing below the breeding population (the number of individuals necessary for the species to breed successfully) because of deaths by automobile. Manatees are equally threatened due to collisions with motorboats.

The California Condor is a welcome instance of an animal almost ready to move from the federally protected Endangered Species list (placed there in 1967). Due to human intervention, the condor has successfully bred in captivity. Most importantly, birds re-introduced into the wild have been surviving.

Among the other threatened species are the whales, who are killed for their body parts. Mountain gorillas and pandas are threatened by shrinking habitat and food sources as human populations press in on their range. Asian tigers, South American jaguars, and snow leopards are disappearing as their pelts are sold as souvenirs. Sea turtles are hunted for their shells, reptiles for their skins, and rare birds are trapped to be sold as pets.

The numbers of unidentified species vanishing forever from the tropical rain forests, home to the greatest amount of life on Earth, has become a cause of great concern to environmentalists. The most disturbing phenomenon connected to the disappearing rain forests is that they are being destroyed to make room for ranches built to breed cattle that will eventually provide inexpensive meat products for developed nations.

Like the dinosaurs 65 million years ago, humanity finds itself at the top of a food chain that is in the midst of a mass extinction. A mass extinction is a traumatic event. As the food chain falls apart, the survivors scramble to reassemble a workable **ecosystem**. For example, should the food of any common prey, such as rabbits or mice, become scarce, the numbers of those species will drop. This will set off a chain reaction that affects all the ground and air predators that feed on them, such as, coyotes, badgers, hawks and owls. The largest, most resourceful consumptive species do not survive. Ultimately, if humans continue to abuse the intricate ecological mechanisms that keep the world running smoothly, humans themselves may prove to be the most threatened species of all. SEE ALSO Endangered Species; Extinction; Habitat Loss; Habitat Restoration.

ecosystem a self-sustaining collection of organisms and their environment

Nancy Weaver

Bibliography

Bailey, Jill, and Tony Seddon. *The Living World.* Garden City, NY: Doubleday, 1986.

Lampton, Christopher. *Endangered Species.* New York: Franklin Watts, 1988.

Tool Use

Until quite recently, tool use was considered to be a uniquely human behavior. Early anthropologists taught that the use of tools was limited to *Homo sapiens* and used the presence of tools as an indicator of the presence of humans. Even after tool use by earlier Homo species was demonstrated, anthropologists still insisted that tool use made the species human.

More recently, scientists have observed many different animals using tools. Sea otters use rocks as anvils to break open shellfish. Galapagos finches mold twigs to probe holes in trees to obtain insect larvae. Egyptian vultures use rocks to crack open ostrich eggs. The burrowing wasp, *Ammophila*, uses a small pebble to hammer down the soil over its nest of eggs. And green herons use bait to attract small fish.

Since nonhuman animals were clearly observed to be using tools, anthropologists reconsidered their earlier position and decided that the *making* of tools was the uniquely human characteristic. However, in 1960 Jane Goodall and others observed chimpanzees in the wild breaking off twigs from trees, stripping away the leaves, and using the twigs to extract termites from their nests. Since the twig had to be modified by removing its leaves, this activity clearly demonstrated toolmaking. Captive Asian elephants have often been observed to use branches to swat flies. The branches are modified by shortening and removing side branches. Recently, wild Asian elephants have been seen demonstrating the same tool-using and toolmaking behavior.

The environment must possess two characteristics in order for tool use to evolve among a **population** of animals. First, there must be some evolutionary advantage in tool use. For example, the animal must be more successful at finding food, avoiding predators, or reproducing. Second, objects in the environment that will make useful tools must be available. Chimpanzees use twigs, wasps use small stones, and finches use cactus spines.

population a group of individuals of one species that live in the same geographic area

Without access to these objects, the tool-using behavior would never evolve. The following examples illustrate how Egyptian vultures, woodpecker finches, green herons, and chimpanzees gained an evolutionary advantage from tool use.

Egyptian Vultures

An Egyptian vulture, *Neophron percnopterus*, has been observed breaking open ostrich eggs, too hard to open by pecking, by throwing a stone held in its beak at the egg shell. The bird's aim is quite good. According to reports by Jane Goodall, the vultures will wander as far as 50 meters (165 feet) from the egg to find a suitable rock.

The rock most often chosen is an egg shaped. This suggests that the vultures have modified an earlier behavior. Many birds throw or drop eggs to break them. John Alcock has suggested that the vultures originally threw or dropped eggs to break them open. The use of rocks to break the eggs open probably began when a vulture accidentally hit an egg with a rock. They then evolved from throwing the eggs to throwing rocks at the eggs. The movement the vulture makes when breaking an egg with a stone is almost the same as the movement the vulture makes when pecking at an egg to break it.

Observations by Chris Thouless and his co-workers of young, hand-reared vultures demonstrated that the stone-throwing behavior is innate or instinctive, not learned. Young vultures exhibit the behavior once it is linked to a food reward. In the wild, encountering a broken ostrich egg probably rewards young vultures. Thouless also observed that all vultures preferred to throw rounded-off, egg-like stones.

Woodpecker Finches

Charles Darwin observed many species of finches inhabiting the Galapagos Islands and theorized that all of them evolved from a single-species population that had somehow made it to the island. The woodpecker finch, *Geospiza pallida*, that resides there is one of Darwin's finches. It is called the woodpecker finch because it has evolved the ability to pry insect larvae out of holes in a tree by using a cactus spine or other long, thin tool.

This woodpecker finch uses a twig to reach an insect.

A woodpecker's long, barbed tongue enables it to extract grubs from branches without the assistance of a tool. The woodpecker finch has a short tongue, however, so it has developed the ability to grasp a cactus spine in its beak and pry grubs out of the hole. After extricating the grub, the finch holds the spine under its foot while eating the grub. The cactus spine is carried from branch to branch and used again and again.

Researchers have discovered that woodpecker finches are more likely to adopt tool-using behaviors as hunger increases. In an experiment a different finch, the cactus ground finch, was placed in a cage near a group of tool-using woodpecker finches. The large cactus ground finch does not normally use tools to probe for grubs in its natural environment but it apparently acquired the habit after observing the woodpecker finches at work. Other species of finches did not learn to use tools after observing woodpecker finches.

One researcher happened to observe a young woodpecker finch apparently perfecting the skill of using the cactus spine by observing another finch.

This young finch first tried to get grubs from a tree branch using its beak. Since this did not work, the young finch tried using a twig. Then it apparently observed another finch modifying a twig for use and copied the behavior. Scientists have also observed woodpecker finches modifying long cactus spines to form more manageable tools. This is a clear example of toolmaking.

Green Heron

innate behavior behavior that develops without influence from the environment

A few green herons have been observed dropping small objects onto the surface of the water. When small fish swim to the surface to investigate the object, the heron grabs the fish. This is apparently not **innate behavior** because only a few individual birds practice it. Attempts to teach herons to use bait have also been unsuccessful, so why a few do it is not clear.

It may be behavior learned through experience. Perhaps a bird accidentally drops a small object in the water and sees that small fish are attracted. If the heron is able to make the connection between dropping the bait and catching a fish, this indicates a level of cognitive ability beyond what is considered normal for these birds. Perhaps only exceptionally intelligent birds are able to learn the behavior.

Chimpanzees

Chimpanzees have given us the first and clearest example of tool use and toolmaking in a nonhuman species. In Tanzania, chimps regularly construct tools from grass and twigs that they use to extract termites from termite holes. The chimp carefully selects an appropriate stem or twig, modifies it as necessary, and then uses its strong fingernail to dig a hole in the termite mound. As termites rush to repair the damage, the chimp carefully inserts the twig into the hole and just as carefully withdraws the twig. Invariably, several termites are clinging to the twig, which the chimp eats.

These insects are a good source of protein and fat, so they are a valuable addition to the chimp's diet. Wild chimpanzees have also been seen using sticks to get honey from beehives and dig up edible roots. They also use sticks to pry up the lids of boxes of bananas left by scientists.

learned behavior behavior that develops with influence from the environment

Twig using is at least partially **learned behavior**. After extensive observations, Jane Goodall concluded that young chimps learn how to break twigs from trees, strip away the leaves, and insert them into termite holes by imitating adults. This is a complex and involved behavior. Without the adults to demonstrate, young chimps would probably never become skillful. However, the behavior is also at least partly innate. All young chimps play with sticks and twigs and entertain themselves by poking the sticks into holes.

If neither tool use nor toolmaking distinguish humans from other animals, is there any aspect of tool use that is still uniquely human? The answer is, possibly, no. It is conceivable that intelligence and tool use lie along a spectrum and humans just have more of the characteristic. The difference may be quantitative instead of qualitative. But, it is also possible that the regular, extensive use of tools to solve everyday problems is a distinctly human characteristic. The regular and consistent use of tools frees humans from limits imposed by our anatomy. It is even possible that regular tool use has somehow encouraged the development of problem-solving skills. SEE ALSO LEARNING.

Elliot Richmond

Bibliography

Alcock, John. *Animal Behavior: An Evolutionary Approach*, 6th ed. Sunderland, MA: Sinauer Associates, 1998.

Beck, Benjamin B. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals.* New York: Garland, 1980.

Ciochon, Russell L., and John. G. Fleagle. *Primate Evolution and Human Origins.* Menlo Park, CA: Benjamin/Cummings, 1985.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Greenhood William, and Robert L. Norton. "Novel Feeding Technique of the Woodpecker Finch." *Journal of Field Ornithology* 70 (1999).

Goodall, Jane. (1986). *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge, MA: Belknap Press, 1986.

Goodall, Jane, and Hugo van Lawick. "Use of Tools by Egyptian Vultures, *Neophron percnopterus.*" *Nature* (1966):468.

Lack, David. "Darwin's Finches." *Scientific American* (April 1953):68.

Roberts, William A. *Principles of Animal Cognition.* New York: McGraw-Hill, 1997.

Schultz, Adolph H. *The Life of Primates.* New York: Universe Books, 1972.

Thouless, C R., J. H. Fanshawe, and B. C. R. Bertram. "Egyptian Vultures *Neophron-percnopterus* and *Ostrich Struthio-camelus* Eggs: The Origins Of Stone-Throwing Behavior." *Ibis* 131 (1989).

Transport

Transport is the controlled movement of substances from one part of a cell to another, or from one side of a cell membrane to the other. Because each cell must maintain an internal environment different from the external environment, it must regulate the movement of ions, proteins, toxins, and other molecules both across the cell membrane and within its **cytoplasm**. This control over its molecular environment may be accomplished through a variety of measures, one of which is the establishment of a barrier membrane between the cell and the external world.

cytoplasm fluid in eukaryotes that surround the nucleus and organelles

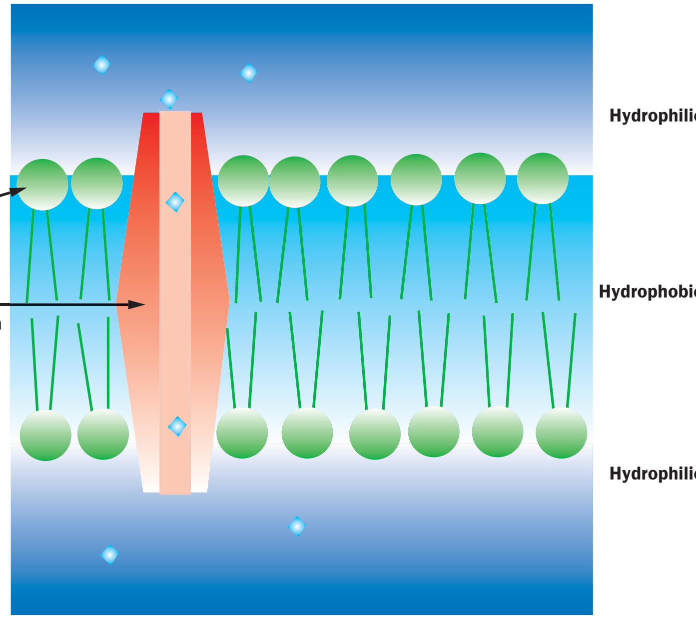
One such barrier, the **bilipid membrane** of a cell, is composed of two hydrophilic, or water-soluble, sheets of molecules separated by an intervening hydrophobic, also called oily or fatty, region. This property results from the structure of the **phospholipid** molecule composing the membrane: a polar, hydrophilic head region, and a nonpolar, hydrophobic tail region. The two layers of membrane are oriented so that the hydrophilic heads face the internal and external cell, and the fatty tails are positioned between the two head layers.

bilipid membrane a cell membrane that is made up of two layers of lipid or fat molecules

phospholipid molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water

The structure of this membrane assures that any polar, water-soluble, molecules in the hydrophilic extracellular space will be unable to pass through the nonpolar, fatty, region within the membrane. If this barrier were completely impermeable, however, the cell would never be able to absorb nutrients or rid itself of wastes, let alone communicate with other cells. Thus the membrane is compromised by proteins that extend through both

The functions of a bilipid membrane.



The cell membrane separates the outside of the cell from the inside with an oily hydrophobic region formed by the tail ends of two phospholipid sheets. Thus water-soluble molecules cannot pass through the oily part of the membrane, but must go through the pore of a membrane-spanning protein.

sides of the bilipid membrane. These proteins provide a watery pore region that connects the extracellular with the intracellular space, thereby allowing hydrophilic molecules to pass through.

There is a wide variety of membrane proteins, some of which are located within the outer cellular membrane, and some of which are imbedded in intracellular **organelles**. In addition to transport across membranes, substances must be transferred from one part of the cell to another, especially in very large cells and in single-celled organisms.

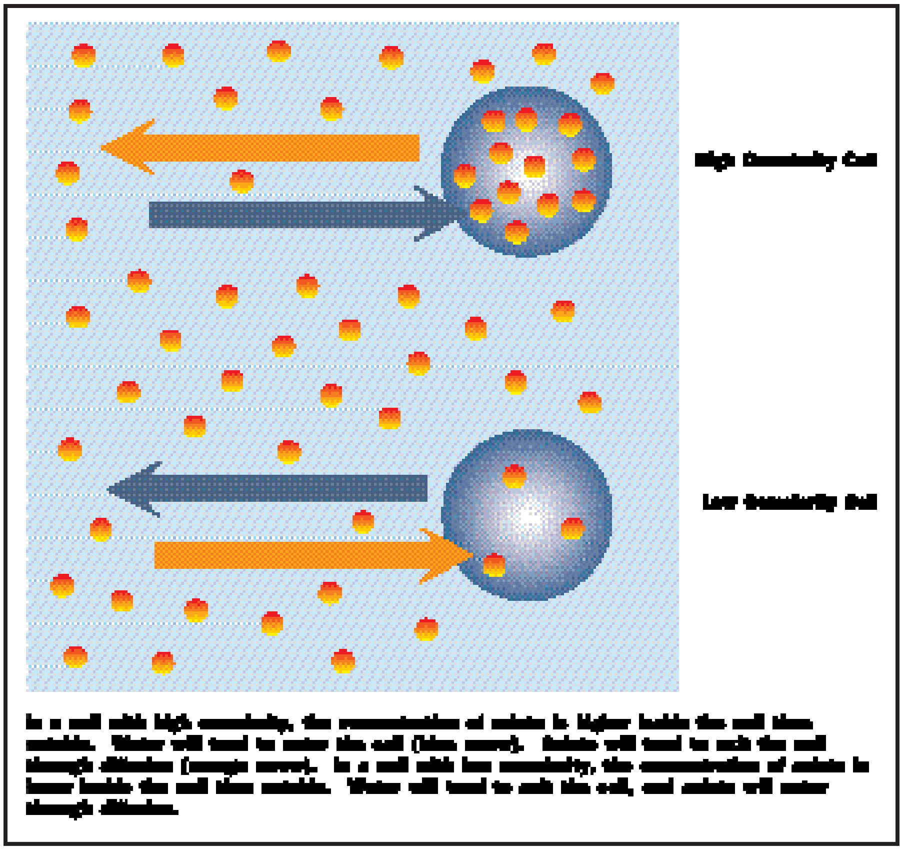
organelles membrane-bound structures found within a cell

Osmosis

The simplest kind of cellular transport is **osmosis**. Osmosis is the passage of water molecules through a semipermeable membrane from a wet environment (a region of high water concentration), to a dry environment (a region of low water concentration). The defining characteristic of a wet environment is a low concentration of dissolved solute in the water. A dry environment has a high concentration of solute. Cells store a high concentration of proteins and other molecules within the membrane. If a cell were removed from biological conditions and placed in distilled water (water containing no dissolved substances), the small water molecules would rush through the bilipid membrane into the relatively dry interior of the cell. The membrane would expand with the increased water intake until the cell exploded.

osmosis the diffusion of water across a membrane

This scenario does not normally occur in nature for two reasons. First, organisms balance their internal osmolarity. Internal osmolarity is the ratio of dissolved substance concentration between the inside and the outside of the cell. This balance is accomplished by maintaining a concentration of



The osmosis process is the simplest kind of cellular transport.

many small ions and molecules in the extracellular space, the areas between cells within an organism. Second, cells store many of their proteins within vesicles, within membranes, and inside organelles; this decreases the apparent concentration of free-floating soluble molecules.

Diffusion

The opposite of osmosis is diffusion, which means the passage of molecules from a region in which they are highly to a region in which they have a low concentration. This only occurs when the molecule has a concentration gradient, meaning that it exists in larger numbers per unit area in one location and in smaller numbers per unit area in an adjacent location. If a high concentration gradient is established, it means that the difference in concentration between two adjacent locations is great. In the case of a cellular membrane, this means that a certain substance is at very high concentrations on one side of the membrane and very low concentrations on the other side. The larger the concentration gradient, the stronger the driving force that powers the diffusion of molecules down the gradient. Whereas osmosis explains the movement of water molecules, diffusion explains the movement of other molecules within a liquid.

Passive Transport

For passive transport, no additional energy is needed to transfer molecules across the membrane. Instead, the concentration gradient of that molecule provides a driving force from high to low concentration, pushing the

facilitated diffusion the spontaneous passing of molecules attached to a carrier protein across a membrane

molecule across the membrane. This process is also known as **facilitated diffusion** because the membrane protein facilitates the natural diffusion tendency of the molecule by providing safe passage across the hydrophobic region of the lipid bilayer. Many sugars and amino acids are transported from the gut into the cells lining the gut through this mechanism.

When the protein forming the pore is constantly open to diffusable molecules, it is called a channel. The size of the pore, and any hydrophilic regions within the pore, can selectively allow certain molecules to pass while barring others. A uniport protein must first bind a molecule and then undergo a conformational change (a change in the shape of the protein) before it releases the molecule on the opposite side of the membrane.

smooth muscle the muscles of internal organs that are not under conscious control

One example of a passive transport mechanism is the gap junction. This is a molecular conduit between two cells formed by a hexagonal array of rigid proteins that leaves a permanent pore open between two cells' cytoplasms. This opening allows inorganic ions and very small hydrophilic molecules to pass directly between cells. Gap junctions are particularly useful in heart muscle cells because they allow ions carrying electrical charge to flow directly from cell to cell, thereby inducing the **smooth muscle** fibers to contract in a coordinated motion. This simple method of communication makes it unnecessary for neuronal connections at each and every heart muscle cell to induce contraction at exactly the right time for a smooth muscle heartbeat. If gap junctions were blocked, heart muscle cells would contract at the incorrect time, or not at all, resulting in irregular or weak heartbeats, or even heart seizure, and death.

Active Transport

active transport process requiring energy where materials are moved from an area of lower to an area of higher concentration

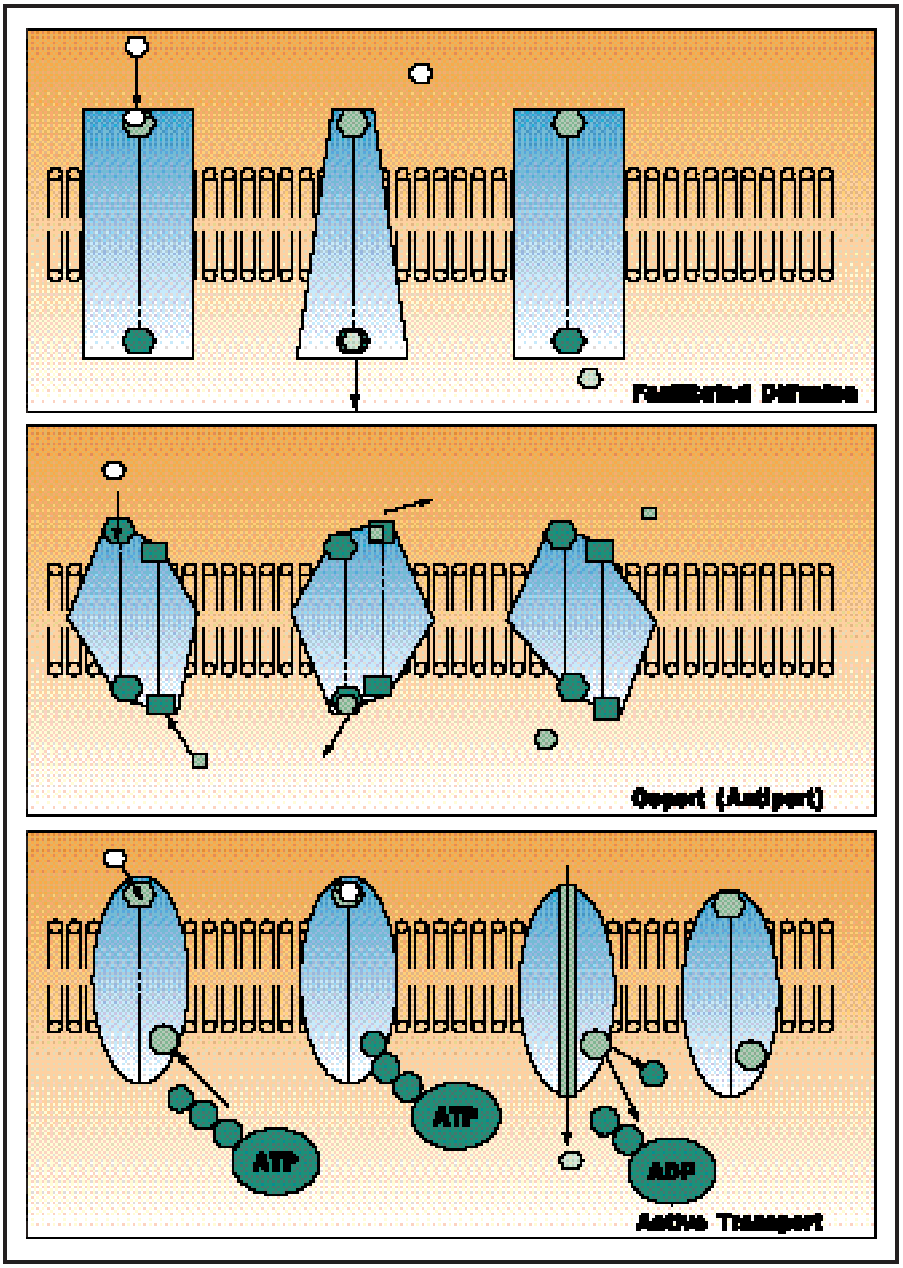
adenosine triphoshate an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

Active transport requires that energy be expended to bring a molecule across the membrane. Most often **active transport** is used when the molecule is to be transferred against its concentration gradient. However, occasionally the target molecule is carried along its concentration gradient, when the gradient is not strong enough to ensure a sufficiently quick flow of molecules across the membrane. For uncoupled active transport, ATP (**adenosine triphosphate**) in the cell's cytoplasm binds to the carrier protein at the same time as the targeted molecule binds. ATP is a cellular molecule that contains a great deal of energy in its molecular bonds. The carrier protein breaks a phosphate off the ATP and uses the energy released from the broken bond to undergo a conformational change that carries the targeted molecule to the other side of the membrane.

neuron a nerve cell

One example of active transport is the sodium/potassium ATPase pump, by which sodium is transferred out of a **neuron** while potassium is transferred into a neuron, both counter to their individual concentration gradients. This is essential for maintaining electrically active nerve cells because it helps to establish a concentration gradient and electrical gradient across the cell membrane. When the cell is active, sodium and potassium are allowed to flow down their electrochemical gradients, whereas during periods of inactivity the sodium/potassium pump restores the resting state polarization of the cell.

There are two kinds of coupled active transport. Symport uses the concentration gradient of one molecule to help transport another molecule. Symport membrane proteins have two binding sites on the same side of the



The diffusion process describes the passage of molecules from a region where they are in high concentration to one in which they have a low concentration.

membrane. The targeted molecule binds at one site, and a coactivating molecule with a high concentration gradient favoring movement across the membrane binds at the other site. The driving force of the coactivating molecule causes a conformational change in the membrane protein, which transports both molecules across the membrane in the same direction. The other type of coupled transport is antiport, by which the coactivating molecule and the targeted molecule bind at sites on different sides of the membrane bilayer. The concentration gradient of the coactivating molecule still provides the energy for the conformational change, but in this case, the molecules are transported simultaneously in opposing directions across the membrane. Symport and antiport systems are also called carrier-assisted transport, because energy from the coactivator helps to carry the target molecule in an energetically unfavorable direction.

