biology

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VOLUME **2**
E–H

Richard Robinson, Editor in Chief

For Your Reference

The following section provides information that is applicable to a number of articles in this reference work. Included are a metric measurement and conversion table, geologic timescale, diagrams of an animal cell and a plant cell, illustration of the structure of DNA nucleotides, detail of DNA nucleotides pairing up across the double helix, and a comparison of the molecular structure of DNA and RNA.

METRIC MEASUREMENT

Definitions

Kilo = 1000
Hecto = 100
Deka = 10
Deci = 0.10 (1/10)
Centi = 0.01 (1/100)
Milli = 0.001 (1/1000)
Micro = 0.000001 (1/1,000,000)
Nano = 0.000000001 (1/1,000,000,000)

Conversions

To convert	Into	Multiply by
Acres	Hectares	0.4047
Centimeters	Inches	0.3937
Feet	Meters	0.3048
Gallons	Liters	3.7853
Grams	Ounces	0.0353
Grams	Pounds	0.0022
Hectares	Acres	2.4710
Inches	Centimeters	2.5400
Kilograms	Pounds	2.2046
Kilometers	Miles	0.6214
Liters	Gallons]	0.2642
Meters	Feet	3.2808
Miles	Kilometers	1.6093
Ounces	Grams	28.3495
Pounds	Kilograms	0.4536
Pounds	Grams	453.59

Temperature Conversion

°F	°C
210	100
200	
190	90
180	80
170	
160	70
150	
140	60
130	
120	50
110	
100	40
90	30
80	
70	20
60	
50	10
40	
30	0
20	
10	−10
0	−20
−10	
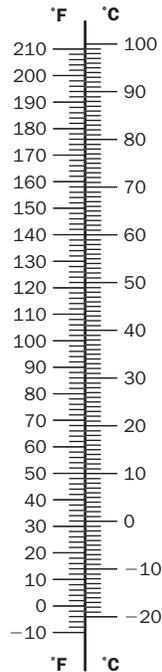
100°C = water boils
0°C = water freezes

GEOLOGIC TIMESCALE

ERA	PERIOD			EPOCH	STARTED (millions of years ago)
Cenozoic: 66.4 millions of years ago–present time	Quaternary			Holocene	0.01
				Pleistocene	1.6
	Tertiary	Neogene		Pliocene	5.3
				Miocene	23.7
		Paleogene		Oligocene	36.6
				Eocene	57.8
				Paleocene	66.4
Mesozoic: 245–66.4 millions of years ago	Cretaceous			Late	97.5
				Early	144
	Jurassic			Late	163
				Middle	187
				Early	208
	Triassic			Late	230
				Middle	240
				Early	245
Paleozoic: 570–245 millions of years ago	Permian			Late	258
				Early	286
	Carboniferous	Pennsylvanian		Late	320
		Mississippian		Early	360
	Devonian			Late	374
				Middle	387
				Early	408
	Silurian			Late	421
				Early	438
	Ordovician			Late	458
				Middle	478
				Early	505
	Cambrian			Late	523
				Middle	540
				Early	570
Precambrian time: 4500–570 millions of years ago					4500

A TYPICAL ANIMAL CELL

Smooth endoplasmic reticulum

Golgi apparatus

Ribosomes

Rough endoplasmic reticulum

Vacuole

Stalk

Basal body — Cilium

Rootlet

Peroxisome

Mitochondrion

Centrioles

Chromosome

Nucleus

Nucleolus

Nuclear membrane

Plasma membrane

Lysosome

A TYPICAL PLANT CELL

Endoplasmic reticulum

Golgi apparatus

Chromosome

Nucleolus

Nucleus

Nuclear membrane

Chloroplast

Ribosomes

Vacuole

Cell wall

Plasma membrane

Mitochondrion

Leucoplast

STRUCTURE OF DNA NUCLEOTIDES

Components of a nucleotide

Nitrogenous base

Phosphate

Sugar
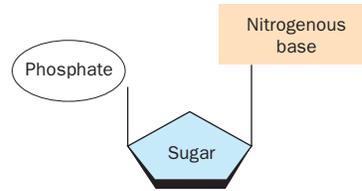
Purine-containing nucleotides

Adenine
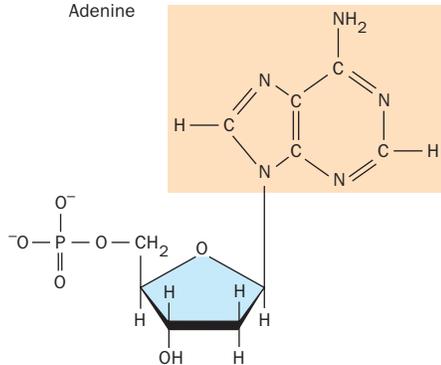
Pyrimidine-containing nucleotides

Thymine
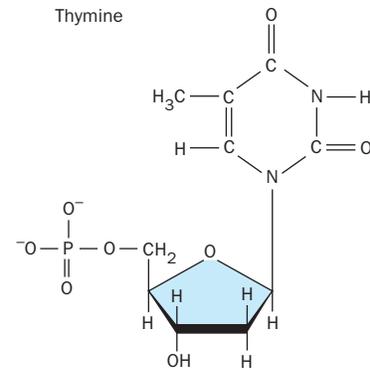
Guanine
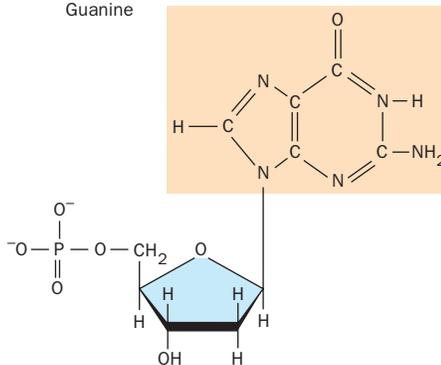
Cytosine
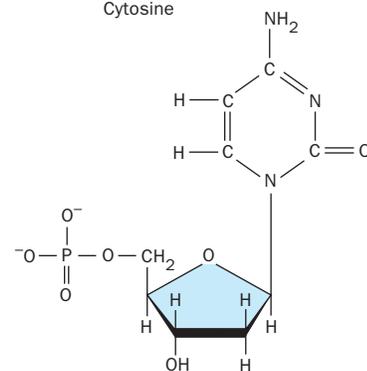
DNA NUCLEOTIDES PAIR UP ACROSS THE DOUBLE HELIX

Thymine (T)

Adenine (A)

5' end

3' end

Cytosine (C)

Guanine (G)

5'

3'

5' to 3' direction

5' to 3' direction

3'

5'

Adenine (A)

Thymine (T)

Guanine (G)

Cytosine (C)

3' end

5' end

Sugar-phosphate backbone of one DNA strand

Nitrogenous bases of the two DNA strands connected by hydrogen bonds

Sugar-phosphate backbone of complementary DNA strand

ix