The most common method for cells to transfer very large molecules across the membrane is through the intermediary of a vesicle. Vesicles are small spheres of membrane that contain large molecules, toxins, nutrients, or signaling molecules. Proteins that are created in the endoplasmic reticulum can be packaged in vesicles in the golgi apparatus. Similarly, vesicles may contain transporter proteins similar to those located in the external cellular membrane, so that they can bring in certain cytoplasmic proteins. Vesicles called lysosomes process and sequester harmful metabolic side-products so that they do not do damage to organelles in the cytoplasm.

In each of these cases, vesicles are transported to the outer cell membrane, a process known as exocytosis. The vesicles travel along a system of structural proteins called microtubules with the help of an associated motor protein called kinesin. Kinesin molecules "grab" vesicles with their globular head region and then take turns binding to the microtubules, so that the net result is that of a cartwheeling vesicle moving in one direction. Some proteins can be transported by binding directly to microtubules and slowly "riding" them as they slide toward the membrane. When it arrives, the vesicle lipid bilayer fuses with that of the outer cell membrane, so that the internal contents of the vesicle are released into the extracellular space. In endocytosis, the mechanism is reversed. Pockets of cell membrane that have bound a particular molecule dimple inwards toward the cell cytoplasm forming a deep pit, and then pinch off so that a vesicle forms on the intracellular side. Phagocytosis refers to the consumption of small cells or cell-pieces by larger cells by surrounding and engulfing them.

Rebecca M. Steinberg

Bibliography

Agutter, Paul S. *Between Nucleus and Cytoplasm.* London and New York: Chapman and Hall, 1991.

Weiss, Thomas Fischer. *Cellular Biophysics.* vol. 1: Transport. Cambridge, MA: MIT Press, 1996.

Wilson, G. *Exploitation of Membrane Receptors and Intracellular Transport Pathways.* New York: Elsevier Science Publishers, 1989.

Trematoda

acoelomate an animal without a body cavity

bilaterally symmetrical an animal that can be separated into two identical mirror image halves

dorsoventrally flattened from the top and bottom

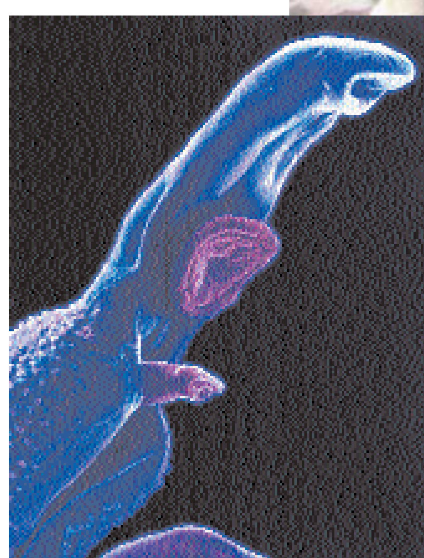
vertebrates animals with a backbone

ventral the belly surface of an animal with bilateral symmetry

Trematodes and flukes are the common names for the flatworms in the class Trematoda, phylum Platyhelminthes. Trematodes have most of the same features as other classes of Platyhelminthes. They are **acoelomate**, unsegmented, **bilaterally symmetrical** triploblasts that are flattened **dorsoventrally**. Trematodes do not have a respiratory system, but do have a mouth and primitive digestive and excretory functions, although these are not developed into full organ system as in higher **vertebrates** like mammals. They have a primitive nervous system with a ganglion, or brainlike structure, in the head region.

All trematodes are parasitic, and most are endoparasitic, living inside other animals. Trematodes infest various organs in a wide variety of animals. Adult trematodes have two specialized suckers. One is an oral sucker that surrounds the mouth. The other is a **ventral** sucker in the middle of the body that helps trematodes hang on to their host. Trematodes have simple sensory organs around the mouth, but do not have some of the more complex sensory organs found in other flatworms, such as the eye spots of turbellarians. The mouth of trematodes is a muscular pharynx, and the larvae and adult stages can suck their food from their host by grabbing on with their powerful mouths. Trematodes expel undigested material through their mouth because they do not have an anus. Nitrogenous waste excretion and other **osmoregulatory functions** are preformed by the protonephridium, which consists of flame cells and tubule networks, all of which act as a primitive kidney.

Most trematodes reproduce sexually. Most species are **hermaphroditic**, but a few have separate sexes. Trematodes have complex life cycles that include eggs, free-swimming ciliated larvae, and adults. Different life stages pass through one or more hosts.



A Bilharzia blood fluke during schistosomiasis.

The two major subclasses of Trematoda are best distinguished by the differences in their life cycles. Trematodes in the subclass Aspidobothria have only a single host in their life cycle. Trematodes in the subclass Digenea have a complex life cycle. These flatworms always pass through a mollusk in the first stage of their life cycle, have at least one additional host (but may have more), and complete their life cycle in the body of a vertebrate. Most trematodes are in Digenea, more than nine thousand known species.

Trematodes are some of the most harmful parasites of humans. Blood flukes (*Shistosoma*) infect more than two million people worldwide with a disease called as schistosomiasis. People become infected by working, bathing, or swimming in water containing **mollusks** such as snails that carry the flatworms. At the beginning of the trematodes' life cycle, fertilized flatworm eggs are passed with human feces into the water, where they infect the mollusk. Once the eggs find a mollusk host the eggs grow into larvae that infect humans when released from the mollusk. The larvae penetrate the skin of humans and migrate through the bloodstream to the liver where they mature into adult flatworms. The adult flatworms can migrate to other organs, and the accumulation of eggs in various organs causes symptoms including acute pain and diarrhea. The adult shistosomes ingest the red blood cells of their host, causing **anemia**. Schistosome larvae that infect birds can also cause problems for humans. Larvae free-floating in water are killed by an immune response when they enter human skin, but the decomposing larvae cause an infection that leads to the bumpy, itchy skin known as "swimmer's itch." Other trematodes can be a problem for humans because they infest domesticated vertebrates such as sheep and cows. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

osmoregulatory functions controlling the water balance within an animal

hermaphroditic having both male and female sex organs

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

anemia a condition that results from a decreased number of red blood cells

Laura A. Higgins

Bibliography

Anderson, D. T. ed. *Invertebrate Zoology.* Oxford: Oxford University Press, 1998.

Barnes, Robert D. *Invertebrate Zoology*, 5th ed. New York: Saunders College Publishing, 1987.

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Purves, William K., Gordon H. Orians, H. Craig Heller, and David Sadava. *Life: The Science of Biology*, 5th ed. Sunderland, MA: Sinauer Associates Inc. Publishers, 1998.

Triassic

The Triassic period is the first of the three divisions of the Mesozoic era, which is known as "The Age of Reptiles." The period lasted for 37 million years, from 245 to 208 million years ago. The Triassic is named after a tricolor sequence of red, white and brown rock layers found in Germany.

Towards the end of the Paleozoic era, which preceded the Triassic, Earth's great crustal plates collided to form the supercontinent Pangaea. Early in the Triassic, Pangaea began to break apart again in a process that is still going on. North America, Europe, and Asia split away as one continent (called Laurasia) from South America, Australia, India, Africa, and Antarctica (known as Gondwanaland). These giant continents continued to break apart into the land masses we have today.

climate long-term weather patterns for a particular region

evaporites rocks formed from evaporation of salty and mineral-rich liquid

The Triassic began with a relatively warm and wet **climate**. However, deposits of fossilized sand dunes and **evaporites** (rocks formed from evaporation of salty and mineral-rich liquid) found in later Triassic strata suggest that the general climate was hot and dry, although some areas may have had defined rainy seasons.

Fossils found in Triassic rocks suggest that this was a period of transition, in which older forms of plants and animals died out and new ones began to appear. A major extinction had occurred at the end of the Paleozoic. Over 90 percent of marine invertebrate species (animals without a backbone) became extinct, as well as many other species of land plants and animals. Scientists hypothesize that a combination of volcanic eruptions, a global drop in sea level, climate change, or loss of habitat during the formation of Pangaea may have contributed to the extinctions.

The Triassic marked the beginning of important advances in plant life. The conifers (including pine trees) appeared to join the already flourishing ferns, cycads (a palmlike plant), horsetail rushes, and now-extinct species like seed ferns. Triassic plants had thick waxy coverings and did not usually grow as tall as modern trees. Scientists hypothesize that the tough coverings on these plants (perhaps developed to keep from drying out in the warm climate) contributed to the development of larger, blunt, rounded teeth (designed for tearing, shredding and chewing) in many animals, including dinosaurs.

invertebrates animals without a backbone

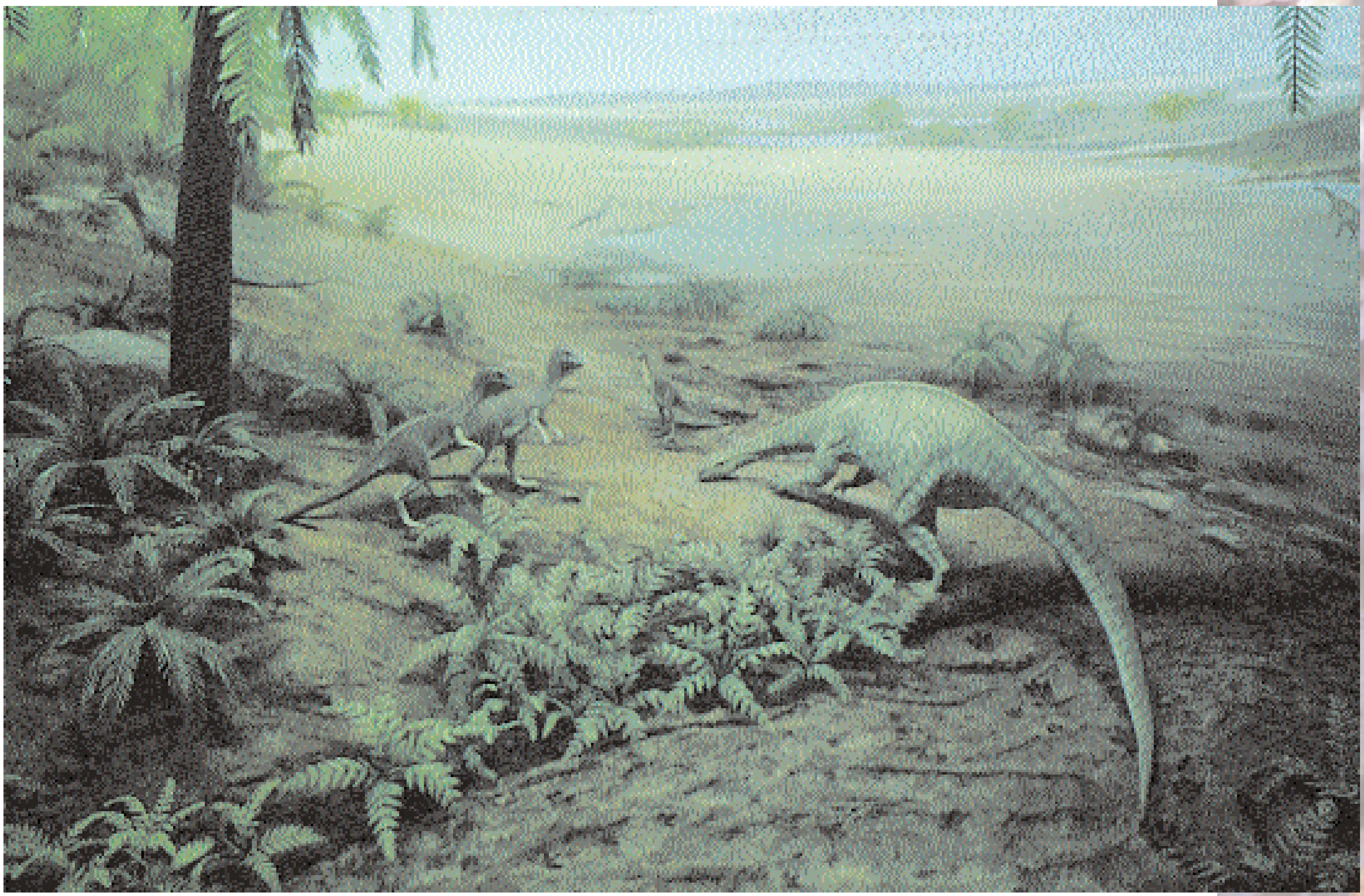
mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

brachiopods a phylum of marine bivalve mollusks

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

Early Triassic oceans contained many different **invertebrates** than before.When seas reflooded the continents during the early Triassic period many changes took place in the composition of species. Many species died out following the Permian extinction and different species began to fill ecological niches. Modern reef-forming corals replaced earlier, more primitive forms.

Clams, snails, scallops, and other **mollusks** weathered the Permian extinction and replaced **brachiopods** as the most common shelled marine invertebrates. Two groups of bryozoans (small seaweed-like colonies attached to objects in shallow seawater), cryptostomate and fenestarte, became extinct. Many families of brachiopods (animals with two shells situated on the top and bottom of the animal) including *productaceans*, *chonetaceans*, *spiriferaceans*, and *richthofeniaceans* became extinct. The entire group of trilobites (early **arthropods** with three lobes—head, abdomen and tail that burrowed



in mud or sand) died out during the Permian extinction. Calms, snails, scallops, and other modern mollusks weathered the Permian extinction. Sea stars, urchins, and sand dollars became the dominant **echinoderms**, over **crinoids** and blastoids.

This museum exhibit depicts two Triassic period dinosaurs, Plateosaurus and Yaleosaurus.

Crinoids and blastoids were two groups that been previously very successful during the flower-like animals known as stalked echinoderms who attached their stalks (or bodies) to the sea floor. They had multiple food gathering "arms" that allowed them to filter water. Fishes continued to evolve and became better adapted to their watery environments. The **cartilaginous** fishes, represented by sharks and rays, had skeletons of **cartilage**, with bony teeth and spines.

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

crinoids echinoderms with radial symmetry that resembles a flower

cartilaginous made of cartilage

cartilage a flexible connective tissue

The skeletons of bony fishes were primarily of bone instead of cartilage. An interesting group of bony fishes included the lungfish and the lobefin fishes. These ancestors of the amphibians had a backbone and small limbs for support, along with an air bladder (a primitive lung) that enabled them to breathe out of water for short periods.

Although, not as numerous as during the Permian period, the amphibians continued to be well represented and diverse.were diverse. One group of common Triassic amphibians was the labyrinthodonts ("labyrinth teeth"). These flat-headed creatures grew several feet in length, had sharp, conical teeth with deeply folded enamel (hence the name of the group), small limbs and very weak backbones, and spent their time in the swampy backwaters

of Triassic rivers. The labyrinthodonts became extinct during the Triassic, but other amphibians, including frogs, became established.

One landmark of animal evolution during the Triassic was the success of the reptiles. Unlike amphibians, which must stay near water for much of their lives, reptiles were completely adapted to life on land and so occupied a variety of habitats, ranging from semidesert to dry uplands, marshes, swamps, and even oceans. Ocean reptiles included the dolphin-like ichthyosaurs, turtles, and large-bodied, long-necked, paddle-flippered reptiles known as plesiosaurs. Except for the turtles, all these marine reptiles are now extinct.

vertebrates animals with a backbone

Triassic land **vertebrates** were dominated by two groups. In the early Triassic, the synapsids, the group that includes mammals and their close relatives, were the most common. One group of synapsids, the "mammal-like reptiles," shared the characteristics of both mammals and reptiles and ultimately gave rise to mammals. True mammals—small, shrewlike creatures—did not appear until the late Triassic. The other large group of terrestrial vertebrates during the Triassic was the archosaurs, which includes dinosaurs, crocodiles, and pterosaurs (flying reptiles), as well as several other now-extinct forms.

bipedal walking on two legs

carnivorous term describing animals that eat other animals

The first dinosaurs appeared in the late Triassic. Early dinosaurs include *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, and *Coelophysis*. These creatures were small, **bipedal**, and **carnivorous**. By the end of the Triassic, dinosaurs had become the most common land vertebrates, along with the pterosaurs, crocodiles, and crocodile-like creatures known as phytosaurs.

Leslie Hutchinson

Bibliography

Lane, Gary A., and William Ausich. *Life of the Past*, 4th ed. Upper Saddle River, NJ: Prentice Hall, 1999.

Trophic Level

zooplankton small animals that float or move weakly through the water

autotroph an organism that makes its own food

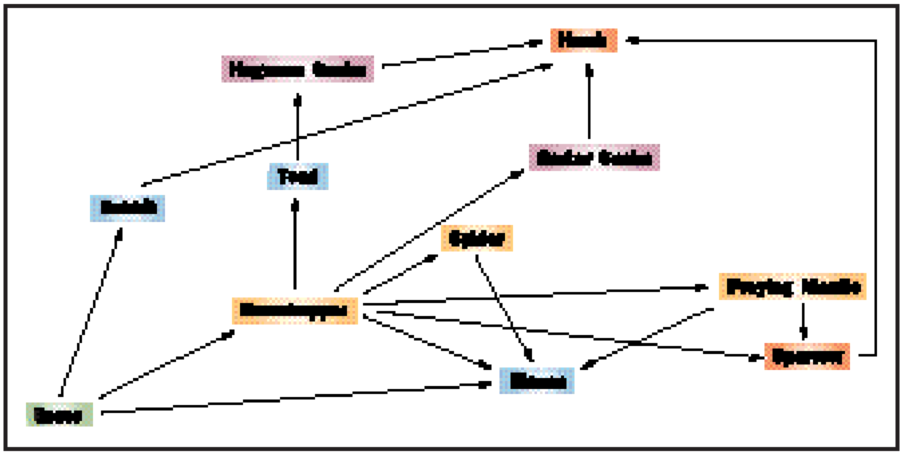
ecosystem a self-sustaining collection of organisms and their environment

herbivore animal who eats plants only

chemotrophs animals that make energy and produce food by breaking down inorganic molecules

A trophic level consists of organisms that get their energy from a similar source. Each step in a food chain is a trophic level. A food chain is a series of organisms each eating or decomposing the preceding organism in the chain. For example, in a lake phytoplankton are eaten by **zooplankton** and zooplankton are eaten by small fish. A food web is similar to a food chain, but in a food web there are many interconnected and interacting food chains. In a typical food chain, a producer or **autotroph** is the source of solar energy that powers the **ecosystem**. For example, in a grazing food web a **herbivore** eats living plant tissue (the producer) and is eaten in turn by an array of carnivores and omnivores. In contrast, a detrivore harvests energy from dead organic material and provides energy for a separate food chain.

There are communities of organisms surrounding deep-ocean hydrothermal vents that obtain their energy from bacteria (known as **chemotrophs** or **chemosynthetic autotrophs**) that harvest heat energy and store it in chemical bonds. These communities are the rare exception.



A simple food web.

Photosynthesis is the ultimate source of energy for every other ecosystem on our planet. **Producers** (autotrophs, or **photosynthesizing autotrophs**) use photosynthesis to harvest energy from the sun. All other organisms obtain their energy, directly or indirectly, from the autotrophs. All of the other organisms in the food chain are **consumers** (known as heterotrophs). The primary consumers eat the producers. Secondary consumers eat the primary consumers, and so on. For example, in a grassland ecosystem, grass is the producer. Grasshoppers are primary consumers. Shrews that prey on the grasshoppers are secondary consumers. Owls, hawks, and snakes prey on the shrews, so they are tertiary consumers. Of course, hawks also prey on snakes and grasshoppers, so the connections get complicated and are usually described as a web of relationships or a food web.

A food chain involves a transfer of matter and energy from organism to organism. As energy is transferred through the food chain or food web, some energy is converted to waste heat at each transfer. The quantity of energy lost is so great that food chains rarely involve more than four or five steps from consumer to top predator. Each level in a food chain or food web is known as a trophic level, a group of organisms that all consume the same general types of food in a food web or a food chain. In a typical food web, all producers belong to the first trophic level and all herbivores (primary consumers) belong to the second trophic level. Using the same grassland as an example, the second trophic level would be all of the herbivores that eat the grass. This group can include a wide variety of different organisms. In the original grasslands of the central United States, the second trophic level included grasshoppers, rabbits, voles and other small rodents, prairie dogs, and American bison. Since they all eat the same grass, they are all at the same trophic level, despite their differences in size, reproductive habits, or any other factors.

The second trophic level in an ecosystem is relatively easy to identify, because the organisms in this level all obtain their energy directly from the autotrophs at the first level. After the second level in a food web, the situation becomes progressively more complex. Many organisms obtain energy from several different sources at different trophic levels. For example, foxes are opportunistic omnivores. They will eat fruits, small herbivores, and small carnivores. Likewise, many birds eat seeds and fruits in one season and switch to eating insects in a different season.

chemosynthetic autotrophs organisms that uses carbon dioxide as a carbon source but obtain energy by oxidizing inorganic substances

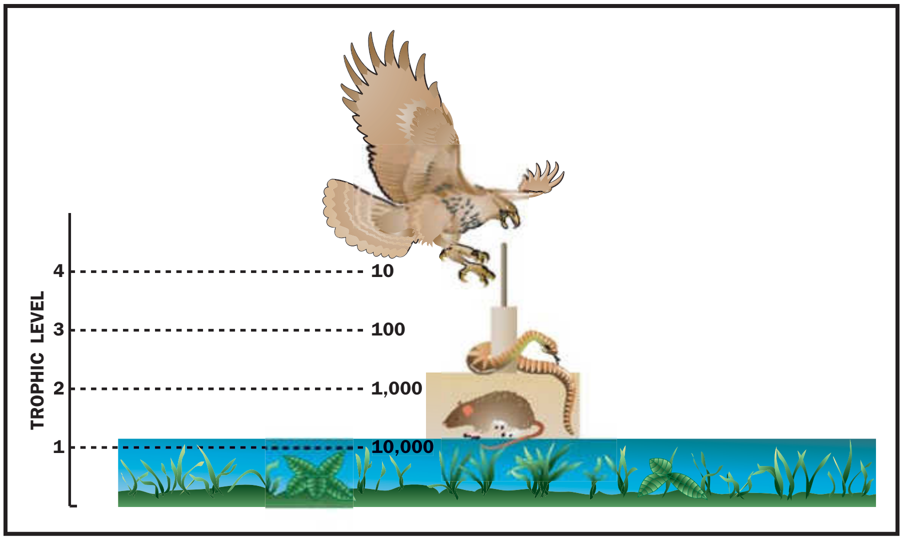
photosynthesis converting sunlight to food

producers organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

photosynthesizing autotrophs animals that produce their own food by converting sunlight to food

consumers animals that do not make their own food but instead eat other organisms

Ecological pyramids illustrate the amount of energy available at each of the four levels of an ecosystem. Redrawn from Johnson.



Another problem in classifying trophic level arises because the energy available at a given trophic level includes many different forms. Plant tissue includes wood, nectar, pollen, seeds, leaves, and fruit. No animal eats all of these different forms of plant tissue. Animals with very different ecological characteristics exploit these various tissues. Termites eat wood; fruit bats eat fruit. Termites offer an additional complication, because it is the organisms in the termite's gut that digest the cellulose who are the actual second-level consumers.

biomass the dry weight of organic matter comprising a group of organisms in a particular habitat

How energy flows through an ecosystem depends on the nature of the producers at the first trophic level. These producers support the entire ecosystem, so their abundance and energy content per kilogram determine the overall energy flow and **biomass** of the ecosystem. Organisms that live on land expend much of their energy in building supporting structures. These supporting structures are not generally available as an energy source to consumers. For example, in a forest, both matter and energy accumulate in the form of wood fibers that cannot be eaten by most animals. On the other hand, grasses have little supporting structure. The herbivores that consume grass are able to eat all of the above ground parts of the plant. With the aid of the specialized bacteria in their guts, grassland herbivores are able to harvest more energy per kilogram of plant material present.

A grassland ecosystem—or any ecosystem—can be represented by an energy pyramid. The base of the pyramid is the community of producers, including various species of grass. The primary consumers, grasshoppers, rodents, rabbits, and bison make up the second level of the pyramid—herbivores. The third level of the pyramid is the secondary consumers, predators that prey on the herbivores. The producers far outnumber the herbivores who far outnumber the carnivores, so the grassland pyramid has a broad base and a narrow tip.

aquatic living in water

population a group of individuals of one species that live in the same geographic area

In **aquatic** environments away from the shoreline, the situation is reversed. The primary photosynthesizing organisms are algae. Small herbivores (grazers) consume the entire organism and harvest almost all of the energy. These grazers decimate the algae **population**, keeping it relatively small. In this ecosystem, most of the energy (and matter) is stored in the second trophic level—the grazers. However, the high reproductive rate and short life cycle of the algae keep the population at a level sufficient to support the grazers. SEE ALSO BIOMASS; FOOD WEB.

Elliot Richmond

Bibliography

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishing, 1989.

Miller, G. Tyler, Jr. *Living in the Environment*, 6th ed. Belmont, CA: Wadsworth Publishing, 1990.

Johnson, George B. *Biology: Visualizing Life.* New York: Holt, Rinehart and Winston, Inc. 1998.

Turbellaria

The class Turbellaria is the most primitive group within the phylum Platyhelminthes, the flatworms. Turbellarians share some important characteristics with other Platyhelminthes. All flatworms are flattened **dorsoventrally**. They are **bilaterally symmetrical**, are unsegmented, and are **acoelomates**, which means they do not have a body cavity. Turbellarians are solid because all the space around their digestive cavity is filled with muscle and other tissue. Turbellarians do not have a respiratory or circulatory system, they exchange gases by diffusion through all their cells. They have a muscular mouth, called a pharynx, as well as a saclike digestive cavity. Turbellarians also have an **osmoregulatory system** called the protonephridium. This system is made up of tubules, a network of little tubes, and specialized cells called flame cells.

dorsoventrally flattened from the top and bottom

bilaterally symetrical an animal that can be separated into two identical mirror image halves

acoelomates animals without a body cavity

osmoregulatory system a system that regulates the water balance between an organism and its environment

The turbellarian nervous system includes a primitive brainlike structure in the head region, called a ganglion. This ganglion is formed by the thickening of the **anterior** part of the **ventral** nerve cords. The head region also has specialized sensory organs, which are more complex in turbellarians than in other flatworms. These organs include eye spots, which are composed of photoreceptors that detect light and are **tactile** and chemical sensory organs that help turbellarians find food. Movement is assisted by receptors that help maintain balance as well as detect movement. The sensory organs of turbellarians are more complex than those of other flatworms because turbellarians are free-living; all other flatworms are parasitic. The free-living turbellarians are ancestors of the parasitic flatworms; parasitism evolved as a specialized form of feeding and reproducing from the scavenger lifestyle of turbellarians. Turbellarians eat both living and dead animal material. Some turbellarians secrete digestive **enzymes** onto their food, then ingest the already-digested food particles through their pharynx. Others digest food in their digestive cavity. All flatworms must expel undigested food out of their mouth; they do not have an anus.

anterior referring to the head end of an organism

tactile the sense of touch

enzymes proteins that act as catalysts to start biochemical reactions

Turbellarians move around using **cilia** on their epidermis or by undulating their body with their muscles. Most turbellarians live in water, either fresh or salt water. A few species live on land in damp habitats like leaf litter. Turbellarians reproduce by **fission** and regeneration, or sexually. Turbellarians that reproduce sexually are hermaphroditic—sperm from one animal will fertilize eggs from another, and the eggs then hatch into small

cilia hair-like projections used for moving

fission dividing into two parts

turbellarians. When reproducing by fission and regeneration, the tail end of the individual turbellarian adheres to a substrate and the head region pulls away from the tail. This eventually splits the flatworm in two, and each piece regenerates the end that is missing. Turbellarians are the only flatworms that can reproduce by fission.

There are more than 4,500 species of turbellarians. Most are less than 5 millimeters (0.2 inches) long, and many are microscopic in size. Planarians (*Dugesia*) are largest turbellarians; they can grow up to 0.5 meter (20 inches) long. SEE ALSO Phylogenetic Relationships of Major Groups.

Laura A. Higgins

Bibliography

Anderson, D. T., ed. *Invertebrate Zoology.* Oxford: Oxford University Press, 1998.

Barnes, Robert D. *Invertebrate Zoology*, 5th ed. New York: Saunders College Publishing, 1987.

Campbell, Neil A., Jane B. Reece, and Lawrence G. Mitchell. *Biology*, 5th ed. Menlo Park, CA: Addison Wesley Longman, Inc., 1999.

Purves, William K., Gordon H. Orians, H. Craig Heller, and David Sadava. *Life: The Science of Biology*, 5th ed. Sunderland, MA: Sinauer Associates Inc. Publishers, 1998.

Urochordata

notochord a rod of cartilage that runs down the back of Chordates

dorsal the back surface of an animal with bilateral symmetry

Urochordates are small marine animals with larvae that swim freely and adults that attach themselves to the ocean floor. The 1,300 species of urochordates, like all members of the phylum Chordata, possess four characteristic anatomical structures as embryos: a flexible body-length rod (the **notochord**) that provides resistance against muscular contractions and allows for more efficient movement; a **dorsal**, hollow, nerve cord that forms the central nervous system; slits in the beginning of the digestive tract (the pharynx) that allow filter feeding and gas exchange; and a postanal tail. Urochordates, commonly known as tunicates, differ from other chordate subphyla (Cephalochordata and Vertebrata) in that the adult form has no notochord, nerve cord, or tail. In fact, an adult tunicate is an immobile, filter-feeding marine animal that in some ways looks more like a sponge or a mollusk than a chordate.

metamorphose drastically changing from a larva to an adult

sexual reproduction a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

metamorphosis a drastic change from a larva to an adult

Tunicate larvae look much more like other chordates than adult tunicates do. Larvae swim using their notochord as structural support for strong, wavelike body movements. However, a larval tunicate cannot eat because both ends of its digestive tract are covered by a skinlike tissue called the tunic. The sole purpose of the larva is to find a place to attach its tail to the ocean floor, where it can **metamorphose** into an adult and begin **sexual reproduction**. **Metamorphosis** involves the loss of the notochord, nerve cord, and tail, and a twisting of the body so that the mouth and the anus both point away from the attachment. The adult can then start filter feeding. It does this by sucking water into its mouth through a pharynx with slits that captures food and spitting the water back out a different opening called the atriopore.

Tunicates might seem like an evolutionary off-shoot, given that the adult form is so different from other chordates. However, based on the similarities between larval tunicates and embryonic **vertebrates**, evolutionary biologists suspect that the first vertebrate chordates were very much like modern-day tunicates. They propose an evolutionary mechanism called paedomorphosis, in which the larval form evolved the ability to reproduce before metamorphosis. No longer requiring a suitable ocean floor to reproduce, these protovertebrates would have been free to exploit and adapt to new niches, eventually giving rise to the vertebrate skeleton.

To say that our vertebrate ancestors resembled tunicates is not to say that those ancestors were tunicates. Modern-day tunicates have had 500 million years to evolve since the days of the ancestors they share with vertebrates. Conceivably, then, protovertebrates did not have an adult form like that of the tunicate, and this adult form evolved later. Without fossil evidence of the earliest vertebrates, it may never be known whether or not they resembled tunicate adults. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Brian R. West

A transparent sea squirt.

vertebrates animals with a backbone

Bibliography

Campbell, Neil A. *Biology*, 2nd ed. Redwood City, CA: Benjamin/Cummings Publishing Company, Inc., 1990.

Curtis, Helena, and N. Sue Barnes. *Biology*, 5th ed. New York: Worth Publishers, 1989.

Ridley, Mark. *Evolution*, 2nd ed. Cambridge, MA: Blackwell Science, Inc., 1996.

Vertebrata

The vertebrates are commonly called "animals with backbones," but this is a simplified description of a group of animals who are the most anatomically and functionally diverse on Earth. As with most major groups of animals, their beginnings are not known. However, scientists have constructed a theory of the origins of vertebrates that is generally well accepted by the academic community.

Scientists base their model of a hypothetical vertebrate ancestor on several primitive living vertebrates. At the forefront is *Amphioxus*, whose body shape is close to what scientists believe resembles that of the ancestral vertebrate. Many researchers have successfully examined the body of this small marine animal and it has become a popular organism for study in biology classes.

Based on *Amphioxus*, scientists believe that the first vertebrates had a fishlike body with individual segmented muscles along its entire length. They were small ocean dwellers who lived close to the bottom and used their muscles to contract and move their bodies and tail in a side-to-side motion. This action propelled them through the water. They had no distinct head. The brain of early vertebrates is a somewhat controversial topic among scientists, but most researchers agree that the early forms had a brain that was more complex than the simple brain of *Amphioxus*. However, the brain was not the highly complicated structure we see in most vertebrates today. The early brain probably carried out only the most basic of body and sensory functions. As with many animals with cerebral

Like other vertebrates, this Cactus Finch has a bilaterally symmetrical body. If divided down the middle, the bird's body will split into two equal halves.

head ganglia, nerve tracts emerged from the brain and ran along the length of the body. Scientists assume the nerve tracts responded to sensory stimuli. The **lateral line** system, present in most fish, was most likely present in early vertebrates.

lateral line a row of pressure sensitive sensory cells in a line on both sides of a fish

Just as in *Amphioxus*, a dorsal (top of body) hollow nerve cord ran the entire length of the body. This nerve cord was supported by an important evolutionary structure made of **cartilage** called the notocord. The notocord, and its role in the evolution of vertebrates, is one of the most important characteristics distinguishing vertebrates from nonvertebrates. Although there are many other characteristics that help to classify the group, the notocord is the structure from which the backbone is believed to have evolved and is the structure from which vertebrates get their name.

cartilage a flexible connective tissue

As vertebrates became more specialized and increased their ability to move and sense their environment, the brain and spine became more complex. In looking at the growth of fetal vertebrates it has been shown that the developing muscles place a strain on the **cartilaginous** notocord. As the strain on the notocord increases with growth of the muscles, deposits of bone replace the cartilage, giving the rod greater strength. This process of replacement eventually produces the bones known as the vertebrae. Each vertebra in a primitive vertebrate corresponds to an individual set of mus-

cartilaginous made of cartilage

cles. This pattern is harder to recognize in more derived vertebrates, like mammals and birds, but it is there nonetheless.

In primitive vertebrates, the mouth is a simple oral opening that leads to the **gill slits** and digestive system. As the vertebrates continued to evolve, the oral cavity was replaced by a more specialized mouth and gill apparatus. Although sharks and their relatives have a primitive type mouth and gills, bony fishes such as salmon and perch have developed complicated gills with a bony covering called an operculum. Sharks are primitive vertebrates in that they do not develop bony skeletons, but even so, the cartilage structure of vertebrates is easy to see.

gills site of gas exchange between the blood of aquatic animals such as fish an the water

As vertebrates become complicated in body structure, the mouth becomes a very characteristic structure. Many have teeth that are actually modified body scales. The increasing specialization of the teeth, such as the pointed, socket-bound teeth of the reptile or the many cusped teeth of the mammals, is a major trait on which groups of vertebrates are identified. Birds have no teeth whatsoever.

Early vertebrates had a simple mouth opening through which they gulped food like a frog or fish. This structure was not only poorly adapted for capturing and holding on to active prey but also prevented the animal from breathing while trying to feed. Hunting and swallowing quick prey, like some flying or hopping insects, was problematic to the ill-equipped vertebrates. As a response to increasingly swift food sources that were adapting to life on land, the vertebrates became swifter and more dangerous. The increased specialization of the mouth proved to be an advantage for the group in capturing food.

As they struggled with larger or stronger prey, it was necessary to bite and hold on to wriggling and unwieldy insects. It was hard for them to breathe and many primitive vertebrates were unable to capture these more agile animals.

A major evolutionary trend in the vertebrates was the development of the secondary palate in the mouth, a platform of bone that separates the nasal cavity from the mouth. Mammals, including humans, have a secondary palate that allows for breathing while feeding. This means that the hunter can bite and hold onto its prey and still breathe. It can chew or tear at its food instead of gulping like a crocodile. Lions are an excellent example of how the secondary palate helps the lion to bite and hold onto its intended victim until it is dead and then tear off portions for eating.

It is difficult to provide a generalized summary of the characters of all vertebrates. The group is extremely diverse and includes fish, sharks and rays, amphibians, reptiles, birds, and mammals. However, there are several characteristics that are common to all vertebrates and four that are completely exclusive to the group.

All vertebrates are bilaterally symmetrical—they have two sides which are identical to each other in one plane only. A vertebrate can be divided down the middle, or **sagital plane**, to produce two equal halves. However, if it is divided down the side, or **transverse plane**, the sides will not be identical.

sagital plane plane long ways through the body

transverse plane a plane perpendicular to the body

The notocord, or skeletal rod, and the **dorsal** hollow nerve cord are present in all vertebrates. These two characters are unique to vertebrates.

dorsal the back surface of an animal with bilateral symmetry

pharyngeal having to do with the tube that connects the stomach and the esophagus

prehensile adapted for siezing, grasping, or holding on

ventral the belly surface of an animal with bilateral symmetry

exoskeleton hard outer protective covering common in invertebrates such as insects

Other characteristics unique to the vertebrates are **pharyngeal** (at the sides of the pharynx, or throat) gill slits and a tail behind the anal opening. The presence of the tail may seem an obvious trait, but no other group of animals has a structure that can be identified as an actual tail behind the anal opening. Some insects have bodies that extend beyond the anus, but they do not have tails. Vertebrate tails can move and provide locomotion, or balance and support, as in birds and dinosaurs. In many vertebrate groups, such as monkeys, which use their **prehensile** tails for swinging through trees, the tail can act as an extra appendage.

The vertebrate circulatory system is always closed, but this is not unique to the group. However, the vertebrate heart is always located in a **ventral** position and the digestive system is complete. Surprising to many, certain vertebrates, especially extinct forms, have an **exoskeleton**. Early fishes, called ostracoderms and placoderms, had bony exoskeletons that protected their head and sensory areas.

The vertebrates have become a highly successful group of animals with an interesting and exciting evolutionary story. Because humans are vertebrates, they have a natural and continuing curiosity about their predecessors who, most likely, had their beginnings about 500 million years ago in the seas of Earth.

Brook Ellen Hall

Veterinarian

Veterinarians are doctors who diagnose and treat the diseases and injuries of animals. Their duties vary depending on the specific type of practice or specialization. In North America, 80 percent of veterinarians are in private practice. The remaining 20 percent work at zoos, inspect meat and poultry for the federal or state government, teach at veterinary universities, or conduct research. When serving in the U.S. Army, Air Force, or Public Health Service, veterinarians are commissioned officers.

A veterinarian listens to this horse's heartbeat during a check-up.

Veterinarians who practice general veterinary medicine are similar to family practitioners. They carry out a number of health services, including giving general checkups, administering tests and immunizations, and advising pet owners on feeding, exercising, and grooming. Veterinarians are called upon to perform routine spaying or neutering, as well as surgery to correct a health problem. Most veterinarians treat small animals and pets exclusively, but others specialize in larger animals such as cattle, horses, and sheep. Veterinarians usually have set office hours, although they may be called to take care of an emergency at any time. Large-animal veterinarians may also be required to visit a farm or ranch when an animal is injured, ill, or expected to give birth under difficult circumstances.

A veterinarian must get along with animals and should have an interest in science. There are a limited number of colleges of veterinary medicine in the United States, and entrance is competitive. Individuals must complete six years of college to receive a Doctor of Veterinary Medicine (D.V.M.) degree. Coursework during the first two years emphasizes physical and biological science. The remaining four years involve classroom work; practical experience in diagnosing and treating animal diseases; surgery; lab courses in anatomy and biochemistry; and other scientific and medical studies. In addition, veterinarians are required to pass an examination in the state, including the District of Columbia, in which they wish to practice.

Stephanie A. Lanoue

Bibliography

Encyclopedia of Careers and Vocational Guidance. Chicago: Ferguson Publishing Company, 2000.

Field, Shelley. *100 Best Careers for the Year 2000.* New York: Prentice Hall, 1992.

VGM's Careers Encyclopedia, 4th ed. Chicago: NTC Publishing Group, 1997.

Viruses

Viruses are infectious agents that have no **organelles** or reproductive machinery of their own. Viruses cannot duplicate their DNA or RNA, nor can they translate their genetic information into protein. Essentially, they are small bags of **genes** that typically encode a comparatively small number of proteins. For example, the human immunodeficiency virus (HIV) is composed of only nine genes, yet with these simple nine bits of protein it can wreak havoc on the human immune system. Others, such as herpes simplex or adenovirus, can have large **genomes** with dozens of genes. Simple or complex, though, all viruses have the same function. As they cannot make protein or reproduce on their own, viruses must force bacteria or animal cells to do their work for them. A virus is, simply put, a genetic parasite.

organelles membrane bound structures found within a cell

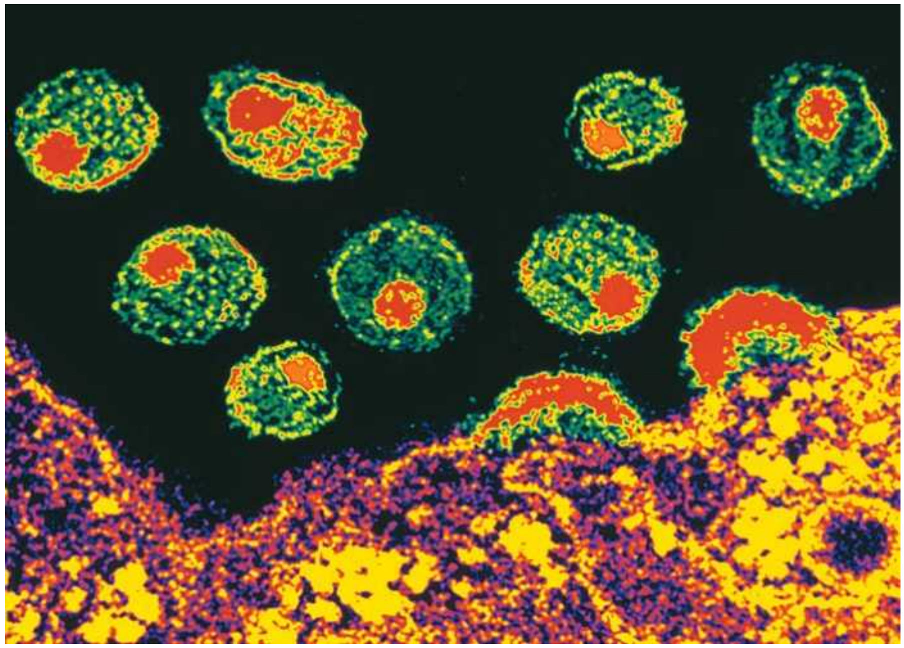
genes segments of DNA located on chromosomes that direct protein production

genomes the sum of all genes in a set of chromosomes

As it does not have to sustain other energetically expensive cellular processes, a virus has a very simple structure. It is usually composed of nucleic acids (DNA or RNA) and a protein coat. This coat may be a very primitive covering (called a capsid) or it may be a complex structure derived from a host's membrane (called an envelope). Viral envelopes may possess a variety of receptors and decoys designed to fool the host's immune system. Avoiding detection is one of a virus's main tasks, and viruses may rely on dummy surface molecules or manipulating the immune system to do so. For example, HIV convinces infected cells to stop producing molecular flags that indicate infection to the rest of the body. In order to be successful, a virus must defeat the immune system and reproduce itself efficiently.

A viral life cycle generally has five distinct phases:

1. Attachment: The virus must connect itself to the target cell. Often, this is accomplished by molecules on the virus that mimic cell surface receptors required to interact with other cells. Rhinoviruses, some of which cause the common cold, bind to intercellular adhesion molecules (ICAMs) on the respiratory tract. ICAMs are meant to help white blood cells find their targets, but rhinoviruses have evolved to use them to get into cells. HIV binds to CD4 and CCR5, two surface markers involved in T-cell trafficking. Such binding may restrict the virus to infecting certain species or certain types of cells within a species.
2. Penetration: Once docked, the virus must get its nucleic material inside the cell. Some viruses are taken entirely into the cell. Others



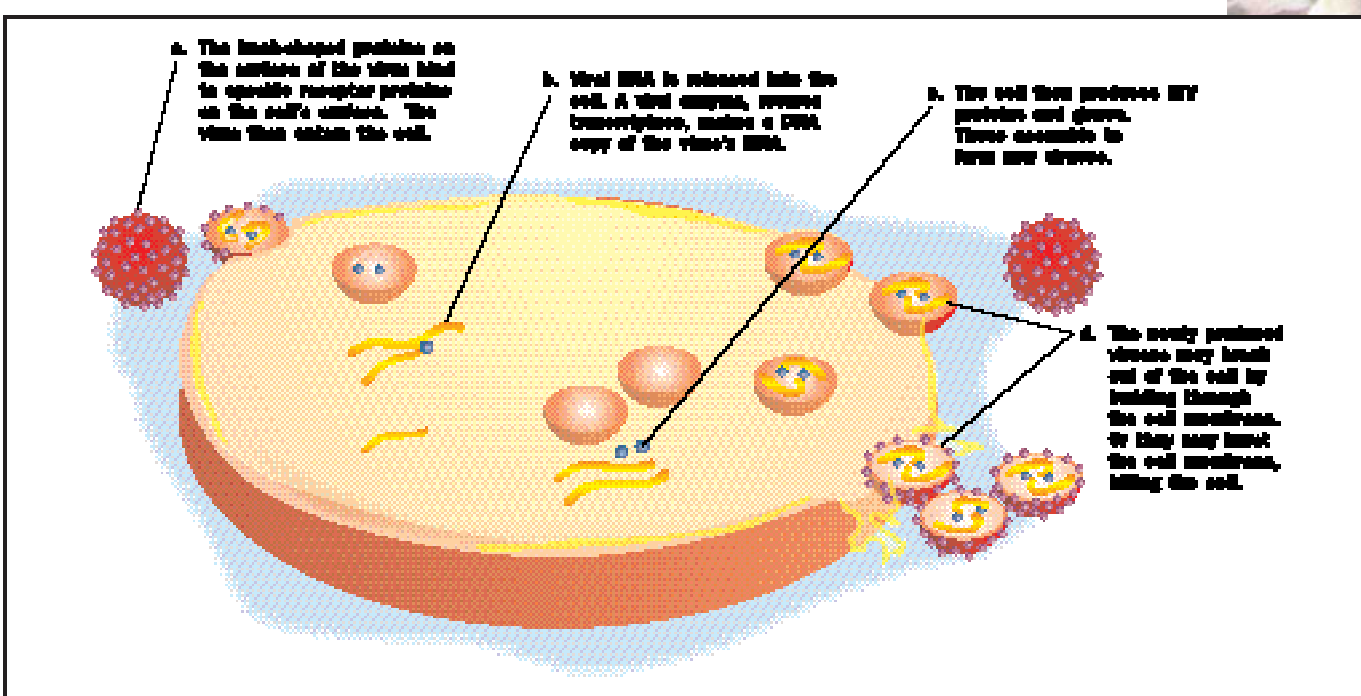
This enhanced photo shows mature HIV viruses.

inject their DNA or RNA through the cell membrane. Still others fuse their membrane with their hosts' and dump the nuclear contents into the cytosol. In order for the virus to use the host's reproduction capabilities, it needs to be inside the cell.

3. Replication: Once the nucleic acids are inside, the virus will use the host's replication machinery to make more copies of itself. Some viruses, such as HIV, are made of RNA instead of DNA. For this reason, these viruses must first transcribe their genomes into DNA in order for cells to copy them. Whether made of DNA or RNA, though, a virus will also force the host cell to make its protein coat and any other proteins necessary to put the virus together. Rather than expending its precious energy on maintenance, the host cell instead is forced to use its energy to make viral parts.
4. Assembly: The various parts of the virus are put together with its freshly copied DNA. Soon the host cell is full of these virions, or individual viral particles, and the virions are ready to infect another cell.
5. Lysis: The virus ruptures the cell and disperses its viral progeny, all off to infect new host cells and begin the cycle again.

Not all viruses lyse (rupture) their host cells. Some may bud off the host cell. Others may become latent and rest in the host's cytosol or even the host's own **chromosomes** for a long time without causing damage. For example, herpes simplex 1 infects individuals and causes cold sores, but does so only intermittently. Cytomegalovirus (CMV) and Epstein-Barr virus (EBV), also known as mononucleosis, both infect the human body and remain latent for life. These viruses are held in check by the immune system and cause no harm, but they never go away completely. Persons with acquired immune deficiency syndrome (AIDS) lose immune function, and CMV and EBV have been known to resurface in persons with AIDS.

chromosomes structures in the cell that carry genetic information



Virus reproduction. Redrawn from Johnson, 1998.

Because some viruses insert themselves into the host's genome, there is a possibility that they might affect normal gene regulation in the host itself. Viruses can be responsible for certain cellular problems that involve gene regulation. For example, some viruses are thought to be the cause of certain types of cancer. Human papilloma virus, for example, has been associated with cervical cancer. Hepatitis B and hepatitis C cause a majority of the world's cases of liver cancer.

While viruses can be specific for a particular species, cross-species infection happens frequently and sometimes with disastrous results. For example, all fifteen known strains of influenza A virus reside in **aquatic** birds, preferring the intestinal tracts of ducks in particular. As such, fowl fecal matter, as well as seals, whales, pigs, horses, and chickens, have been implicated in a number of human influenza outbreaks.

aquatic living in water

As a parasite, the best evolutionary strategy for a virus is for it not to harm the host. It is thought that HIV-1 and HIV-2 were introduced to humanity through the ingestion of uncooked monkeys (a chimpanzee and a sooty mangabey, respectively) sometime in the early twentieth century. These monkeys had been infected with simian immunodeficiency virus (SIV), which is fairly benign to its host. In species such as the mangabeys, African green monkeys, and pigtailed macaques, SIV causes no detectable problems and infection is widespread (it is estimated that some 80 percent of captive sooty mangabeys carry the disease). Infected rhesus monkeys, however, lose their ability to fight disease and waste away. Likewise, when the virus mutated to HIV in humans, it infected human **populations** and continues to cause widespread sickness and death. If HIV is to be with humanity for a long time, then it must become a little less virulent, lest it kill off all of its hosts. SEE ALSO Animal Testing.

populations groups of individuals of one species that live in the same geographic area

Ian Quigley

Bibliography

Cann, Alan J., ed. *DNA Virus Replication.* New York: Oxford University Press, 2000.

Dalgleish, Angus, and Robin Weiss. *HIV and the New Virus.* San Diego: Academic, 1999.

Johnson, George B. *Biology: Visualizing Life.* New York: Holt, Rinehart and Winston, Inc., 1998.

Vision

Different levels of vision correlate to the different types of eyes found in various species. The simplest eye receptor is that of planarians, a flatworm that abounds in ponds and streams. Planarians are moderately cephalized and have eye cups (or eyespots) located near the ganglia, a dense cluster of nerve cells with **ventral** nerve cords running along the length of the body.

ventral the belly surface of an animal with bilateral symmetry

The receptor cells within the cup are formed by layers of darkly pigmented cells that block light. When light is shined on the cup, stimulation of the photoreceptors occurs only through an opening on one side of the cup where there are no pigmented cells. As the mouth of one eye cup faces left and slightly forward, and the other faces right and forward, the light shining on one side can enter the eye cup only on that side.

This allows the ganglia to compare rates of nerve impulses from the two cups. The planarian will turn until the sensations from the two cups have reached an **equilibrium** and decreased. The observable behavior of the planarian is to turn away from the light source and seek a dark place under an object, an adaptation that protects it from predators.

equilibrium a state of balance

As evolution progressed and cephalization increased, vison became more complex as well. There are true image-forming eyes of **invertebrates**: compound eyes and **single-lens eyes**. Compound eyes are found in insects and **crustaceans** (phylum Arthropoda) and in some polychaete worms (phylum Annelida). The **compound eye** has up to several thousand light detectors called *ommatidia*, each with its own cornea and lens. This allows each ommatidium to register light from a tiny part of the field of view. Differences in light intensity across the many ommatidia result in a mosaic image.

invertebrates animals without a backbone

single-lens eyes an eye that has a single lens for focusing the image

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

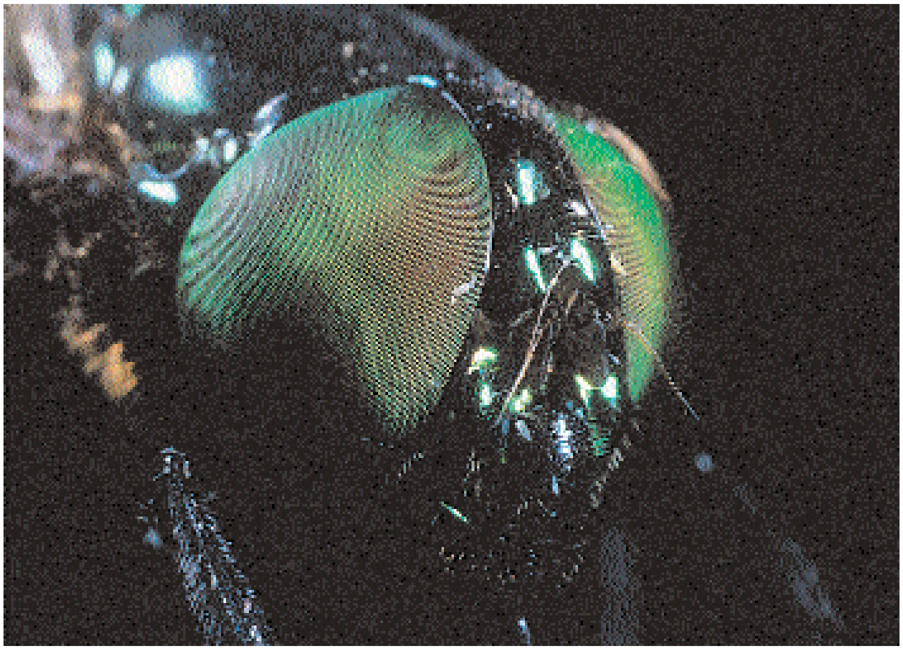
compound eye a multifaceted eye that is made up of thousands of simple eyes

Although the image is not as sharp as that of a human eye, there is greater acuity at detecting movement—an important adaptation for catching flying insects or to avoid threats of predation. This ability to detect movement is partly due to the rapid recovery of the photoreceptors in the compound eye. Whereas the human eye can distinguish up to 50 flashes per second, the compound eye recovers from excitation rapidly enough to distinguish flashes of at the rate of 330 per second. Compound eyes also allow for excellent color vision, and some insects can even see into the UV range of the spectrum.

The second type of invertebrate eye, the single-lens eye, is found in jellyfish, polychaetes, spiders, and many **mollusks**. Its workings are similar to that of a camera. The single lens focuses light onto the retina, a bilayer of cells that are photosensitive, allowing for an image to be formed.

mollusks large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

Vertebrate vision also uses single-lens vision, but it evolved independently and differs from the single-lens eyes of invertebrates. Vertebrate eyes



The compound eye of a horsefly.

have the ability to detect an almost countless variety of colors and can form images of objects that are miles away. It can also respond to as little as one photon of light. But as it is actually the brain that "sees," one must also have an understanding of how the eye generates sensations in the form of **action potentials** and how the signals travel to the visual centers of the brain.

action potential a rapid change in the electric charge of the cell membrane

Structure of the Vertebrate Eye

The globe of the eyeball is composed of the *sclera*, a tough, white outer layer of **connective tissue**, and of the *choroid*, a thin, pigmented inner layer. The sclera becomes transparent at the cornea, which is at the front of the eye where light can enter. The **anterior** choroid forms the iris, the colored part of the eye. By changing size, the iris regulates the amount of light entering the pupil, the hole in the center of the iris. Just inside the choroid is the retina, which forms the innermost layer of the eye and contains the photoreceptor cells.

connective tissue cells that make up bones, blood, ligaments, and tendons

anterior referring to the head end of an organism

Information from the photoreceptor cells of the retina passes through the optic disc, where the optic nerve attaches to the eye. The optic disc can be thought of as a blind spot in a vertebrate's field of vision because no photoreceptors are present in the disc. Any light that is focused on the lower outside part of the retina, the area of the optic disc, cannot be detected.

The eye is actually composed of two cavities, divided by the lens and the ciliary body. The anterior, smaller cavity is between the lens and the cornea and the **posterior**, larger one is behind the lens, within the eyeball itself.

posterior behind or the back

The ciliary body is involved in constant production of the clear, watery aqueous humor that fills the anterior cavity of the eye. (Blockage of the ducts from which the aqueous humor drains can lead to glaucoma and eventually blindness, as the increased pressure compresses the retina.) The posterior cavity is lubricated by the vitreous humor, a jellylike substance that occupies most of the volume of the eye. Both humors function as liquid lenses that help focus light on the retina.

The lens itself is a transparent protein disc that focuses images on the retina. Many fish focus by moving the lens forward and backward, camera-style. In humans and other mammals, focusing is achieved through accommodation, the changing of the shape of the lens. For viewing objects at a distance, the lens is flattened and when viewing objects up close, the lens is almost spherical.

Accommodation is controlled by the ciliary muscle, which contracts to pull the border of the choroid layer of the eye to the lens, causing suspensory ligaments to slacken. There is a decrease in tension and the lens becomes more elastic, allowing the lens to become rounder. For viewing at a distance, the ciliary muscle relaxes, allowing the choroid to expand, thus placing more tension on the suspensory ligament and pulling the lens flatter.

Signal Transduction

The photoreceptor cells in the retina are of two types: rods and cones. The rods are more sensitive to light but are not involved in distinguishing color. They function in night vision and then only in black and white. Cones require greater amounts of light to be stimulated and are, therefore, not initiated in night vision. However, they are involved in distinguishing colors.

diurnal active in the daytime

The human retina has approximately 125 million rod cells and approximately 6 million cone cells. The rods and cones account for nearly 70 percent of all receptors in the body, emphasizing the importance of vision in a human's perception of the environment. The numbers of photoreceptors are partly correlated with nocturnal or **diurnal** habits of the species, with nocturnal mammals having a maximum number of rods.

In humans the highest density of rods is at the lateral regions of the retina. Rods are completely absent from the fovea, the center of the visual field. This is why it is harder to see a dim star at night if you look at it directly than if you look at the star at an angle, allowing the starlight to be focused onto rod-populated regions of the retina. However, the sharpest day vision is achieved by looking directly at an object because the cones are most dense in the fovea, approximately 150 thousand cones per square millimeter. Some birds actually have more than one million cones per square millimeter, enabling species such as hawks to spot mice from very high altitudes.

Photoreceptor cells have an outer segment with folded membrane stacks with embedded visual pigments. Retinal is the light-absorbing molecule synthesized from vitamin A and bonded to *opsin*, a membrane protein in the photoreceptor. The opsins vary in structure from one type of photoreceptor to another. The light-absorbing ability of retinal is affected by the specific identity of the opsin partner.

neurotransmitters chemical messengers that are released from one nerve cells that cross the synapse and stimulate the next nerve cell

synapse the space between nerve cells across which impulses are chemically transmitted

The chemical response of retinal to light triggers a chain of metabolic events, which causes a change in membrane voltage of the photoreceptor cells. The light hyperpolarizes the membrane by decreasing its permeability to sodium ions, so there are fewer **neurotransmitters** being released by the cells in light than in dark. Therefore a decrease in chemical signals to cells with which photoreceptors **synapse** serves as a message that the photoreceptors have been stimulated by light.

The **axons** of rods and cones synapse with **neurons**, bipolar cells, which synapse with ganglion cells. The horizontal cells and amacrine cells help integrate information before it is transmitted to the brain.

axons cytoplasmic extension of a neuron that transmits impulses away from the cell body

neurons nerve cells

The axons of the ganglion cells form optic nerves that meet at the optic chiasma near the center of the base of the cerebral cortex. The nerve tracts are arranged so that what is in the left field of view of both eyes is transmitted to the right side of the brain (and vice versa).

The signals from the rods and cones follow two pathways: the vertical pathway and the lateral pathway. In the vertical pathway, the information goes directly from receptor cells to the bipolar cells and then to the ganglion cells. In the lateral pathway, the horizontal cells carry signals from one photoreceptor to other receptor cells and several bipolar cells. When the rods or cones stimulate horizontal cells, these in turn stimulate nearby receptors but inhibit more distant receptor and bipolar cells that are not illuminated. This process, termed **lateral inhibition**, sharpens the edges of our field of vision and enhances contrasts in images.

lateral inhibition a phenomenon that amplifies the differences between light and dark

The information received by the brain is highly distorted. Although the anatomy and **physiology** of vision has been extensively studied, there is still much to learn about how the brain can convert a coded set of spots, lines, and movements to perceptions and recognition of objects. SEE ALSO NERVOUS SYSTEM; GROWTH AND DIFFERENTION OF THE NERVOUS SYSTEM.

physiology the study of the normal function of living things or their parts

Danielle Schnur

Bibliography

Bradbury, Jack W., and Sandra L. Vehrencamp. *Principles of Animal Communication.* Sunderland, MA: Sinauer, 1998.

Campbell, Neil A., Lawrence G. Mitchell, and Jane B. Reece. *Biology: Concepts and Connections*, 3rd ed. Menlo Park, California: Benjamin/Cummings Publishing Company, 1993.

Vocalization

Many animals communicate with acoustic signals. Crickets rub a hind leg along a row of protruding spikes; rattlesnakes shake a set of beads in their tail. But vocalization is by far the most common mechanism of acoustic communication. Found only among **vertebrates**, vocalization involves forcing air through a tube across one or more thin membranes located in a tube between the **lungs** and the mouth. These membranes vibrate, producing rapid fluctuations in air pressure in the outgoing air stream that can be detected as sound by a receiver that is tuned to the appropriate frequencies.

vertebrates animals with a backbone

lungs sac-like, spongy organs where gas exchange takes place

Vocalization results from the interaction of four forces acting on each membrane. The first force is air pressure, which is generated by expelling air from a flexible sac, such as a lung. The second force is the elasticity of the membrane, which returns the membrane to its original position after it is disturbed. The third force, which is muscular, forces the membrane into the airflow. The fourth force is called Bernoulli's force, which sucks the membrane into the airflow.

To produce a vocal sound, air is forced through the tube by the contraction of the air sac. Simultaneously, a muscle thrusts the membrane into

A coyote howls during a snowstorm in Yellowstone National Park.

the airflow, causing air pressure to build up. Eventually, this air pressure forces the membrane out of the airflow, rapidly releasing air from the tube. The rapid flow of air past the membrane generates Bernoulli's force, which pulls the membrane back into the airflow.

This cycle repeats until the muscles forcing the membrane into the airflow relax and the elasticity of the membrane pulls it out of the airflow. The rate at which the cycle repeats is equivalent to the frequency of the sound produced and is dependent on the degree of muscular contraction blocking the airflow.

Mammals, **anurans**, and birds each have a unique mechanism of vocalization. All possess a tube called a trachea, which connects the bronchi (tubes leading to the lungs) to the mouth and nose. In mammals, a set of two membranes called the glottis, or vocal cords, partially blocks the airflow through the trachea when a pair of muscles contracts. The diaphragm, an abdominal muscle underneath the lungs and above the intestines, contracts to expand the lungs and relaxes to expel air. Thus, the rate of airflow during vocalization, which can occur only during exhalation, is not under direct muscular control.

anurans the order of amphibians that contains frogs and toads

The signal produced is periodic and nonsinusoidal, meaning that the rate of airflow varies regularly, but not continuously, around the mean. This produces harmonics, which are sounds at higher multiples of the fundamental frequency. These harmonics can be altered by downstream cavities, such as the mouth, to produce different tones, such as the vowels.

Frogs and toads have two consecutive sets of membranes: the one closer to the lungs acting as the vocal cords, and the farther one referred to as the glottis. The vocal cords control the frequency of the signal, whereas the glottis provides periodic amplitude modulation (AM, as in a radio signal). Expelled air is captured in a throat sac and returned to the lungs to be reused, thereby reducing the amount of work required of the diaphragm. The throat sac also serves as a resonant coupler, its vibrations transferring the signal to the outside air.

Bernoulli's force, also known as Bernoulli's principle, draws its name from its discoverer, Daniel Bernoulli (1700–1782). The principle relates fluid velocity and pressure. Among many other applications, the principle provides an explanation for aircraft lift. The wing shape and the angle of its tip relative to the flow of air are configured so that the air flowing over the wing moves faster than the air under the wing. The pressure difference between the two makes the lift possible.

Birds have two separate membranes: one between each bronchus and the trachea, together referred to as the syrinx. Each membrane functions independently, allowing birds to produce two different sounds simultaneously. Muscles cause the membranes, which line the side of the syrinx, to buckle, allowing Bernoulli's force to pull them into the airflow.

In addition to lungs, birds possess air sacs throughout the body that are connected to the bronchi and subject to muscular contraction. Thus, exhalation is under direct muscular control, allowing for finely calibrated amplitude modulation. Furthermore, many species employ a labium to control the aperture of the syrinx, and therefore amplitude, onset, and offset of the signal. Finally, the degree of tension in the membranes affects both frequency and amplitude, which are often correlated in bird calls.

Although mammals, anurans, and birds differ in the way they control the frequency and amplitude of their acoustic signals, they share an ability to exploit air as a medium for the rapid transmission of information. This is especially important for animals that live in visually cluttered **habitats** such as trees, or those that communicate over long distances. Sounds do not require localization by the receiver in order to be recognized, whereas

habitats physical locations where an organism lives in an ecosystem visual signals must be noticed first. Therefore, acoustic signals serve well as alarm calls and to attract attention from potential competitors or mates. SEE ALSO ACOUSTIC SIGNALS; COMMUNICATION.

Brian R. West

Bibliography

Hopp S. L., M. J. Owren, and C. S. Evans. *Animal Acoustic Communication: Sound Analysis and Research Methods.* Berlin: Springer-Verlag, 1997.

Von Baer's Law

Early developmental stages of a characteristic tend to be more similar among related species than later stages. This means that most characteristics that differentiate **taxa**, and which are commonly used to distinguish among species, represent later modifications to a fundamentally similar developmental plan. Von Baer's Law states that structures that form early in development are more widely distributed among groups of organisms than structures that arise later in development.

taxa named taxonomic units at any given level

This law of embryology is named after the nineteenth-century German biologist Karl Ernst von Baer, who first articulated it. Although von Baer was not an evolutionist, his concept of increasing **differentiation** between species during **ontogeny**, or embryonic development, fits well with an evolutionary view of embryology. His law comes from the first two of four generalizations he made in 1828:

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

ontogeny the embryonic development of an organism

1. General features common to a large group of animals appear earlier in the embryo than do specialized features.
2. The development of particular embryonic characters progresses from general to specialized during their ontogeny.
3. Each embryo of a given species, instead of passing through the adult stages of other animals, departs more and more from them as ontogeny progresses (in direct contrast to the invalid biogenetic law of Ernst Haeckel, discussed below).
4. Therefore, the early embryo of a higher animal is never like the adult of a lower animal, only similar to its early embryo.

Karl Ernst von Baer was the first researcher to explain the law of embryology.

Von Baer's Law dictates that a generalized state is present in the early embryo. This generalized state gives way to more specialized states as the embryo develop, as can be seen by direct observation of embryos. In other words, an early stage of a chick embryo might be recognizable as a member of the phylum Vertebrata, but not as any particular subtaxon. Later, as structural specialization continues, it is recognizable as a member of the class Aves, and finally as a member of a particular species, *Gallus domesticus.*

Charles Darwin recognized that von Baer's Law provides a connection between embryology and biological evolution, namely that primitive features tend to be generalized and derived features tend to be specialized. Darwin realized that evolutionary change could be inferred from changes in development.

An example of the connection between embryonic development and evolutionary history is the development of the vertebrate limb. Structures of the limb develop in a proximodistal sequence, or from nearest to most distant from the body: shoulder bones develop first, and bones of the digits develop last. Lungfish and coelacanths, distant living relatives of the ancestral tetrapod, have fins with well-developed "shoulders," but their appendages do not contain bones **homologous** to the digits of tetrapods (their similarity in various taxa derives from their common origin in a shared ancestor). Digits appear as specialized, derived features in early tetrapods. Limb morphology, or form, proceeds from generalized to specialized as we climb the **phylogenetic**, or evolutionary, tree, and limb development in the embryos of advanced tetrapods parallels the evolutionary history of these tetrapods.

homologous similar but not identical

phylogenetic relating to the evolutionary history of a species or group of related species

An additional example of von Baer's Law is seen in the development of the **notocord**. All **vertebrates** develop a **dorsal** cartilaginous rod called the notochord and gill pouches in the pharyngeal, or throat, region. Both are early developmental traits and are common to many species. Later in development, however, these traits are lost and replaced by traits that are distinctive to different groups of vertebrates.

notochord a rod of cartilage that runs down the back of chordates

vertebrates animals with a backbone

dorsal the back surface of an animal with bilateral symmetry

Thus, early embryos of different vertebrate species are remarkably similar. For example, the early embryos of fishes, salamanders, tortoises, chickens, pigs, cows, rabbits, and humans appear similar, yet each species follows its own embryonic developmental trajectory (sequence of events during development) to develop distinctive traits.

Mutations that alter early development are usually lethal because they can introduce drastic changes to subsequent development. Because of these developmental constraints, early developmental stages are less likely to change through evolutionary time. These early stages are likely to be similar among taxa and differences among them are more likely to arise later in ontogeny, or embryonic development.

mutations abrupt changes in the genes of an organism

Another nineteenth-century German biologist, Ernst Haeckel, proposed what he thought was a law of evolution. Although Haeckel's law is invalid, it is widely known and resulted in the familiar phrase "ontogeny recapitulates phylogeny." Haeckel's biogenic law thus claims that embryonic development repeats evolutionary history. Embryos, he was saying, repeat the adult stages of ancestral species in chronological order from primitive to most recent and changes are added only during final stages, called terminal addition.

In some cases, the **ontogeny** of a trait does go through stages much like the adult forms of ancestral species. However, although Haeckel's biogenic law describes a possible evolutionary pattern, it provides no causal explanation for the pattern. The biogenetic law eventually lost credibility with the rise of experimental embryology and Mendelian **genetics**. Embryological studies showed that many types of change in developmental timing (heterochrony) are possible and that different parts of the organism may differ in rates of development. Genetic studies have demonstrated that **genes** could effect changes at any stage of development so that terminal addition was not the only possibility. SEE ALSO EMBRYONIC DEVELOPMENT.

ontogeny the embryonic development of an organism

genetics the branch of biology that studies heredity

genes segments of DNA located on chromosomes that direct protein production

Andrew G. Gluesenkamp

Bibliography

Futuyma, Douglas J. *Evolutionary Biology.* Sunderland, MA: Sinauer Associates, Inc., 1986.

Gould, Stephan J. *Ontogeny and Phylogeny.* Cambridge, MA: Belknap Press, 1977.

Raff, Rudolf A. *The Shape of Life.* Chicago: University of Chicago Press, 1996.

Raff, Rudolf A., and Thomas C. Kaufman. *Embryos, Genes, and Evolution: The Developmental-Genetic Basis of Evolutionary Change.* New York: Macmillan, 1983.

Wallace, Alfred Russel

Naturalist

1823–1913

Alfred Russel Wallace was born on January 8, 1823, in Usk, Great Britain (Wales). He died at the age of 90 on November 7, 1913. Wallace developed a theory of evolution by **natural selection** independently of Charles Darwin but at nearly the same time. He also founded the field of animal geography, the study of where animals occur on Earth.

natural selection a process by which organisms best suited to their environment are most likely to survive and reproduce

naturalists scientists who study nature and the relationships among the organisms

As a boy Wallace had a great interest in plants and collected them. In 1844 he began teaching at a boy's school, the Collegiate School in Leicester, Leicestershire, England. There he met the British **naturalist** Henry Walter Bates, who got him interested in insects. In 1848 Wallace and Bates began a four-year expedition to the Amazon. Unfortunately, the ship sank on the return voyage, and most of Wallace's collected specimens were lost. In 1853 he published a book about the journey. In 1854 Wallace began an eight-year tour of the Malay Archipelago in the East Indies. He studied the culture of the native people and the geographical distribution of the animals. He collected and described thousands of new tropical species, and was the first European to see an orangutan in the wild. Wallace discovered that the animals of the Malay Archipelago are divided into two groups of species following an imaginary line, now known as "Wallace's Line." Species west of the line are more closely related to mammals of Asia. Those east of the line are more closely related to mammals of Australia.

While in Malaysia, Wallace thought of the concept of "survival of the fittest" as the key to evolution. In 1858 he wrote about his theory in a paper that he sent to Charles Darwin. Darwin realized that they both had the same revolutionary ideas. The men presented their ideas together in a joint paper to the Linnaean Society in 1858. Darwin is given most of the credit for the theory of evolution by natural selection because he developed the idea in much more detail than Wallace did. Also, Darwin was the person most responsible for its acceptance in the scientific community. Both Wallace and Darwin believed that man evolved to his present bodily form by natural selection. However, Wallace insisted that man's complex mental abilities must have been due to a different, nonbiological force. His activities in spiritual and psychic circles caused many of his fellow scientists to avoid him.

Wallace went on to write many influential books about evolution as well as tales of his journeys. He was an outspoken supporter of socialism, women's rights, and pacifism. He was awarded the Order of Merit by the British government in 1910.

Denise Prendergast

Bibliography

Muir, Hazel, ed. *Larousse Dictionary of Scientists.* New York: Larousse Kingfisher Chambers Inc., 1994.

Internet Resources

Alfred Russel Wallace. <http://www.wku.edu/%7Esmithch/index1.htm>.

Water Economy in Desert Organisms

The white-throated wood rat, *Neotoma albigula*, may go its whole life without ever taking a drink of water. It does not need to. The rat obtains all the water it needs from its food. The fact that the rat's diet includes dry seeds and cactus makes this even more surprising. It obtains about half of the water it needs from succulent plants. The white-throated wood rat is also able to chemically synthesize water from the molecules in the food it eats. It shares this adaptation with many other *Neotoma* species, also known as pack rats. The wood rat has many other adaptations that allow it to thrive with little or no water.

The small kit fox, *Vulpes velox*, rarely drinks water. It will if it is thirsty and has the opportunity, but it is generally a long way from the fox's den to any reliable source of water. Therefore, the fox consumes much more prey than it needs for energy requirements. The excess prey is consumed simply for the water it contains. Along with this behavior, the fox has evolved a digestive system that allows it to survive while rarely drinking water.

Both of these are examples of water economy as practiced by desert organisms. Many desert organisms, both plants and animals, have evolved strategies that allow then to survive on little or no water.

Plant Adaptations

Desert plants have many adaptations that reduce water loss, including extensive root systems to capture as much water as possible and thickened stems to store water. Plants also have waxy or resinous coatings on their leaves and a thick epidermis, and they keep their stomata closed much of the time. However, keeping the stomata closed causes another problem. Since the carbon dioxide molecule is even bigger than the water molecule, anything that reduces water loss also prevents carbon dioxide from entering the leaf. In these plants, the carbon dioxide levels can drop so low that normal **photosynthesis** cannot function.

photosynthesis converting sunlight to food

To compensate, many desert plants have evolved a much more efficient form of photosynthesis that uses a molecule with four carbon atoms. Photosynthesis in non-desert plants uses a molecule with three carbon atoms. The two reactions are commonly known as C3 photosynthesis and C4 photosynthesis respectively. The corresponding plants are called C3 plants and C4 plants. Desert plants are frequently C4 plants.

This roadrunner will extract water from its lizard prey. This is one of several adaptations the roadrunner has made in order to exist in an environment with a very limited water supply.

C4 photosynthesis is more efficient at low levels of carbon dioxide. It is more costly in energy terms, but since deserts have plenty of sunlight, low light levels are not a problem.

Animal Adaptations

Kangaroo rats (*Dipodomys* sp.), small rodents closely related to pocket gophers that are not rats at all, exhibit many of the adaptations common to desert mammals. They have highly efficient kidneys that excrete almost solid urine, thus conserving water. To do this, they have evolved adaptations that allow salt concentration in their urine to be as high as 24 percent, compare to 6 percent in humans.

Also, kangaroo rats have complex passages in their nostrils that condense, collect, and recycle moisture. The temperature at the tips of their noses is 28°C (82°F) while their body temperature is 38°C (100°F). So, as they exhale, the air is cooled and water is condensed and recycled. Humans lose twenty times more water through respiration than do kangaroo rats.

A camel, donkey, and man walk through a desert in Pakistan. Many desert animals have evolved systems for surviving on little or no water.

Kangaroo rats also plug their burrows during the day to maintain a relative humidity in the burrow of 50 percent or higher while the humidity above ground drops to as low as from 10 to 15 percent. Kangaroo rats can also obtain water metabolically from the seeds they eat. Captive kangaroo rats may become stressed enough to drink water, but a wild kangaroo rat may go its entire life without drinking water.

The kangaroo rat is not unique. Many other animals have adaptations that allow them to live in the desert by practicing water economy. Several small rodents share some or all the adaptations of the kangaroo rat. These include the white-throated wood rat (also known as pack rat, *Neotoma* sp.), the canyon mouse (*Peromyscus crinitus*) and many others. Birds also exhibit some adaptations, although most simply escape the dry conditions. The Phainopepla, *Phainopepla nitens*, breeds in the desert in the springtime and escapes to the mountains in summer.

The roadrunner, *Geococcyx californianus*, cannot easily escape the desert, nor does it try. It has several adaptations that allow it to thrive. It reabsorbs water from feces, it excretes excess salt through a nasal gland (other than the roadrunner, an adaptation found only in marine birds), and it is able to utilize effectively the water in its prey. Behavioral modifications include reducing its activity by 50 percent during the heat of midday.

Desert bighorn sheep (*Ovis canadensis nelsoni*) do not drink water in the winter. They obtain all of the water they need from the vegetation they eat. In the summer they must drink about every three days. If water is not available, then the bighorn changes its behavior to rest during daylight hours and feed at night. Since they must rely on plants to supply all their water, they select succulent plants and the tender young pads of prickly pear (after scraping off the thorns with their hooves).

Here are three of the other **physiological** and **behavioral** adaptations for minimizing water loss:

physiological the basic activities that occur in the cells and tissues of an animal

behavioral relating to actions or a series of actions as a response to stimuli

- Many animals are active only at night. Others are crepuscular (active only at dusk and dawn);
- A few desert animals enter a period of dormancy during the heat of summer. These include the round-tailed ground squirrel and several species of desert toads; and
- Birds and reptiles excrete **uric acid** in the form of a semi-solid paste.

uric acid an insoluble form of nitrogenous waste excreted by many different types of animals

Of all the adaptations shared by desert-dwelling animals, the most amazing must be the kangaroo rat's ability to chemically synthesize water. Wild kangaroo rats get by on nothing but dry seeds. They do not drink water even if it is available. So the kangaroo rat is not practicing efficient water economy: it simply does not need to drink water. However, the kangaroo rat must have water in its blood and tissues just like other animals and will die from dehydration if the water in its tissues is deficient. The kangaroo rat gets the water it needs exclusively from digestion of carbohydrates. All animals produce some water, the water of metabolism, this way. But the kangaroo rat metabolizes all the water it ever needs. SEE ALSO DIURNAL; NOCTURNAL.

Elliot Richmond

Bibliography

Burt, William Henry, and Richard Phillip Grossenheider. *The Peterson Field Guide Series: A Field Guide to the Mammals*, edited by R. A. Peterson. Boston: Houghton Mifflin, Company, 1976.

Hoffmeister, Donald Frederick. *Mammals of Arizona.* Tucson: University of Arizona Press, 1986.

Findley, James S., et al. *Mammals of New Mexico.* Albuquerque: University of New Mexico Press, 1975.

Findley, James S. *The Natural History of New Mexican Mammals.* Albuquerque: University of New Mexico Press, 1987.

Krutch, Joseph Wood. *The Voice of the Desert: A Naturalist's Interpretation.* New York: William Sloan Associates, 1962.

MacMahon, James A. *The Audubon Society Nature Guides: Deserts.* New York: Alfred A. Knopf, 1985.

MacMillen, R. E., and E. A. Christopher. "The Water Relations of Two Populations of Non-captive Desert Rodents." In N. F. Hadley ed., *Environmental Physiology of Desert Organisms.* New York: Dowden, Hutchison, and Ross, 1975.

Nowak, Ronald M. *Walker's Mammals of the World*, 5th ed. 2 vols. Baltimore: Johns Hopkins University Press, 1991.

Whales

See Morphological Evolution in Whales.

Wild Game Manager

A wild game manager oversees wildlife species of game (animals hunted for sport) in their **habitats**, the natural areas where they live. Game includes animals such as deer, elk, wild pigs, duck, geese, and fish. A wild game manager may work for the private sector at sporting clubs or large ranches. Wild game managers may also work for the government (state or federal). They

habitats physical locations where an organism lives in an ecosystem

These game wardens tag a white-tailed fawn for population research studies.

populations groups of individuals of one species that live in the same geographic area

may be involved in establishing hunting and fishing seasons and regulations. As hunting and fishing on private land become more and more profitable for landowners, there will be more job opportunities in this sector.

Wild game managers make certain that the animals are in good health. They monitor **populations** to see if there are threatening diseases. They may collect population data to ensure that the game exist in sufficient numbers to be safely hunted without being wiped out. Depending on the size of a population, the manager may recommend more or less hunting in a particular season.

Managers study the animals' habitats to see if they are being negatively affected by human activities. This career demands excellent physical condition since the work is outdoors in all kinds of weather. Duties may be difficult, and work hours may be long. A wild game manager may work in remote areas where survival and practical skills are important. The job demands working with people as well as animals. A wild game manager should therefore have good communication skills. Wild game managers should be good at completing tasks on their own and making decisions.

Those who want to work in the field of wild game management can start preparing for this career in high school by taking courses in science, chemistry, math, computers, and English. Outdoor activities such as camping, hunting, fishing, and wildlife photography provide valuable knowledge and experience regarding wildlife and the environment. A college education (bachelor's degree at the minimum) is normally required. In college, potential wild game managers should take courses in the physical and biological sciences, as well as English, statistics, geography, economics, and computers. College training should be supplemented with practical experience. Many students spend their summer months working on a farm or ranch, or working with wildlife, parks, or outdoor recreational agencies.

Denise Prendergast

Bibliography

Cook, John R., Jr., president, and Kevin Doyle, ed. *The Complete Guide to Environmental Careers in the 21st Century.* Covelo, CA: Island Press, 1999.

Internet Resources

Colorado Division of Wildlife Department of Natural Resources. <http://www.dnr.state.co.us/wildlife/about/careers.htm>.

Wildlife Biologist

A career in wildlife biology may consist of conducting research through a university, zoo, or science museum or of working for the government or private corporations. When based out of an academic organization, wildlife biologists dedicate their time to modeling the lives and interactions of particular species or particular environments. Governmental wildlife biologists make recommendations on new legislation that may affect the survival of endangered animals or environments. Wildlife management administrators oversee the running of state and national parks. Governments of countries that strongly rely on **ecotourism** employ wildlife biologists and environmental technicians to create tourist-friendly parks or to reconstruct environments that were damaged in the past. In work for business and corporations, wildlife biologists test the effects of factory pollutants on the environment, advise businesses on where to build new structures, and sometimes actively monitor wildlife preserves located on corporation property.

ecotourism tourism that involves travel to areas of ecological or natural interest, usually with a naturalist guide

Wildlife biologists must be able to calculate and predict population sizes, migration patterns, birth and death rates, and environmental interactions, all of which necessitate a strong background in mathematics, physics, and computer science. Most positions offered in this field require a strong background in natural sciences, with a graduate degree in wildlife biology or fishery. Recommended course work includes habitat design, wild bird management, large mammal conservation, wildlife **ecology**, and fisheries ecology. Courses in wild animal veterinary science may also be valuable for some positions. To pursue a career in wildlife biology, it is best to begin early: volunteer at a local zoo, veterinary clinic, or landscaping firm. Seek out wildlife researchers from among college professors and offer to help them with their research. In addition to mathematics and science classes, take

ecology the study of how organisms interact with their environment

A group of wildlife biologists examine a tranquilized giant panda.

classes in public speaking, economics, or political science. A bachelor's degree can be followed by graduate studies, and by volunteer or salaried work in a national park.

Rebecca M. Steinberg

Bibliography

Leopold, Aldo. *Game Management.* Boulder, CO: Johnson Books, 2000.

Maynard, Thane, and Jane Goodall. *Working with Wildlife: A Guide to Careers in the Animal World.* New York: Franklin Watts, 1999.

Wildlife Photographer

Wildlife photography is a loosely-defined profession which demands a passion for nature and art. Wildlife photographers make a career of traveling to remote areas and taking pictures of wild animals and natural scenery.

Wildlife photography began as a hobby of safari hunters, in the early 1900s, who found photographs to be less violent and more permanent reminders of their adventures than the slaying and stuffing of a wild animal. Modern photographers often began as artists, biologists, or park rangers, and taught themselves the technical aspects of the field.

Classes in wildlife photography are offered at colleges and art schools around the world, and many organized safaris and expeditions also provide training and photographic opportunities. Wildlife photographs can be sold to greeting card companies, printed as posters, sold as stock photography, collected into a book, displayed in an art gallery, or sold to a magazine. Ad-

These king penguins pose for a wildlife photographer.

ditionally, some wildlife photographers are hired full-time by nature magazines.

Wildlife photography is a demanding and competitive vocation. Traveling to isolated areas is expensive, as is the photographic equipment necessary for professional quality photos. The work itself is physically and mentally taxing, requiring patience and perfectionism. Because wild animals are wary of humans, wildlife photographers must use a *hide* to get close enough for a clear photograph. Hides are made of anything that conceals form and movement, such as a tiny tent with an opening for the camera, or a car with tinted windows.

Even with a hide, the photographer may have only several seconds in which to take the photo, due to the unpredictability of wild animals, making agility and patience necessary traits. Persistence is also useful. Obtaining special permission to visit national parks in restricted regions or after hours is often essential, although it can be very difficult to accomplish. In addition, the photographer must research the photographic site to understand local lighting conditions, weather, the habits of local wildlife, and the customs of local peoples. Only the best wildlife photographers earn enough money to support themselves entirely with their photographs.

Rebecca M. Steinberg

Bibliography

Shaw, John. *The Nature Photographer's Complete Guide to Nature Photography*. New York: Garsington, 2000.

Angel, Heather. *Natural Visions: Creative Tips for Wildlife Photography*. New York: Amphoto Books, 2000.

Wilson, Edward Osborne

American Biologist
1929–

Edward O. Wilson developed the field of sociobiology.

Edward Osborne Wilson was born in Birmingham, Alabama. Wilson originated the field of science called sociobiology, which argues that social animals, including humans, behave mainly according to rules written in their **genes**. Wilson is also considered the world's leading expert on ants.

genes segments of DNA located on chromosomes that direct protein production

Wilson's interest in biology began in childhood. He attended the University of Alabama, obtaining a bachelor of science degree in 1949 and a master of science degree in 1950. After obtaining his Ph.D. at Harvard University in 1955, he joined the Harvard faculty. He became a professor in 1964 and curator of entomology (the study of ants) at the university's Museum of Comparative Zoology in 1971.

Wilson has written many important books. In 1971 he published *The Insect Societies*, his definitive work on ants and other social insects. His second major work, *Sociobiology: The New Synthesis* (1975), presented his theories about the biological basis of social behavior. These ideas proved controversial among some scientists and made Wilson famous. His theories caused scientists to discuss and further research the long-standing argument about "nature versus nurture." This is the debate over how much of human behavior is determined by **genetics** and how much by the environment in which a person is raised. Two of Wilson's books won a Pulitzer Prize for general nonfiction: *On Human Nature* in 1979, and *The Ants* (cowritten with Bert Holldobler) in 1991. Wilson's other books include *The Diversity of Life* (1992) and his autobiography, *Naturalist* (1994).

genetics the branch of biology that studies heredity

Wilson has made many important scientific discoveries and contributions to biology. He was the first to determine that ants communicate mainly through the exchange of chemical substances called **pheromones**. Wilson worked with the American scientist Robert MacArthur to develop a theory on **populations** of species living on islands. Working with another scientist, W. L. Brown, Wilson developed the concept of **character displacement**. This is the theory that when two closely related species first come into contact, they undergo relatively rapid evolutionary changes. This ensures that they will not have to compete fiercely with one another and that they will not interbreed.

pheromones small, volatile chemicals that act as signals between animals that influence physiology or behavior

populations groups of individuals of one species that live in the same geographic area

character displacement a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

Alarmed by the loss of species throughout the world, Wilson has taken an active role in alerting policymakers and the public about this crisis. Wilson argues that humans are causing the greatest mass extinction of plant and animal species since the extinction of the dinosaurs 65 million years ago. He is an outspoken and active advocate of conserving Earth's resources.

Wilson has received many scientific awards throughout his distinguished career. He was named by Time magazine as one of America's twenty-five most influential people of the twentieth century. He was awarded the National Medal of Science by President Jimmy Carter in 1977. In 1990 he shared Sweden's Crafoord Prize with the American biologist Paul Ehrlich. In 1996, Wilson was named by Time magazine as one of America's twenty-five most influential people of the twentieth century.

Denise Prendergast

Bibliography

Daintith, John, Sarah Mitchell, Elizabeth Tootil, and Derek Jertson. *Biographical Encyclopedia of Scientists*, vol. 2, 2nd ed. Bristol, U.K.: Institute of Physics Publishing, 1994.

Wilson, Edward O. *The Diversity of Life*. Cambridge, MA: Belknap Press, 1992.

Internet Resources

"Edward Osborne Wilson." *Sociobiology: The New Synthesis*. <http://www.2think.org/sociobiology.shtml>.

Xenopus

X

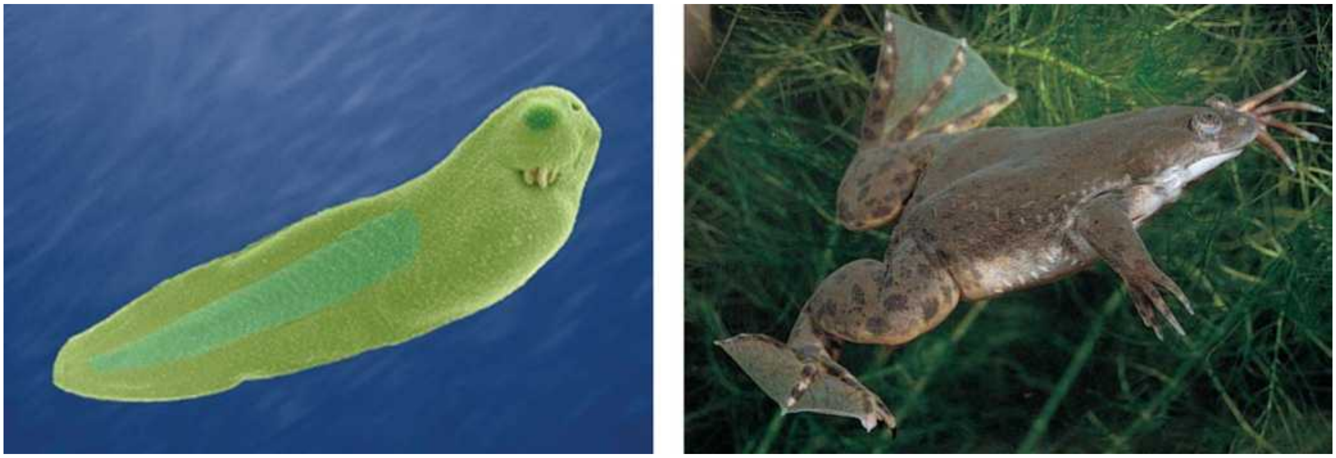
The South African clawed frog *Xenopus laevis* is a flat, smooth frog with lidless eyes and webbed feet (in Latin, *xenopus* means "peculiar foot," and *laevis* means "smooth"). The lateral-line system, which consists of sensory hair cells covering the body that are used to detect movements in the water column, persists in adults. The lidless eyes, webbed feet, and maintenance of the lateral-line system in the adult stage are all adaptations to these frogs' lifelong environment. *Xenopus* can live in virtually any amount or quality of water, a necessary adaptation when ponds begin to dry up and become stagnant in the summer. They may also **aestivate** in the mud of dried up ponds, shutting down most of their life processes until more favorable (i.e., wet) conditions arise. These frogs can survive for several months without food or water in aestivation. *Xenopus* are not entirely out of their element on land, either. They have been known to migrate overland in times of drought and to move from overcrowded ponds to colonize new areas at the onset of torrential rains.

aestivate a state of lowered metabolism and activity that permits survival during hot and dry conditions

Xenopus has become a model organism for studies of vertebrate development, and can be found in labs around the world. In fact, escapees have established themselves in a number of wild areas in the Americas. Several characteristics make *Xenopus* amenable to laboratory experimentation. First, they are **aquatic** and can complete their entire life cycle in water. Thus, unlike most amphibians, they can be kept in water tanks instead of **terraria**, which are harder to maintain. Second, they are hardy animals. They eat virtually any type of food and are not prone to disease. Third, they are

aquatic living in water

terraria a small enclosure or closed container in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed



Comparison of the scanning electron micrograph of the African clawed frog tadpole (left) to the adult frog demonstrates the significant changes undergone during metamorphosis.

fertilization the fusion of male and female gametes

detritus dead organic matter

metamorphosis a drastic change from a larva to an adult

extremely fertile and have a relatively short life cycle. Females can lay up to 1,000 eggs at one spawning, and these eggs can develop into reproductive adults within one year.

The life cycle of *Xenopus*, as in most other frogs, is made up of three main stages: fertilized egg, tadpole, and adult frog. Mating occurs in fresh water with the male clinging to the back of the larger female. **Fertilization** occurs externally—the female lays her eggs in the water while the male releases sperm over them. The tadpoles hatch within three days and start to filter-feed from **detritus** in the water. After about two months, the tadpoles undergo **metamorphosis**, a marked structural transformation in which the legs sprout and the tail is lost. Internally, the skeleton of the head changes shape and teeth appear; and the circulatory, digestive, immune, and other systems are differentiated. Adult *Xenopus* use the claws of their front forelimbs to tear up food which they then manipulate into their tongueless mouths.

hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

Xenopus first gained widespread use in labs when researchers discovered that they could be used in human pregnancy tests. The injection of a small amount of urine from a pregnant female under the skin of female *Xenopus* causes them to lay eggs. In fact, an injection of reproductive **hormones** from many vertebrate species causes the same reaction. This proved to be an extremely useful trait, as biologists could now induce egg laying to study the embryology and development of *Xenopus* eggs at any time of year.

vertebrates animals with a backbone

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

Another reason that *Xenopus* are useful in labs is that the large size of their embryos and cells makes visualization of the various developmental stages significantly easier than in most other **vertebrates**. Various staining and labeling techniques are used to follow the cellular and molecular changes occurring in the developing embryo. For example, specific tissues of the embryo may be stained, and then several of these stained embryos may be collected at later life stages. To determine the distribution of this tissue in the embryo, histological sections, or thin slices of embryos from each life stage, are made and observed for staining patterns. In this way, scientists can follow the three-dimensional migration and **differentiation** of a particular tissue type over time.

Scientists use similar techniques to follow spatial and temporal gene **transcription** patterns. For example, to determine when the embryo begins making its own mRNA (and thus its own proteins), rather than relying on maternal mRNA, scientists inject radioactively labeled mRNA **precursors** into developing embryos. As before, sections of the embryos are then made and analyzed for mature radioactive mRNAs. Scientists can also follow the function of a particular gene over time by injecting developing embryos with radioactive probes that bind specifically to mRNA of that gene. This is a very important technique as it lends insight into which **genes** control which developmental processes.

transcription process where enzymes are used to make an RNA copy of a strand of DNA

precursors a substance that give rise to a useful substance

genes segments of DNA located on chromosomes that direct protein production

Probably the most striking aspect of *Xenopus* development is metamorphosis. The tadpole and adult stages have fundamentally different **body plans** and life styles. This leads to the question: How are the cells and tissues of the larval stage rearranged and redistributed to form the adult stage, at the same time allowing the developing organism to maintain necessary life functions?

body plan the overall organization of an animals body

Metamorphosis is initiated by hormones released from the pituitary and thyroid glands. One hormone in particular, thyroxine, affects several tissues and organs of the larvae. In the brain, thyroxine causes most cells to undergo **mitosis**, and the brain becomes larger. However, in the hindbrain, giant Mauthner's cells, which extend down the **spinal chord** and allow the rapid darting movements tadpoles use to avoid predation, degenerate when exposed to thyroxine. Similarly, thyroxine causes the deposition of collagen, a fibrous skin protein, in most areas of the body, but causes the breakdown of collagen in the regressing tail. Thyroxine also causes the initiation of bone development in the limbs.

mitosis a type of cell division that results in two identical daughter cells from a single parent cell

spinal cord a thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

Thyroxine sets off a cascade of developments in the maturing frog. The **resorption** of the tadpole's tail begins with the resorption of the **notochord** from the tip of the tail to the base. Next the vertebral rudiments and **connective tissue** that surrounded the notochord degenerate. Finally the tail muscles are resorbed and disappear rapidly. This may be because the organism does not want to lose the tadpole form of locomotion (its tail) before the adult form of locomotion (webbed feet) is fully developed. Once the webbed feet are developed, the tail becomes a hindrance and is quickly lost.

resorption absorbing materials that are already in the body

notochord a rod of cartilage that runs down the back of Chordates

connective tissue cells that make up bones, blood, ligaments, and tendons

The appearance of limbs occurs in the following manner. The hind legs start to bud off just before the front limbs, and shortly thereafter are innervated by new nerve cells. The pelvic girdle (the hip) ossifies first, then the bones of the legs ossify one by one outward from the body. The forelimbs, however, ossify before the shoulder girdle is completed. This is possibly an adaptation which allows filter feeding from the mouth through the gills to continue during development of the forelimbs.

Other than metamorphosis, another unique feature of amphibians such as *Xenopus* is their ability to regenerate their limbs, tail, and many internal organs. If a limb is severed, dead cells at the site are quickly removed through the blood stream. Then nearby **mesodermal** cells, cells with specialized functions in connective or other tissues, multiply and "dedifferentiate" so that they can act as precursors for the new types of cells necessary to form

mesoderm the middle layer of cells in embryonic cells

a complete limb. In general, the ability to regenerate body parts declines over time, especially after metamorphosis is completed.

Todd A. Schlenke

Bibliography

Bernardini, Giovanni, M. Prati, E. Bonetti, and G. Scari. *Atlas of* Xenopus *Development.* New York: Springer-Verlag, 1999.

Deuchar, Elizabeth M. Xenopus: *The South African Clawed Frog.* New York: John Wiley and Sons, 1975.

Duellman, William E., and Linda Trueb. *Biology of Amphibians.* Baltimore: Johns Hopkins University Press, 1986.

Nieuwkoop, Pieter D., and Jacob Faber, eds. *Normal Table of* Xenopus *Development (Daudin): A Systematical and Chronological Survey of the Development from the Fertilized Egg until the End of Metamorphosis*, 2nd ed. Amsterdam: North-Holland Publishing Company, 1975.

Tinsley, R. C., and H. R. Kobel. *The Biology of* Xenopus. Oxford, U.K.: Oxford University Press, 1996.

Zoological Parks

As far back as the historical record goes, there is evidence of people keeping wild animals in cages. During the Middle Ages in Europe, rare and exotic animals, and occasionally even foreign natives, were displayed in traveling caravans called menageries. Stationary collections of animals then developed, where the captives were kept in small dark cells, usually alone, with no privacy and nothing to do. They frequently died in a short time and were replaced with new animals captured in the wild. Private zoos on the estates of the wealthy were also popular, with animal dealers supplying birds, reptiles, and mammals from around the world. Often as many as a dozen animals would be killed in captivity or in transport for every one that survived to be sold.

Protected Environments

habitat physical location where an organism lives in an ecosystem

In the late 1800s, a German animal dealer, Carl Hagenbeck, first envisioned the modern zoo. His dream was to create a spacious zoological park where animals could be seen in something resembling their native **habitat**. His park was built in 1907, near Stellingen, Germany, with no fences. Different species such as lions and zebras were kept in the same enclosure, separated by deep moats. Despite commercial popularity, Hagenbeck's ideas did not catch on until the mid-1900s. Animal behaviorists began to emphasize the importance of giving captive animals enough room for some activity and allowing social animals such as monkeys to be in the same cage. They concluded that animals kept in such environments would be healthier, more active, and more interesting to the paying public.

Worldwide, unspoiled habitats began disappearing at an alarming rate by the late twentieth century, as did their inhabitants; more and more wild animals became increasingly rare. Many larger zoos transformed from competing fiefdoms into cooperating members of zoological organizations whose mission became wildlife conservation, research, education of the public, and captive breeding of endangered species.

Proboscis monkeys at the Bronx Zoo in New York. Many zoos try to incorporate native flora into habitat design.

Disagreements Over the Best Strategies

As **populations** of some species plummet because of habitat destruction, illegal **poaching**, **pesticides**, and pollution of air and water, conservationists in the United States divide along two lines of thought. The first, which includes the Sierra Club and Friends of the Earth, believes that animals must be protected and saved in their own habitat, that a species is not saved unless it continues to exist in the wild. The second group is led by the U.S. Fish and Wildlife Service, the National Audubon Society, and the American Association of Zoological Parks and Aquariums. They believe that endangered species must be brought into zoos and wildlife parks where new generations can be raised, frequently with much human intervention, and then released back into the wild. Many zoos participate in species survival plans (SSPs), which coordinate breeding efforts for more than fifty species, including cheetahs, rhinoceros, Asian elephants, orangutans, pandas, Puerto Rican crested toads, tamarins, zebras, tapirs, lemurs and Komodo dragons. The long-range goal of the SSP program is to build up large enough populations so that these animals can be returned to their natural habitat. A

populations groups of individuals of one species that live in the same geographic area

poaching hunting game outside of hunting season or by using illegal means

pesticides substances that control the spread of harmful or destructive organisms central computer system, the International Species Inventory System, keeps detailed records of the genetic background of the animals in the program. In order to avoid **inbreeding depression**, which can cause weakened resistance to disease and infertility, animals may be shipped from one part of the world to another to arrange genetically diverse matches. Ultimately, even this tiny gene pool will need to be replenished from the wild to stay vital.

inbreeding depression the loss of fitness due to breeding with close relatives

Captive breeding programs have had mixed results. Some species respond well and others, for reasons not yet understood, but probably related to psychological stress, refuse to breed in captivity or, after birth, abandon their offspring.

New Ideas for Zoological Parks

At the beginning of the twenty-first century, zoos are moving in several directions. As local wild habitats vanish, some small zoos are specializing in local wildlife, providing a glimpse of how indigenous plants and animals interact. Large wildlife parks incorporate hundreds of acres of bogs, woods, meadows, and grasslands and feature native and exotic species that thrive in local conditions. These parks are frequently driven through or have walking trails where people are inobtrusively separated from the animals.

Some zoos have become "bioparks," using aerial walkways, watery moats, and one-way security glass to offer visitors the opportunity to see animals in something resembling natural conditions. These immersion exhibits are sometimes huge re-creations of specific **ecosystems**. Amazonia, at the National Zoo in Washington, D.C., is a 1,400-square-meter (15,000-square-foot) dome filled with thousands of tropical plants, fish, birds, insects, reptiles, amphibians, and mammals. With careful attention to temperature and humidity, it offers a taste of a real tropical jungle. Other immersion exhibits include replicas of Antarctic penguin islands and sandy deserts. Moonlight houses have also become common in many zoos. In these buildings day and night are reversed. **Infrared** lighting allows people to view nocturnal species who rest during the day and are active at night. In large enclosures that have artificial caves and tunnels, bats fly about in search of fruit, nectar, and insects. Desert animals emerge from burrows, coyotes stalk and howl, raccoons hunt for food to wash beside streams, and crocodiles and alligators wallow in marshes before setting off in search of dinner. As people live increasingly urbanized lives, they are looking for zoos to provide a way to get closer to nature and an experience of the wild.

ecosystems self-sustaining collections of organisms and their environments

infrared an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red, heat is carried on infrared waves

Modern zoos are extremely expensive operations. It is a massive undertaking to meet the daily nutritional needs of hundreds of animals of different species. The food must be as appropriate as possible to each animal and delivered in a way that mimics its natural eating habits. Carnivores need whole animals or large chunks of meat and bone. Primates need to search out fruits, nuts, and seeds that have been hidden in their enclosures. Each elephant requires 45 kilograms (100 pounds) of grass and 14 kilograms (30 pounds) of vegetables a day. Live worms, crickets, guppies, lizards, and mice are all kept on hand for specialized appetites. And some **herbivores** need specific leaves from their homes: acacia for giraffes, eucalyptus for koalas, bamboo for pandas, and hibiscus for leaf-eating monkeys. Abandoned or orphaned infants require precise formulas and extensive care. Some baby birds need to be fed every few minutes to survive.

herbivores animals who eat plants only

In nature, sick or injured animals die swiftly. In zoos, each animal represents such a costly investment that most major zoos have full-time medical teams to diagnose and treat disease and provide preventive health care. Tigers and gorillas get dental checks. Females are tested for fertility and carefully monitored during pregnancy. New animals and sick ones are quarantined, and surgeries are performed on broken limbs or tumors.

> The Zoological Society of San Diego has developed a different and engaging interface for accessing information on its web site. This new site is titled "E-Zoo," and is available at http://www.sandiegozoo.org/virtualzoo/homepage.html. Between the interactive games, the videos, and the e-postcards, the Zoological Society has helped to make learning about animals fun from any location—even your desk chair.

Naturalistic zoo exhibits attempt to recreate the environment of a given species. This involves scientists, designers, architects, and curators. The exhibit must take into account every detail of each animal's life: breeding, social interaction, exercise, and the food gathering method for which the animal is genetically designed. The insects, plants, and geologic features need to be recreated. Careful regulation of temperature, humidity, and the length and variation of daylight needs to be maintained. The amount of effort involved in recreating even a small ecosystem is beyond the capability of all but the largest zoos.

Although one of the stated goals of zoos is to replenish wild populations, almost no animals have ever been returned to their native habitat. Restoring wild animals is difficult, expensive, and requires the cooperation of the local people to succeed. Craig Hoover, program manager of the Wildlife Trade Monitoring Arm of the World Wildlife Fund, stated that "Zoos have been very successful breeding grounds for many species. But what do you do with those animals when they're not babies anymore? Certainly the open market is the best place to sell them" (Merritt 1991, p. 32). And dozens of major zoos admit to supplying the multibillion dollar a year trade in exotic animals, where rare and endangered species wind up in the private collections of celebrities or as trophy targets on profitable hunting ranches.

Critics of zoos contend that while zoos justify their existence by claiming to educate children, they are teaching the wrong lesson: that it is acceptable to keep wild animals in captivity. Nor is warehousing animals the answer to saving them from extinction. The ultimate salvation of endangered species is in protecting their natural habitats. Perhaps the future of zoos lies in the vision of the Worldlife Center in London, a high-tech zoo with no animals. Visitors observe animals via live satellite links with the Amazon rain forest, the Great Barrier Reef off Australia, and the African savanna and jungle. Rather than putting money into all the infrastructure of a modern zoo, it goes directly to habitat protection to developing nonprofit sanctuaries where hunters and poachers are kept at bay and through which the local people are given an economic incentive to participate in wildlife preservation.

The greatest contribution that zoos may have made is to highlight how little humans understand the incredibly intricate mechanisms of life on Earth. Human technology, while capable of destroying vast ecosystems, is insufficient to create and maintain them. Zoos began as a symbol of human conquest of wild animals. Perhaps modern zoos can serve as sanctuaries for animals rescued from ill treatment and as reminders to be more respectful of nature and the place of humans in it. SEE ALSO Habitat Loss; Habitat Restoration; Natural Selection; Populations; Selective Breeding.

Nancy Weaver

Bibliography

Challindor, David, and Michael H. Robinson. *Zoo Animals: A Smithsonian Guide.* New York: Macmillan, 1995.

Merritt, Clifton. "Low Class, No Class Scumballs." *Animals Agenda* 11, no. 10 (1991):32.

Zoologist

Zoology is a branch of biology that involves the study of animals. Zoology is a very broad field; zoologists study subjects ranging from single-celled organisms to the behavior of groups of animals. Some zoologists study the biology of a particular animal, others study the structure and function of the bodies of animals. Some zoologists are interested in **heredity**, how the characteristics of animals are passed from one generation to the next. Others study the way animals interact with other animals or their surrounding environment. Many zoologists are classified by the animal they study. For example, herpetologists study reptiles and amphibians. Entomologists specialize in insects. Ornithologists study birds. Mammalogists specialize in mammals.

heredity the passing on of characteristics from parents to offspring

Many zoologists are involved in research and development. Some conduct basic research to expand knowledge about animals. Others may conduct applied research, which is used to directly benefit humans. Applied research may be used to develop new medicines, make livestock more resistant to disease, control pests, or help the environment. Researchers may be employed at universities, government agencies, nonprofit organizations, scientific institutions, or private industries. Many zoologists work at zoos, aquariums, and museums. Research can involve fieldwork, laboratory work, and writing up the results for publication. Most zoologists spend only two to eight weeks in the field each year. Junior scientists spend more time in the field than senior scientists, observing animals and collecting data. Senior scientists spend much of their time coordinating research, overseeing junior staff, and writing grant proposals, or obtaining funds in some other way. Zoologists involved in research need at least a bachelor's degree. Advanced degrees (master's and Ph.D.) can also be very helpful.

This zoologist weighs a polar bear cub.

The following types of companies/organizations may employ zoologists:

- animal hospitals
- pet stores
- food companies
- biotechnology firms
- humane societies
- pharmaceutical companies
- chemical companies
- medical laboratories
- clinics/hospitals
- research laboratories
- veterinarian schools

- national parks
- dog-training schools
- natural history museums
- environmental companies
- veterinarian-supply houses
- pest-control agencies
- government agencies

Some zoologists are primarily teachers. They can teach at the high-school level or at the university/college level. Teaching at the high-school level requires a bachelor's degree and state certification. Teaching at the university level generally requires a doctoral (Ph.D.) degree.

At the high-school level, persons interested in becoming zoologists should study mathematics, chemistry, physics, biology, English, writing, and computer studies. In college, persons obtaining a bachelor's degree in zoology will study these same types of subjects. In graduate school, a student specializes in a particular area of interest. SEE ALSO Animal.

Denise Prendergast

Bibliography

Cosgrove, Holli R., ed. *Encyclopedia of Careers and Vocational Guidance*, 11th ed. Chicago: Ferguson Publishing Company, 2000.

Zooplankton

The word "plankton" refers to the floating marine organisms that live on the surface of oceans. These organisms can be plants or animals. The plant forms are microscopic algae whose photosynthesis reactions provide the Earth's atmosphere with the majority of its oxygen. The other type of plankton, composed of tiny animals, is called zooplankton.

Zooplankton is made up of hundreds of thousands of different species of animals. Some are baby or larval forms of the animals while others spend their whole life as free-floating organisms. The entire scope of species of zooplankton is enough for scientists to have identified whole communities of these organisms. These communities are very dynamic in that they change their structure and **populations** on a seasonal basis.

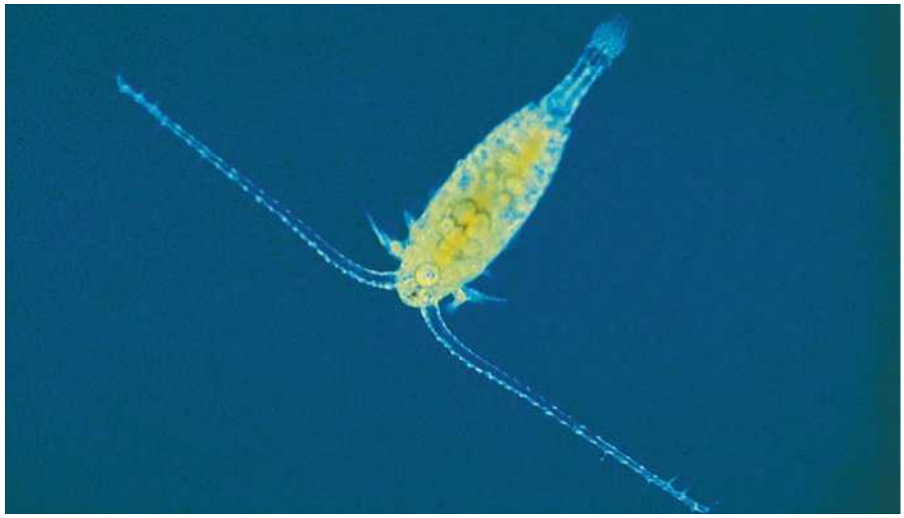
Many members of a zooplankton community begin their lives in **estuaries** where crabs, fishes, and a whole host of various **invertebrates** come to breed. The calm and relatively shallow waters of an estuary provide a safe place for eggs to survive and hatch. Upon hatching, the tiny larvae are too small to succumb to the effects of gravity in the water and so begin their journeys as floating animals.

populations groups of individuals of one species that live in the same geographic area

estuaries an area of brackish water where a river meets the ocean

invertebrates animals without a backbone

In many species of zooplankton, the larval forms look nothing like the adults they will become. A remarkable example is the flounder fish. It starts its life as a small larval floating form that looks very much like a common fish. It drifts in the water for about forty or forty-five days until it begins its transformation into a bottom-dwelling flat adult. While drifting in the



A living crustacea copepoda.

ocean it feeds on other plankton and begins to grow until it begins its juvenile phase. As a juvenile, it drifts to the ocean bottom and flattens out, with one of its eyes rotating around its head to sit next to the other eye. As a bottom-dwelling adult it becomes a flat fish with eyes on the upper surface of its body. Then it is ready to produce more planktonic larvae.

Many members of the zooplankton community feed on other members of the population, and in turn become the meals of other larger predators. Eventually, the whole zooplankton community becomes the bottom of a food chain for an entire food web stretching from the smallest fish to the largest whale. Many of the ocean's largest animals feed on zooplankton. Many whales have feeding structures called **baleen** that filter the zooplankton from the water. In the polar regions, a small component of the zooplankton community called **krill** is the basic diet of the many summer-feeding whales.

baleen fringed filter plates that hang from the roof of a whale's mouth

krill an order of crustaceans that serves a food source for many fish, whales, and birds

One of the benefits of becoming a pelagic, or open ocean-dwelling, organism for a specific population is that the drifting currents move the offspring from one place to another. This ensures species distribution, which is critical to the survival of many species. It keeps genetic diversity high and populations healthy.

The waterborne distribution of zooplankton helps its population survive harsh environmental conditions such as freezing, high heat, large storms, and other severe natural phenomena. Because riding the ocean currents distributes many species worldwide, only small portions of a population may be seriously affected by these conditions.

For many planktonic forms, their lifestyleas organisms suspended on the ocean surface, means that they can avoid unfavorable conditions in the deeper regions of the water column. Those species that eventually drift to the bottom and complete their **metamorphosis** avoid some forms of predation until they are of a suitable size or form to avoid attack.

metamorphosis a drastic change from a larva to an adult

One of the concerns raised by the increasing depletion of the ozone layer is how the increased influx of ultraviolet radiation that it causes will affect zooplankton. Because they are the basis of the food chain for a great many animals in lakes and oceans, many scientists and others are concerned that the tiny covering around these larval animals may not be strong enough to withstand the impact of increased radiation. As in all food web chains, the zooplankton provide a foundation for so many other and larger food species that some forms of higher predators may be seriously impacted.

Until the increasing ozone loss is curbed, the protection of estuaries, deltas, and other coastal planktonic breeding grounds is crucial for the continued production of zooplankton. More and more, scientists are discovering how important zooplankton are for the health of the marine ecosystems. SEE ALSO Food Web; Plankton.

Brook Ellen Hall

Bibliography

Pechnik, J. *Biology of the Invertebrates.* Boston: Prindle, Weber, & Schmidt, 1985.

Nybakken, J. *Marine Biology: an Ecological Approach.* New York: Harper & Row, 1988.

Moyle, P., and J. Chech Jr. *Fishes: An Introduction to Icthyology.* Upper Saddle River, NJ: Prentice Hall, 1996.

Photo and Line Art Credits

The illustrations and tables featured in Animal Sciences were created by GGS Information Services. The photographs appearing in the text were reproduced by permission of the following sources:

Volume One

Acoustic Signals (**4**): Zig Leszczynski/Animals Animals; *Adaptation* (**7**): JLM Visuals, Ken Cole/Animals Animals; *African Cichlid Fish* (**9**): Gerard Lacz/Animals Animals; *Aggression* (**11**): Lynn Stone/Animals Animals; *Agnatha* (**14**): Omikron, National Audobon Society Collection/Photo Researchers, Inc.; *Allometry* (**16**): Redrawn from Scott Gilbert; *Allometry* (**15**): Redrawn from Scott Gilbert; *Altruism* (**18**): Robert J. Huffman/Field Mark Publications; *Amphibia* (**20**): Robert J. Huffman/Field Mark Publications; *Animal Rights* (**25**): AP/Wide World Photos; *Animal Testing* (**29**): Yann Arthus-Bertrand/Corbis; *Annelida* (**31**): E. R. Degginger/Animals Animals; *Antibody* (**34**): Redrawn from Hans and Cassady; *Antlers and Horns* (**35**): Kennan Ward/Corbis; *Apiculture* (**37**): Breck P. Kent/Animals Animals; *Aposematism* (**39**): R. Andrew Odum, Toledo Zoological Society; *Aquaculture* (**42**): David Samuel Robbins/Corbis; *Aristotle* (**45**): UPI/Bettmann Newsphotos/Corbis; *Arthropoda* (**47**): Dr. Dennis Kunkel/Phototake; *Arthropoda* (**50**): JLM Visuals; *Aves* (**53**): Joe McDonald/Animals Animals; *Bailey, Florence Augusta Merriam* (**57**): Courtesy of the Library of Congress; *Bates, Henry Walter* (**58**): Courtesy of the Library of Congress; *Behavior* (**60**): Ross, Edward S., Dr.; *Behavior* (**61**): Carl Purcell/Corbis; *Binomial (Linnaean System)* (**64**): Archive Photos, Inc.; *Biodiversity* (**68**): Joerg Sarback/AP/Wide World Photo; *Bioethics* (**71**): Jacques M. Chenet/Corbis; *Bioethics* (**70**): Robyn Beck/Corbis; *Biological Evolution* (**75**): Sally Morgan/Ecoscene/Corbis; *Biological Evolution* (**76**): P. Parks-OSF/Animals Animals; *Biological Pest Control* (**80**): Bill Beatty/Animals Animals; *Biomechanics* (**84**): Brad Nelson/Phototake; *Biomes* (**88**): W. Wayne Lockwood, M.D./Corbis; *Biomes* (**89**): Robert J. Huffman/Field Mark Publications; *Blood* (**98**): Richard T. Nowitz/Phototake; *Body Cavities* (**100**): Redrawn from Holt, Rinehart and Winston; *Body Cavities* (**101**): Nancy Sefton, National Audobon Society Collection/Photo Researchers, Inc.; *Body Plan* (**108**): JLM Visuals; *Bone* (**111**): CNRI/Phototake; *Burgess Shale and Ediacaran Faunas* (**113**): Lowell Laudon/JLM Visuals; *Cambrian Explosion* (**117**): Robert J. Huffman/Field Mark Publications; *Cambrian Period* (**119**): Mickey Gibson/Earth Scenes; *Camouflage* (**120**): Art Wolfe/The National Audubon Society Collection/Photo Researchers, Inc.; *Cancer* (**123**): Luis M. De La Maza/Phototake; *Carson, Rachel* (**128**): UPI/Bettmann Newsphotos/Corbis; *Cartilage* (**129**): Dr. Mary Notter/Phototake; *Cell Division* (**134**): Redrawn from Gale Research; *Cells* (**136**): Redrawn from New York Public Library Desk Reference; *Cephalization* (**139**): P. Parks-OSF/Animals Animals; *Cestoda* (**142**): Custom Medical Stock Photo, Inc.; *Chitin* (**143**): Chris McLaughlin/Animals Animals; *Chondricthyes* (**145**): Joyce and Frank Burek/Animals Animals; *Chordata* (**147**): Ralph White/Corbis; *Circadian Rhythm* (**150**): George McCarthy/Corbis; *Circulatory system* (**152**): GCA/CNRI/Phototake; *Cnidaria* (**155**): Nancy Rotenberg/Animals Animals; *Coevolution* (**161**): Robert J.

Huffman/Field Mark Publications; *Coevolution* (**159**): Michael and Patricia Fogden/Corbis; *Communication* (**165**): James E. Lloyd/Animals Animals; *Community Ecology* (**168**): Richard Baetson/U.S. Fish and Wildlife Service, Washington D.C.; *Competition* (**174**): Ross, Edward S., Dr.; *Conservation Biology* (**177**): Fred Whitehead/Animals Animals; *Constraints on Animal Development* (**179**): Robert Lubeck/Animals Animals; *Convergence* (**185**): E. R. Degginger/Animals Animals; *Courtship* (**186**): Michael Fogden/Animals Animals.

Volume Two

Cretaceous (**2**): Richard P. Jacobs/JLM Visuals; *Cultures and Animals* (**6**): Duluth Convention and Visitor's Bureau; *Cultures And Animals* (**8**): Craig Lovell/Corbis; *Darwin, Charles* (**10**): Courtesy of the Library of Congress; *DDT* (**12**): AP/Wide World Photos; *Defense* (**14**): Mark N. Boulton/The National Audubon Society Collection/Photo Researchers, Inc.; *Diamond, Jared* (**18**): AP/Wide World Photos; *Digestive System* (**22**): Roger De La Harpe/Animals Animals; *Dinosaurs* (**25**): Graves Museum of Archaeology and Natural History/AP/Wide World Photos; *Domestic Animals* (**29**): Tim Thompson/Corbis; *Dominance Hierarchy* (**32**): Tim Wright/Corbis; *Drosophila* (**34**): UPI/Bettmann Newsphotos/Corbis; *Echinodermata* (**36**): Herb Segars/Animals Animals; *Ecology* (**42**): U.S. National Aeronautics and Space Administration (NASA); *Ecosystem* (**47**): James Watt/Animals Animals; *Elton, Charles Sutherland* (): Animals Animals/©; Scott Johnson; *Embryology* (**52**): Science Pictures Limited/Corbis; *Embryonic Development* (**54**): Redrawn from Scott Gilbert; *Embryonic Development* (**59**): Redrawn from Scott Gilbert; *Endangered Species* (**62**): Vince Streano/The Stock Market; *Entomology* (**72**): Doug Wechsler/Earth Scenes; *Environmental Degradation* (**74**): George H. H. Huey/Earth Scenes; *Environmental Impact* (**78**): David Barron/Earth Scenes; *Excretory and Reproductive Systems* (**88**): Joe McDonald/Animals Animals; *Exotic Species* (**91**): C. C. Lockwood/Animals Animals; *Extinction* (**100**): Glen Smart/U.S. Fish and Wildlife Service/Washington, D.C.; *Extremophile* (**103**): TC Nature/Animals Animals; *Farming* (**105**): Tim Page/Corbis; *Feeding* (**111**): Malcolm S. Kirk/Peter Arnold, Inc.; *Feeding Strategies* (**114**): Bruce Davidson/Animals Animals; *Fertilization* (**117**): Hank Morgan/National Audobon Society Collection/Photo Researchers, Inc.; *Flight* (**122**): Zefa Germany/The Stock Market; *Foraging Strategies* (**130**): Suzanne Danegger/Photo Researchers, Inc.; *Fossey, Dian* (**131**): AP/Wide World Photos; *Fossil Fuels* (**133**): H. David Seawell/Corbis; *Functional Morphology* (**137**): Tim Davis/Photo Researchers; *Genes* (**140**): Biophoto Associates/National Audobon Society Collection/Photo Researchers, Inc.; *Genetic Engineering* (**149**): Lowell Georgia/Corbis; *Genetic Variation In A Population* (**153**): Eastcott-Momatiuk/Animals Animals; *Genetically Engineered Foods* (**156**): Lowell Georgia/Corbis; *Geneticist* (**157**): Photo Researchers, Inc.; *Genetics* (**160**): AP/Wide World Photos; *Gills* (**164**): Breck P. Kent/Animals Animals; *Global Warming* (**168**): Bernard Edmaier/Science Photo Library/Photo Researchers, Inc.; *Goodall, Jane* (**171**): AP/Wide World Photos; *Gould, Steven Jay* (**172**): Wally McNamee/Corbis; *Habitat* (**178**): Johnny Johnson/Animals Animals; *Habitat Loss* (**180**): Ecoscene/Corbis; *Habitat Loss* (**182**): Francois Gohier/National Audubon Society Collection/Photo Researchers, Inc.

Volume Three

Habitat Restoration (**3**): Eastcott-Momatiuk/Earth Scenes; *Haeckel's Law Of Recapitulation* (**5**): Courtesy of the Library of Congress; *Haldane, J. B. S.* (**6**): Courtesy of the Library of Congress; *Heterochrony* (**9**): Christian Testu/BIOS; *Home Range* (**11**): Darren Bennet/Animals Animals; *Hormones* (**17**): Barbra Leigh/Corbis; *Horse Trainer* (**19**): Jerry Cooke/Animals Animals; *Human Commensal and Mutual Organisms* (**31**): LSF OSF/Animals Animals; *Human Evolution* (**35**): John Reader/Science Photo Library/Photo Researchers, Inc.; *Human Populations* (**41**): AP/Wide World Photos; *Human–Animal Conflicts* (**28**): John Nees/Animals Animals; *HunterGatherers* (**44**): Anthone Bannister/Earth Scenes; *Hunting* (**46**): Raymond Gehman/Corbis; *Imprinting* (**50**): Robert J. Huffman/Field Mark

Publications; *Instinct* (**52**): Anup Shah/Animals Animals; *Interspecies Interactions* (**55**): JLM Visuals; *Iteroparity And Semelparity* (**58**): Kennan Ward/The Stock Market; *Jurassic* (**60**): E. R. Degginger/Earth Scenes; *Keratin* (**63**): L. Lauber-OSF/Animals Animals; *Lamarck* (**69**): Courtesy of the Library of Congress; *Leakey, Louis And Mary* (**70**): UPI/Bettmann Newsphotos/Corbis; *Learning* (**72**): Erwin and Peggy Bauer/Animals Animals; *LeviMontalcini, Rita* (**74**): AP/Wide World Photos; *Linnaeus, Carolus* (**77**): U.S. National Library of Science; *Living Fossils* (**80**): Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc.; *Locomotion* (**88**): Jeffrey L. Rotman/Corbis, Richard Alan Wood/Animals Animals, Ross, Edward S., Dr., Robert Winslow/Animals Animals; *Lorenz, Konrad* (**91**): UPI/Bettmann Newsphotos/Corbis; *Malaria* (**95**): Redrawn from Hans and Cassady; *Malthus, Thomas Robert* (**98**): Archive Photos, Inc.; *Mammalia* (**103**): Leonard Lee Rue III/Animals Animals; *Mayr, Ernst* (**106**): AP/Wide World Photos; *Mendel, Gregor* (**108**): Archive Photos, Inc.; *Mesenchyme* (**110**): Lester V. Bergman/Corbis; *Migration* (**117**): AP/Wide World Photos; *Mimicry* (**122**): Breck P. Kent/Animals Animals; *Molecular Biologist* (**126**): Philippe Plailly/National Audubon Society Collection/Photo Researchers, Inc.; *Molting* (**135**): Ross, Edward S., Dr.; *Morphological Evolution in Whales* (**137**): Bomford/T.Borrill-OSF/Animals Animals; *Mouth, Pharynx, Teeth* (**141**): H. Pooley/OSF/Animals Animals; *Muscular System* (**143**): Custom Medical Stock Photo, Inc.; *Museum Curator* (**145**): Robert J. Huffman/Field Mark Publications; *Natural Resources* (**147**): Richard Hamilton Smith/Corbis; *Nematoda* (**151**): Eric V. Grave/Photo Researchers, Inc.; *Nervous System* (**157**): Redrawn from Neil Campbell.; *Nervous System* (**155**): Secchi-Lecague/Roussel-UCLAF/CNRI/Science Photo Library/National Audubon Society Collection/Photo Researchers, Inc.; *Osteichthyes* (**169**): A. Kuiter/OSF/Animals Animals; *Parasitism* (**179**): Frank Lane Picture Agency/Corbis; *Pasteur, Louis* (**180**): Courtesy of the Library of Congress; *Peppered Moth* (**186**): Breck P. Kent/Animals Animals.

Volume 4

Permian (**2**): Richard P. Jacobs/JLM Visuals; *Pesticide* (**4**): Arthur Gloor/Earth Scenes; *Phylogenetic Relationships of Major Groups* (**6**): Redrawn from Caroline Ladhani.; *Plankton* (**12**): Douglas P. Wilson/Frank Lane Picture Agency/Corbis; *Pleistocene* (**16**): Breck P. Kent/Earth Scenes; *Pollution* (**21**): Wesley Bocxe/National Audubon Society Collection/Photo Researchers, Inc.; *Population Dynamics* (**26**): Wolfgang Kaehler/Corbis; *Populations* (**32**): JLM Visuals; *Predation* (**37**): Johnny Johnson/Animals Animals; *Primates* (**40**): Barbara Vonn Hoffmann/Animals Animals; *Reproduction, Asexual and Sexual* (): Animals Animals/©; Zig Leszczynski; *Reptilia* (**52**): Animals Animals/©; Zig Leszczynski; *Respiration* (**55**): Ron Boardman, Frank Lane Picture Agency/Corbis; *Respiratory System* (**58**): Photo Researchers, Inc.; *Rotifera* (**60**): P. Parks/OSF/Animals Animals; *Scales, Feathers, and Hair* (**62**): Dr. Dennis Kunkel/Phototake; *Selective Breeding* (**65**): George Bernard/Animals Animals; *Sense Organs* (**68**): Robert J. Huffman/Field Mark Publications; *Sexual Dimorphism* (**74**): Gregory G. Dimijian/Photo Researchers, Inc.; *Sexual Selection* (**77**): Animals Animals/©; Darren Bennett; *Shells* (**81**): Spreitzer, A.E., Mr.; *Simpson, George Gaylord* (**85**): Courtesy of the Library of Congress; *Skeletons* (**86**): E. R. Degginger/Animals Animals; *Social Animals* (**91**): G. I. Bernard/OSF/Animals Animals; *Sociality* (**95**): JLM Visuals;*Stevens, Nettie Maria* (**99**): Science Photo Library/Photo Researchers, Inc.; *Sustainable Agriculture* (**101**): Michael Gadomski/Earth Scenes; *Territoriality* (**106**): Jack Wilburn/Animals Animals; *Threatened Species* (**113**): Kenneth W. Fink/Photo Researchers, Inc.; *Tool Use* (**115**): C. Bromhall/OSF/Animals Animals; *Trematoda* (**123**): Photo Researchers, Inc.; *Triassic* (**125**): Robert J. Huffmann/Field Mark Publications; *Urochordata* (**130**): Joyce and Frank Burek/Animals Animals; *Vertebrata* (**132**): Breck P. Kent/JLM Visuals; *Veterinarian* (**134**): Peter Weiman/Animals Animals; *Viruses* (**136**): Scott Camazinr/National Audubon Society Collection/Photo Researchers, Inc.; *Vision* (**139**): J. A. L. Cooke/OSF/Animals Animals;

Vocalization (**142**): Victoria McCormick/ Animals Animals; *Von Baer's Law* (**143**): Courtesy of the Library of Congress; *Water Economy In Desert Organisms* (**147**): Langley, Cory, Mr., (**148**): Maslowski/Photo Researchers, Inc.; *Wild Game Manager* (**150**): Raymond Gehman/Corbis; *Wildlife Biologist* (**152**): Mark Stouffer/Animals Animals; *Wildlife Photographer* (**153**): Johnny Johnson/ Animals Animals; *Wilson, E. O.* (**154**): AP/ Wide World Photos; *Xenopus* (**156**): Zig Leszczynski/Animals Animals, Dr. Dennis Kunkel/Phototake; *Zoological Parks* (**159**): Alfred B. Thomas/Animals Animals; *Zoologist* (**162**): N. Rosing/OSF/Animals Animals; *Zooplankton* (**164**): M. I. Walker/Science Photo Library/National Audubon Society Collection/Photo Researchers, Inc.

Glossary

abiogenic: pertaining to a nonliving origin

abiotic: nonliving parts of the environment

abiotic factors: pertaining to nonliving environmental factors such as temperature, water, and nutrients

absorption: the movement of water and nutrients

acid rain: acidic precipitation in the form of rain

acidic: having the properties of an acid

acoelomate: an animal without a body cavity

acoelomates: animals without a body cavity

acoustics: a science that deals with the production, control, transmission, reception, and effects of sound

actin: a protein in muscle cells that works with myosin in muscle contractions

action potential: a rapid change in the electric charge of the cell membrane

active transport: a process requiring energy where materials are moved from an area of lower to an area of higher concentration

adaptive radiation: a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

adenosine triphoshate: an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

aestivate: a state of lowered metabolism and activity that permits survival during hot and dry conditions

agnostic behavior: a type of behavior involving a contest of some kind that determines which competitor gains access to some resource such as food or mates

alkaline: having the properties of a base

allele: one of two or more alternate forms of a gene

alleles: two or more alternate forms of a gene

allometry: relative growth of one part of an organism with reference to another part

allopatry: populations separated by a barrier

alluvial: sediments from flowing water such as silt, sand, mud, and gravel

alpha: the dominant member of a group

altruistic behavior: the aiding of another individual at one's own risk or expense

alveoli: thin-walled sacs in the lungs where blood in capillaries and air in the lungs exchange gases

ameloblasts: cells that form dental enamel

amiote: embryo of a vertebrate that is surrounded by a fluid-filled sac

ammonites: an extinct group of cephalopods with a curled shell

amnion: the membrane that forms a sac around an embryo

amniote: a vertebrate which has a fluid-filled sac that surrounds the embryo

amniotes: vertebrates which have a fluid-filled sac that surrounds the embryo

anadromous: moving from the ocean up a river to spawn

analogous: a similarity in structures between two species that are not closely related

anemia: a condition that results from a decreased number of red blood cells

angiosperms: a flowering plant that produces seeds within an ovary

annelids: segmented worms

anoxic: an environment that lacks oxygen

anterior: referring to the head end of an organism

anterior pituitary: the front part of the pituitary gland that produces hormones that stimulate the production of sperm and testosterone in the testes

antibodies: proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

antigen: foreign substances that stimulate the production of antibodies in the blood

anurans: the order of amphibians that contains frogs and toads

aphrodisiac: a substance or object that is thought to arouse sexual desire

aphrodisiacs: substances or objects that are thought to arouse sexual desire

aposematic: a feature or signal that serves to warn

aposematic coloration: a bright coloration in animals with physical or chemical defenses that act as a warning to predators

appendicular: having to do with arms and legs

appendicular skeleton: part of the skeleton with the arms and legs

aquatic: living in water

aragonite: a mineral form of calcium carbonate

arboreal: living in trees

Archae: an ancient lineage of prokaryotes that live in extreme environments

arthropod: a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

arthropods: members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

artificial pollination: manual pollination methods

asexual reproduction: a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

asymmetrical: lacking symmetry, having an irregular shape

aural: related to hearing

autonomic nervous system: division of the nervous system that carries nerve impulses to muscles and glands

autotroph: an organism that makes its own food

autotrophs: organisms that make their own food

axial skeleton: the skeleton that makes up the head and trunk

axon: cytoplasmic extension of a neuron that transmits impulses away from the cell body

axons: cytoplasmic extensions of a neuron that transmit impulses away from the cell body

B-lymphocytes: specialized cells produced from stem cells in the bone marrow that secrete antibodies that bind with antigens to form a pathogen fighting complex

bacterium: a member of a large group of single-celled prokaryotes

baleen: fringed filter plates that hang from the roof of a whale's mouth

Batesian mimicry: a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

behavioral: relating to actions or a series of actions as a response to stimuli

benthic: living at the bottom of a water environment

bilateral symmetry: characteristic of an animal that can be separated into two identical mirror image halves

bilaterally symmetrical: describes an animal that can be separated into two identical mirror image halves

bilateria: animals with bilateral symmetry

bilipid membrane: a cell membrane that is made up of two layers of lipid or fat molecules

bio-accumulation: the build up of toxic chemicals in an organism

bioactive protein: a protein that takes part in a biological process

bioactive proteins: proteins that take part in biological processes

biodiversity: the variety of organisms found in an ecosystem

biogeography: the study of the distribution of animals over an area

biological control: the introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

biological controls: introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

biomagnification: increasing levels of toxic chemicals through each trophic level of a food chain

biomass: the dry weight of organic matter comprising a group of organisms in a particular habitat

biome: a major type of ecological community

biometry: the biological application of statistics to biology

biotic: pertaining to living organisms in an environment

biotic factors: biological or living aspects of an environment

bipedal: walking on two legs

bipedalism: describes the ability to walk on two legs

birthrate: a ratio of the number of births in an area in a year to the total population of the area

birthrates: ratios of the numbers of births in an area in a year to the total population of the area

bivalve mollusk: a mollusk with two shells such as a clam

bivalve mollusks: mollusks with two shells such as clams

bivalves: mollusks that have two shells

body plan: the overall organization of an animal's body

bone tissue: dense, hardened cells that makes up bones

botany: the scientific study of plants

bovid: a member of the family bovidae which is hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

bovids: members of the family bovidae which are hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

brachiopods: a phylum of marine bivalve mollusks

brackish: a mix of salt water and fresh water

brood parasites: birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

buccal: mouth

budding: a type of asexual reproduction where the offspring grow off the parent

buoyancy: the tendency of a body to float when submerged in a liquid

Burgess Shale: a 550 million year old geological formation found in Canada that is known for well preserved fossils

calcified: made hard through the deposition of calcium salts

calcite: a mineral form of calcium carbonate

calcium: a soft, silvery white metal with a chemical symbol of Ca

capture-recapture method: a method of estimating populations by capturing a number of individuals, marking them, and then seeing what percentage of newly captured individuals are captured again

cardiac: relating to the heart

cardiac muscle: type of muscle found in the heart

cardiopulmonary: of or relating to the heart and lungs

carnivorous: describes animals that eat other animals

carrying capacity: the maximum population that can be supported by the resources

cartilage: a flexible connective tissue

cartilaginous: made of cartilage

catadromous: living in freshwater but moving to saltwater to spawn

character displacement: a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

chelicerae: the biting appendages of arachnids

chemoreceptors: a receptor that responds to a specific type of chemical molecule

chemosynthesis: obtaining energy and making food from inorganic molecules

chemosynthetic autotrophs: an organism that uses carbon dioxide as a carbon source but obtains energy by oxidizing inorganic substances

chemotrophs: animals that make energy and produce food by breaking down inorganic molecules

chitin: a complex carbohydrate found in the exoskeleton of some animals

chitinous: made of a complex carbohydrate called chitin

chloroquine: a drug commonly used to treat malaria

chromosomes: structures in the cell that carry genetic information

cilia: hair-like projections used for moving

circadian rhythm: daily, 24-hour cycle of behavior in response to internal biological cues

clades: a branching diagram that shows evolutionary relationships of organisms

Class Branchiopoda: a group of marine bivalve mollusks

Class Malacostraca: crustaceans such as lobsters, crabs, and shrimp

Class Maxillopoda: crustaceans such as barnacles, ostracods, and copepods

Class Merostomata: crustaceans such as horseshoe crabs and eurypterids

Class Pycnogonida: crustaceans such as sea spiders

cleavage: the process of cytokinesis in animal cells; as cells multiply, the plasma membrane pinches off to make two cells from one

climate: long-term weather patterns for a particular region

cnidaria: a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

cnidarians: aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

codominance: an equal expression of two alleles in a heterozygous organism

codon: the genetic code for an amino acid that is represented by three nitrogen bases

codons: the genetic code for an amino acid that is represented by three nitrogen bases

coelom: a body cavity

coevolution: a situation in which two or more species evolve in response to each other

coexist: live together

commensal: a symbiotic relationship wherein which one species benefits and the other is neither helped nor harmed

competitive exclusion principle: the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

compound eye: a multifaceted eye that is made up of thousands of simple eyes

compound eyes: multifaceted eyes that are made up of thousands of simple eyes

concentric: having the same center

conchiolin: a protein that is the organic basis of mollusk shells

coniferous, conifers: having pine trees and other conifers

connective tissue: cells that make up bones, blood, ligaments, and tendons

consumers: animals that do not make their own food but instead eat other organisms

continental drift: the movement of the continents over geologic time

contour feather: a feather that covers a bird's body and gives shape to the wings or tail

contour feathers: feathers that cover a bird's body and give shape to the wings or tail

controversy: a discussion marked by the expression of opposing views

convergence: animals that are not closely related but they evolve similar structures

copulation: the act of sexual reproduction

crinoids: an echinoderm with radial symmetry that resembles a flower

critical period: a limited time in which learning can occur

critical periods: a limited time in which learning can occur

crustaceans: arthropods with hard shells, jointed bodies, and appendages that mainly live in the water

ctenoid scale: a scale with projections on the edge like the teeth on a comb

cumbersome: awkward

cytoplasm: fluid in eukaryotes that surrounds the nucleus and organelles

cytosolic: the semifluid portions of the cytoplasm

death rate: a ratio of the number of deaths in an area in a year to the total population of the area

deciduous: having leaves that fall off at the end of the growing season

denaturing: break down into small parts

dendrites: branched extensions of a nerve cell that transmit impulses to the cell body

described: a detailed description of a species that scientists can refer to identify that species from other similar species

dessication: drying out

detritus: dead organic matter

deuterostome: animal in which the first opening does not form the mouth, but becomes the anus

deuterostomes: animals in which the first opening does not form the mouth, but becomes the anus

diadromous: animals that migrate between freshwater and saltwater

differentiation: differences in structure and function of cells in multicellular organisms as the cells become specialized

diffusion: the movement of molecules from a region of higher concentration to a region of lower concentration

dioecious: having members of the species that are either male or female

diploblastic: having two germ layers; ectoderm and endoderm

diploid cells: cells with two sets of chromosomes

direct fitness: fitness gained through personal reproduction

diurnal: active in the daytime

DNA replication: the process by which two strands of a double helix separate and form two identical DNA molecules

dominance hierarchies: the structure of the pecking order of a group of individuals of a group where the multiple levels of dominance and submission occur

dominant: an allele that is always an expressed trait

dorsal: the back surface of an animal with bilateral symmetry

dorsal root ganglia: nervous tissue located near the backbone

dorsoventrally: flattened from the top and bottom

dysentery: inflammation of the intestines that is characterized by pain, diarrhea, and the passage of mucous and blood

ecdysis: shedding the outer layer of skin or exoskeleton

ecdysone: hormone that triggers molting in arthropods

echinoderms: sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

ecological: relating to an organism's interaction with its environment

ecology: study of how organisms interact with their environment

ecosystem: a self-sustaining collection of organisms and their environment

ecosystems: self-sustaining collections of organisms and their environments

ecotourism: tourism that involves travel to areas of ecological or natural interest usually with a naturalist guide

ectodermal: relating to the outermost of the three germ layers in animal embryos

ectoparasite: an organism that lives on the surface of another organism and derives its nutrients directly from that organism

ectoparasites: organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

edentates: lacking teeth

El Niño: a periodic condition characterized by a warming of the central Pacific Ocean and the changes in global weather patterns that are brought about

emit: to send out or give off

endocrine system: the grouping of organs or glands that secrete hormones into the bloodstream

endoparasite: an organism that lives inside another organism and derives its nutrients directly from that organism

endoparasites: organisms that live inside other organisms and derive their nutrients directly from those organisms

endoskeleton: a skeleton that is surrounded by muscle tissue

endosymbionts: the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

endotrophic: deriving nourishment from within

enterocoelous: a cavity formed by the in-folding of the wall of the intestinal cavity in a gastrula

enzyme: a protein that acts as a catalyst to start a biochemical reaction

enzymes: proteins that act as catalysts to start biochemical reactions

epidermis: the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

epistasis: a phenomenon in which one gene alters the expression of another gene that is independently inherited

epithelial cells: cells that occur in tightly packed sheets that line organs and body cavities

epithelial lining: sheets of tightly packed cells that cover organs and body cavities

epitope: a localized region on an antigen that is recognized chemically by antibodies

equilibrium: a state of balance

erythrocytes: red blood cells, cells containing hemoglobin that carry oxygen throughout the body

estuaries: an area of brackish water where a river meets the ocean

ethology: animal behavior

eucoelomates: animals that have a true body cavity that is completely surrounded by mesoderm

eukaryota: a group of organisms containing a membrane bound-nucleus and membrane-bound organelles

eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles

eukaryotic cells: contains a membrane-bound nucleus and membrane-bound organelles

euryhaline: animals that can live in a wide range of salt concentrations

eusocial: animals that show a true social organization

evaporites: rocks formed from evaporation of salty and mineral-rich liquid

excrescence: an abnormal growth

excrescences: abnormal growths

exons: the coding region in a eukaryotic gene that is expressed

exoskeleton: a hard outer protective covering common in invertebrates such as insects

exoskeletons: hard outer protective coverings common in invertebrates such as insects

exponential growth: a population growing at the fastest possible rate under ideal conditions

extant: still living

facilitated diffusion: the spontaneous passing of molecules attached to a carrier protein across a membrane

facultative parasites: organisms that can survive either as a parasite or free-living

falconry: a sport where falcons are used for hunting

fascicle: a close cluster

fauna: animals

fertilization: the fusion of male and female gametes

fibroblasts: type of cells found in loose connective tissue that secretes the proteins for connective fibers

fight or flight response: an automatic, chemically controlled response to a stimulus that causes increased heart and breathing rates for increased activity

filter feeders: animals that strain small food particles out of water

fission: dividing into two parts

fixed action pattern: behaviors that are common to all members of a species

flagella (flagellum): cellular tail that allows the cell to move

flagellae: cellular tails that allow cells to move

flora: plants

fossil record: a collection of all known fossils

frequency-dependant selection: a decline in the reproductive success of a particular body type due to that body type becoming common in the population

frugivores: fruit-eating animals

functional morphology: studying form and function

fusion: coming together

gametes: reproductive cells that only have one set of chromosomes

gametocyte: cell that produces gametes through division

gametocytes: cells that produce gametes through division

ganoid scale: hard, bony, and enamel covered scales

gastropods: mollusks that are commonly known as snails

gastrovascular cavity: a single cavity where digestion occurs

gastrulation: the formation of a gastrula from a blastula

gene therapy: a process where normal genes are inserted into DNA to correct a genetic disorder

genes: segments of DNA located on chromosomes that direct protein production

genetic trait: trait related to biological inheritance

genetics: the branch of biology that studies heredity

genome: an organism's genetic material

genomes: the sum of all genes in a set of chromosomes

genotype: the genetic makeup of an organism

germ cell: an egg or sperm cell, a gamete

germ cells: egg or sperm cells, gametes

gill arches: arches of cartilage that support the gills of fishes and some amphibians

gill filaments: the site of gas exchange in aquatic animals such as fish and some amphibians

gills: site of gas exchange between the blood of aquatic animals such as fish and the water

gizzard: the muscular part of the stomach of some animals where food is ground

global warming: a slow and steady increase in the global temperature

glycoprotein: an organic molecule that contains a carbohydrate and a protein

gonad: the male and female sex organs that produce sex cells

gonads: the male and female sex organs that produce sex cells

granulocytes: a type of white blood cell where its cytoplasm contains granules

green house effect: a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

habitat: the physical location where organisms live in an ecosystem

habitat loss: the destruction of habitats through natural or artificial means

habitat requirement: necessary conditions or resources needed by an organism in its habitat

habitats: physical locations where organisms live in an ecosystem

Hamilton's Rule: individuals show less agression to closely related kin than to more distantly related kin

haplodiploidy: the sharing of half the chromosomes between a parent and an offspring

haploid cells: cells with only one set of chromosomes

hemocoel: a cavity between organs in arthropods and mollusks through which blood circulates

hemocyanin: respiratory pigment found in some crustaceans, mollusks, and arachnids

hemoglobin: an iron-containing protein found in red blood cells that binds with oxygen

hemolymph: the body fluid found in invertebrates with open circulatory systems

herbivore: an animal that eats plants only

herbivores: animals that eat only plants

herbivorous: animals that eat plants

heredity: the passing on of characteristics from parents to offspring

heritability: the ability to pass characteristics from a parent to the offspring

hermaphodite: an animals with both male and female sex organs

hermaphroditic: having both male and female sex organs

heterodont: teeth differentiated for various uses

heterotrophic eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles and do not make their own food

heterotrophs: organisms that do not make their own food

heteroxenous: a life cycle in which more than one host individual is parasitized

heterozygote: an organism whose chromosomes contain both genes of a contrasting pair

heterozygote advantage: a condition where a heterozygous individual has a reproductive advantage over a homozygous individual

Hippocrates: a central figure in medicine in ancient Greece, he is considered the father of modern medicine

home range: the area where an animal lives and eats

homeostasis: a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

homeothermic: describes animals able to maintain their body temperatures

hominid: belonging to the family of primates

hominids: belonging to the family of primates

homodont: teeth with a uniform size and shape

homologous: similar but not identical

homology: correspondence in the type of structure and its origin

homoplastic: similar but of different origins

homozygote: an animal with two identical alleles for one trait

hormone: a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

hormones: chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

Horseshoe crabs: "living fossils" in the class of arthropods

Hox genes: also known as selector genes because their expression leads embryonic cells through specific morphologic development

Human Genome Project: a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

hunting season: a period of time during which hunting is permited

hunting seasons: periods of time during which hunting is permited

hybrid: offspring resulting from the cross of two different species

hydrostatic skeleton: a pressurized, fluid-filled skeleton

hyperpolarizing potential: any change in membrane potential that makes the inside of the membrane more negatively charged

hypothalamus: part of the upper end of the brain stem that regulates activities in the nervous and endrocrine systems

IgA: imunoglobin A; a class of proteins that make up antibodies

IgD: imunoglobin D; a class of proteins that make up antibodies

IgE: imunoglobin E; a class of proteins that make up antibodies

IgG: imunoglobin G; a class of proteins that make up antibodies

IgM: imunoglobin M; a class of proteins that make up antibodies

inbreeding depression: loss of fitness due to breeding with close relatives

incomplete dominance: a type of inheritance where the offspring have an intermediate appearance of a trait from the parents

incus: one of three small bones in the inner ear

indirect fitness: fitness gained through aiding the survival of non-descendant kin

infrared: an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red; heat is carried on infrared waves

innate behavior: behavior that develops without influence from the environment

innervate: supplied with nerves

inoculation: introduction into surroundings that support growth

insectivore: an animal that eats insects

insectivores: animals that eat insects

instars: the particular stage of an insect's or arthropod growth cycle between moltings

integument: a natural outer covering

intercalation: placing or inserting between

intraspecific: involving members of the same species

introns: a non-coding sequence of base pairs in a chromosome

invagination: a stage in embryonic development where a cell layer buckles inward

invertebrates: animals without a backbone

involuntary muscles: muscles that are not controlled by will

isthmus: a narrow strip of land

iteroparous: animals with several or many reproductive events in their lives

***k*-selected species:** a species that natural selection has favored at the carrying capacity

***k*-selecting habitat:** habitat where there is a high cost of reproduction and is sensitive to the size of the offspring

key innovation: a modification that permits an individual to exploit a resource in a new way

keystone species: a species that controls the environment and thereby determines the other species that can survive in its presence

krill: an order of crustaceans that serves as a food source for many fish, whales, and birds

lancelet: a type of primitive vertebrate

lancelets: primitive vertebrates

lateral inhibition: phenomenon that amplifies the differences between light and dark

lateral line: a row of pressure sensitive sensory cells in a line on both sides of a fish

learned behavior: behavior that develops with influence from the environment

learning: modifications to behavior motivated by experience

leukocytes: a type of white blood cells that are part of the immune system

life history strategies: methods used to overcome pressures for foraging and breeding

life history strategy: methods used to overcome pressures for foraging and breeding

lipids: fats and oils; organic compounds that are insoluble in water

logistic growth: in a population showing exponential growth the individuals are not limited by food or disease

lungs: sac-like, spongy organs where gas exchange takes place

lymphocytes: white blood cell that completes development in bone marrow

macroparsite: a parasite that is large in size

macroparasites: parasites that are large in size

macrophages: white blood cell that attacks anything foreign such as microbes

malleus: the outermost of the inner ear bones

mantle: the tissue in mollusks that drapes over the internal organs and may secrete the shell

mantles: tissues in mollusks that drape over the internal organs and may secrete the shell

matrix: the nonliving component of connective tissue

megachiroptera: fruit bats and flying foxes

meiosis: a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

merozoite: a motile stage in some parastic protozoa

mesenchyme: the part of the mesoderm from which the connective tissues (bone, cartilage, and vascular system) arise

mesenteries: the membrane that suspends many internal organs in the fluid-filled body cavity of vertebrates

mesoderm: the middle layer of cells in embryonic tissue

messenger RNA: a type of RNA that carries protein synthesis information from the DNA in to the nucleus to the ribosomes

metamorphose: to change drastically from a larva to an adult

metamorphoses: changes drastically from its larval form to its adult form

metamorphosing: changing drastically from a larva to an adult

metamorphosis: a drastic change from a larva to an adult

metazoan: a subphylum of animals that have many cells, some of which are organized into tissues

metazoans: a subphylum of animals that have many cells, some of which are organized into tissues

microchiroptera: small bats that use echolocation

microparasite: very small parasite

microparasites: very small parasites

midoceanic ridge: a long chain of mountains found on the ocean floor where tectonic plates are pulling apart

mitochondria: organelles in eukaryotic cells that are the site of energy production for the cell

Mitochondrial DNA: DNA found within the mitochondria that control protein development in the mitochondria

mitosis: a type of cell division that results in two identical daughter cells from a single parent cell

modalities: to conform to a general pattern or belong to a particular group or category

modality: to conform to a general pattern or belong to a particular group or category

molecular clock: using the rate of mutation in DNA to determine when two genetic groups spilt off

molecular clocks: using the rate of mutation in DNA to determine when two genetic groups spilt off

mollusks: large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

molted: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

molting: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

monoculture: cultivation of a single crop over a large area

monocultures: cultivation of single crops over large areas

monocytes: the largest type of white blood cell

monophyletic: a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

monotremes: egg-laying mammals such as the platypus and echidna

monoxenous: a life cycle in which only a single host is used

morphogenesis: the development of body shape and organization during ontogeny

morphological: the structure and form of an organism at any stage in its life history

morphological adaptation: an adaptation in form and function for specific conditions

morphological adaptations: adaptations in form and function for specific conditions

morphologies: the forms and structures of an animal

mutation: an abrupt change in the genes of an organism

mutations: abrupt changes in the genes of an organism

mutualism: ecological relationship beneficial to all involved organisms

mutualisms: ecological relationships beneficial to all involved organisms

mutualistic relationship: symbiotic relationship where both organisms benefit

mutualistic relationships: symbiotic relationships where both organisms benefit

mutualists: a symbiotic relationship where both organisms benefit

myofibril: longitudinal bundles of muscle fibers

myofilament: any of the ultramicroscopic filaments, made up of actin and myosin, that are the structural units of a myofibril

myosin: the most common protein in muscle cells, responsible for the elastic and contractile properties of muscle; it combines with actin to form actomyosin

natural selection: the process by which organisms best suited to their environment are most likely to survive and reproduce

naturalist: a scientist who studies nature and the relationships among the organisms

naturalists: scientists who study nature and the relationships among the organisms

neuromuscular junction: the point where a nerve and muscle connect

neuron: a nerve cell

neurons: nerve cells

neurotransmitters: chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

niche: how an organism uses the biotic and abiotic resources of its environment

nocturnal: active at night

notochord: a rod of cartilage that runs down the back of Chordates

nucleotide: the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

nucleotide chain: a chain composed of five-carbon sugar groups that forms the basis for nucleic acid

nucleotides: building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

obligative mutualism: an animal that must exist as part of a mutually beneficial relationship

obligatory parasites: an animal that can only exist as a parasite

olfactory: relates to the sense of smell

omnivorous: eating both plants and animals

ontogeny: the embryonic development of an organism

oocyst: a cyst in sporozoans that contains developing sporozoites

operculum: a flap covering an opening

operculum chamber: space covered by a flap

organelles: membrane-bound structures found within a cell

ornithology: the study of birds

osmoregulatory functions: controlling the water balance within an animal

osmoregulatory system: system that regulates the water balance between an organism and its environment

osmosis: the diffusion of water across a membrane

ossification: deposition of calcium salts to form hardened tissue such as bone

osteoblasts: potential bone forming cells found in cartilage

oviparous: having offspring that hatch from eggs external to the body

ovoviparity: having offspring that hatch from eggs retained in the mother's uterus

ovoviviparous: having offspring that hatch from eggs retained in the mother's uterus

paleoanthropology: the study of ancient humans

parasitology: the study of parasites

parasympathetic division: part of the nervous system that generally enhances body activities that gain and conserve energy such as digestion and heart rate

parental imprinting: a process by which a gene's expression in a child depends on which parent donated it before development

passive diffusion: the passing of molecules across a membrane from an area of higher concentration to an area of lower concentration without any energy input

pathogens: disease-causing agents such as bacteria, fungi, and viruses

pecking order: the position of individuals of a group wherein multiple levels of dominance and submission occur

pectoral: of, in, or on the chest

pedipapls: one pair of short appendages near the mouth in some arthropods used for feeding and copulation

pericardial cavity: the space within the membrane that surrounds the heart

peripheral nervous system: the sensory and motor nerves that connect to the central nervous system

peritoneum: the thin membrane that lines the abdomen and covers the organs in it

pesticide: any substance that controls the spread of harmful or destructive organisms

pesticides: substances that control the spread of harmful or destructive organisms

pH: a measure of how acidic or basic a substance is by measuring the concentration of hydrogen ions

phalanges: bones of the fingers and toes

pharyngeal: having to do with the tube that connects the stomach and the esophagus

phenotype: physical and physiological traits of an animal

phenotypes: the physical and physiological traits of an animal

phenotypic: describes the physical and physiological traits of an animal

phenotypic trait: physical and physiological variations within a population

phenotypic variation: differences in physical and physiological traits within a population

pheromones: small, volatile chemicals that act as signals between animals that influence physiology or behavior

phlogenetic: relating to the evolutionary history

phospholipid: molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water

photoreceptors: specialized cells that detect the presence or absence of light

photosynthesis: the combination of chemical compounds in the presence of sunlight

photosynthesizing autotrophs: animals that produce their own food by converting sunlight to food

phyla: broad, principle divisions of a kingdom

phylogenetic: relating to the evolutionary history of species or group of related species

phylogeny: the evolutionary history of a species or group of related species

physiological: relating to the basic activities that occur in the cells and tissues of an animal

physiology: the study of the normal function of living things or their parts

placenta: the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placental: having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placoid scale: a scale composed of three layers and a pulp cavity

placoid scales: scales composed of three layers and a pulp cavity

plankton: microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

plate tectonics: the theory that Earth's surface is divided into plates that move

platelet: cell fragment in plasma that aids clotting

platelets: cell fragments in plasma that aid in clotting

pleural cavity: the space where the lungs are found

plumose: having feathers

pluripotent: a cell in bone marrow that gives rise to any other type of cell

poaching: hunting game outside of hunting season or by using illegal means

poikilothermic: an animal that cannot regulate its internal temperature; also called cold blooded

polymer: a compound made up of many identical smaller compounds linked together

polymerase: an enzyme that links together nucleotides to form nucleic acid

polymerases: enzymes that link together nucleotides to form nucleic acid

polymodal: having many different modes or ways

polymorphic: referring to a population with two or more distinct forms present

polymorphism: having two or more distinct forms in the same population

polymorphisms: having two or more distinct forms in the same population

polyploid: having three or more sets of chromosomes

polysaccharide: a class of carbohydrates that break down into two or more single sugars

polysaccharides: carbohydrates that break down into two or more single sugars

population: a group of individuals of one species that live in the same geographic area

population density: the number of individuals of one species that live in a given area

population dynamics: changes in a population brought about by changes in resources or other factors

population parameters: a quantity that is constant for a particular distribution of a population but varies for the other distrubutions

populations: groups of individuals of one species that live in the same geographic area

posterior: behind or the back

precursor: a substance that gives rise to a useful substance

prehensile: adapted for siezing, grasping, or holding on

primer: short preexisting polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase

producers: organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

progeny: offspring

prokaryota: a group of organisms that lack a membrane-bound nucleus and membrane-bound organelles

prokaryotes: single-celled organisms that lack a true cell nucleus

prokaryotic endosymbionts: single-celled organisms that lack a true cell nucleus that live inside of other cells

proprioceptors: sense organs that receive signals from within the body

protostome: animal in which the initial depression that starts during gastrulation becomes the mouth

protostomes: animals in which the initial depression that starts during gastrulation becomes the mouth

protozoa: a phylum of single-celled eukaryotes

protozoan: a member of the phylum of single-celled organisms

pseudocoelom: a body cavity that is not entirely surrounded by mesoderm

pseudocoelomates: animals with a body cavity that is not entirely surrounded by mesoderm

pterylae: feather tracks

quadrupedal: describes an animal with four legs

quadrupeds: animals with four legs

quinine: substance used to treat malaria

***r*-selected species:** a species that shows the following characteristics: short lifespan; early reproduction; low biomass; and the potential to produce large numbers of usually small offspring in a short period of time

***r*-selecting habitat:** the concept where a high reproductive rate is the chief determinant of life history

radially symmetric: wheel-like symmetry in which body parts radiate out from a central point

radially symmetrical: describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

recessive: a hidden trait that is masked by a dominant trait

recombinant DNA: DNA that is formed when a fragment of DNA is incorporated into the DNA of a plasmid or virus

regeneration: regrowing body parts that are lost due to injury

relative abundance: an estimate of population over an area

rennin: an enzyme used in coagulating cheese; is obtained from milk-fed calves

resorbed: absorption of materials already in the body

resorption: absorbing materials that are already in the body

respiratory pigments: any of the various proteins that carry oxygen

restriction enzymes: bacterial proteins that cut DNA at specific points in the nucleotide sequence

retina: a layer of rods and cones that line the inner surface of the eye

riparian: habitats in rivers and streams

ruminants: plant-eating animals with a multicompartment stomach such as cows and sheep

sagital plane: a plane that runs long-ways through the body

salamanders: four-legged amphibians with elongated bodies

sarcomere: one of the segments into which a fibril of striated muscle is divided by thin dark bands

scavengers: animals that feed on the remains of animals it did not kill

schizocoelous: the mesoderm originates from existing cell layers when the cells migrate

scleroblasts: cells that give rise to mineralized connective tissue

sedimentary rock: rock that forms when sediments are compacted and cemented together

semelparous: animals that only breed once and then die

serial homology: a rhythmic repetition

sessile: not mobile, attached

sexual reproduction: a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

sexual selection: selection based on secondary sex characteristics that leads to greater sexual dimorphorphism or differences between the sexes

sexual size dimorphism: a noticeable difference in size between the sexes

shoals: shallow waters

single-lens eyes: an eye that has a single lens for focusing the image

skeletal muscle: muscle attached to the bones and responsible for movement

smooth muscle: muscles of internal organs which is not under conscious control

somatic: having to do with the body

somatic nervous system: part of the nervous system that controls the voluntary movement of skeletal muscles

somatosensory information: sensory information from different parts of the body except for the eyesm tongue, ears, and other primary sense organs

somites: a block of mesoderm along each side of a chordate embryo

sonar: the bouncing of sound off distant objects as a method of navigation or finding food

spinal cord: thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

splicing: spliting

spongocoel: the central cavity in a sponge

sporozoa: a group of parasitic protozoa

sporozoans: parasitic protozoans

sporozoite: an infective stage in the life cycle of sporozoans

stapes: innermost of the three bones found in the inner ear

stimuli: anything that excites the body or part of the body to produce a specific response

stimulus: anything that excites the body or part of the body to produce a specific response

strata: layers of sedimentary rock consisting of approximately the same kinds of material

striated muscle: a type of muscle with fibers of cross bands usually contracted by voluntary action

striated muscles: muscles with fibers of cross bands usually contracted by voluntary actions

superposition: the order in which sedimentary layers are found with the youngest being on top

symbiosis: any prolonged association or living together of two or more organisms of different species

symbiotic relationship: close, long-term relationship where two species live together in direct contact

symbiotic relationships: close, long-term relationships where two species live together in direct contact

symmetrical: a balance in body proportions

synapse: the space between nerve cells across which impulses are chemically transmitted

systematic: study of the diversity of life

tactile: the sense of touch

tapetum: a reflective layer in the eye of nocturnal animals

taxa: named taxonomic units at any given level

taxon: named taxonomic unit at any given level

taxonomy: the science of classifying living organisms

terraria: a small enclosure or closed container in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrariums: small enclosures or closed containers in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrestrial: living on land

thoracic: the chest area

thromboplastin: a protein found in blood and tissues that promotes the conversion of prothrombin to thrombin

torpid: a hibernation strategy where the body temperature drops in relation to the external temperature

trachea: the tube in air-breathing vertebrates that extends from the larynx to the bronchi

transcription: process where enzymes are used to make an RNA copy of a strand of DNA

transgenic: an organism that contains genes from another species

transgenic organism: an organism that contains genes from another species

translation: process where the order of bases in messenger RNA codes for the order of amino acids in a protein

transverse plane: a plane perpendicular to the body

trilobites: an extinct class of arthropods

triploblasts: having three germ layers; ectoderm, mesoderm, and endoderm

trophic level: the division of species in an ecosystem by their main source of nutrition

trophic levels: divisions of species in an ecosystem by their main source of nutrition

ungulates: animals with hooves

urea: soluble form of nitrogenous waste excreted by many different types of animals

urethra: a tube that releases urine from the body

uric acid: insoluble form of nitrogenous waste excreted by many different types of animals

ventral: the belly surface of an animal with bilateral symmetry

vertebrates: animals with a backbone

viviparity: having young born alive after being nourished by a placenta between the mother and offspring

viviparous: having young born alive after being nourished by a placenta between the mother and offspring

vocalization: the sounds used for communications

voluntary muscles: a type of muscle with fibers of cross bands usually contracted by voluntary action

wavelength: distance between the peaks or crests of waves

zooplankton: small animals who float or weakly move through the water

zygote: a fertilized egg

zygotes: fertilized eggs

zymogens: inactive building-block of an enzyme

Topic Outline

ADAPTATIONS

Adaptation
Antlers and Horns
Aposematism
Biological Evolution
Biomechanics
Blood
Camouflage
Catadromous—Diadromous and Anadromous Fishes
Colonization
Communication
Community Ecology
Comparative Biology
Defense
Echolocation
Egg
Extremophile
Locomotion
Mimicry
Peppered Moth
Tool Use
Water Economy in Desert Organisms

AGRICULTURE

Apiculture
Aquaculture
Classification Systems
Dinosaurs
Domestic Animals
Farmer
Farming
Selective Breeding
Sustainable Agriculture

ANIMAL DIVERSITY

Animal
Biodiversity
Biogeography
Biological Evolution
Cambrian Explosion
Camouflage
Cephalization
Coevolution
Colonization
Community Ecology
Constraints on Animal Development
Diversity of Major Groups
Extremophile
Functional Morphology
Kingdoms of Life
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Prokaryota
Sexual Dimorphism
Taxonomy

ANIMAL GROUPS

Agnatha
Amphibia
Annelida
Arthropoda
Aves
Cephalochordata
Cestoda
Chondricthyes
Chordata
Cnidaria
Dinosaurs
Echinodermata

Eukaryota
Mammalia
Metazoan
Molluska
Nematoda
Osteicthyes
Platyhelmithes
Porifera
Primates
Prokaryota
Reptilia
Rotifera
Trematoda
Turbellaria
Urochordata
Vertebrata

ANIMAL HISTORY

African Cichlid Fishes
Animal
Burgess Shale and Ediacaran Faunas
Cambrian Explosion
Coevolution
Colonization
Constraints on Animal Development
Domestic Animals
Eukaryota
Extinction
Fossil Record
Horses
Kingdoms of Life
Living Fossils
Paleontologist
Paleontology
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Tetropods—From Water to Land
Xenopus

ANATOMY

Acoustic Signals
Biomechanics
Body Cavities
Body Plan
Bone
Cartilage
Cells
Cephalization
Comparative Biology
Echolocation
Embryology
Embryonic Development
Feeding
Functional Morphology
Gills
Growth And Differentiation of the Nervous System
Homology
Keratin
Locomotion
Mouth, Pharynx, and Teeth
Muscular System
Neuron
Scales, Feathers, and Hair
Sense Organs
Skeletons
Vision

BEHAVIOR

Acoustic Signals
Aggression
Altruism
Behavior
Behavioral Ecology
Circadian Rhythm
Courtship
Crepuscular
Diurnal
Dominance Hierarchy
Ethology
Homeostasis
Imprinting
Instinct
Learning
Migration
Nocturnal
Social Animals
Sociality
Sociobiology
Territoriality

BIOCHEMISTRY AND PHYSIOLOGY

Absorption
Allometry
Antibody

Blood
Cancer
Cell Division
Cells
Digestion
Egg
Homeostasis
Hormones
Keratin
Molecular Biologist
Molecular Biology
Molecular Systematics
Physiologist
Physiology
Respiration
Transport

BIODIVERSITY

Biodiversity
Biogeography
Biomass
Biomes
Colonization
Community Ecology
Diversity of Major Groups
Eukaryota
Habitat
Habitat Loss
Habitat Restoration
Zooplankton

CAREERS IN ANIMAL SCIENCE

Ecologist
Environmental Lawyer
Farmer
Functional Morphologist
Geneticist
Horse Trainer
Human Evolution
Livestock Manager
Marine Biologist
Medical Doctor
Molecular Biologist
Museum Curator
Paleontologist
Physiologist
Scientific Illustrator
Service Animal Trainer
Systematist
Taxonomist
Veterinarian
Wild Game Manager
Wildlife Biologist
Wildlife Photographer
Zoologist

CELL BIOLOGY

Absorption
Blood
Cell Division
Cells
Viruses

ECOLOGY

African Cichlid Fishes
Behavioral Ecology
Biotic Factors
Camouflage
Community Ecology
Competition
Competitive Exclusion
Conservation Biology
DDT
Ecologist
Ecology
Ecosystem
Evolutionary Stable Strategy
Exotic Species
Expenditure per Progeny
Feeding Strategies
Fitness
Food Web
Foraging Strategies
Growth And Differentiation of the Nervous System
Habitat
Habitat Loss
Habitat Restoration
Home Range
Human Commensals and Mutual Organisms
Interspecies Interactions
Iteroparity and Semelparity
Keystone Species
Life History Strategies

ENVIRONMENT

ETHICS

EVOLUTION

FORM AND FUNCTION

Nervous System
Respiratory System
Sexual Selection
Shells
Vision
Vocalization

GENETICS

Drosophila
Genes
Genetic Engineering
Genetic Variation in a Population
Genetically Engineered Foods
Geneticist
Genetics
Mendel, Gregor
Modern Synthesis
PCR
Viruses

GEOLOGIC HISTORY

Cambrian Period
Carboniferous
Continental Drift
Cretaceous
Devonian
Geological Time Scale
Jurassic
K/T Boundary
Oligocene
Ordovician
Permian
Pleistocene
Quaternary
Silurian
Tertiary
Triassic

GROWTH AND DEVELOPMENT

Allometry
Antlers and Horns
Body Cavities
Body Plan
Bone
Cartilage
Cell Division
Cells
Comparative Biology
Constraints on Animal Development
Egg
Embryology
Embryonic Development
Haeckel's Law of Recapitulation
Heterochrony
Mesenchyme
Metamorphosis
Molting
Ontogeny
Serial Homology
Von Baer's Law

HISTORICAL FIGURES IN SCIENCE

Aristotle
Bailey, Florence Augusta Merriam
Bates, Henry Walter
Carson, Rachel
Darwin, Charles
Diamond, Jared
Elton, Charles Sutherland
Fausto–Sterling, Anne
Fossey, Dian
Goodall, Jane
Gould, Steven Jay
Haldane, J. B. S.
Lamarck, Jean-Baptiste
Leakey, Louis and Mary
Linnaeus, Carolus
Lorenz, Konrad
Malthus, Thomas Robert
Mayr, Ernst
McArthur, Robert
Mendel, Gregor
Montalcini, Rita Levi
Pasteur, Louis
Simpson, George Gaylord
Stevens, Nettie Maria
Wallace, Alfred Russel
Wilson, E. O.

HUMANS AND THE ANIMAL WORLD

Cultures and Animals
Human Commensals and Mutual Organisms
Human Populations
Human–Animal Conflicts

Hunter-Gatherers
Hunting
Malaria

LIFE CYCLES

Catadromous—Diadromous and Anadromous Fishes
Cell Division
Colonization
Courtship
Endosymbiosis
Iteroparity and Semelparity
Malaria
Metamorphosis
Parasitism

REPRODUCTION

Antlers and Horns
Asexual And Sexual Reproduction
Cell Division
Excretory and Reproductive Systems
Fertilization

SCIENTIFIC FIELDS OF STUDY

Behavioral Ecology
Community Ecology
Comparative Biology
Conservation Biology
Ecology
Embryology
Entomology
Functional Morphology
Herpetology
Icthyology
Molecular Biology
Morphology
Mouth, Pharynx, and Teeth
Paleontology
Physiology
Sociobiology
Taxonomy

Cumulative Index

*Page numbers in **boldface type** indicate article titles; those in italic type indicate illustrations. The number preceding the colon indicates the volume number.*

A

C

F

G

H

O

P

Q

R

T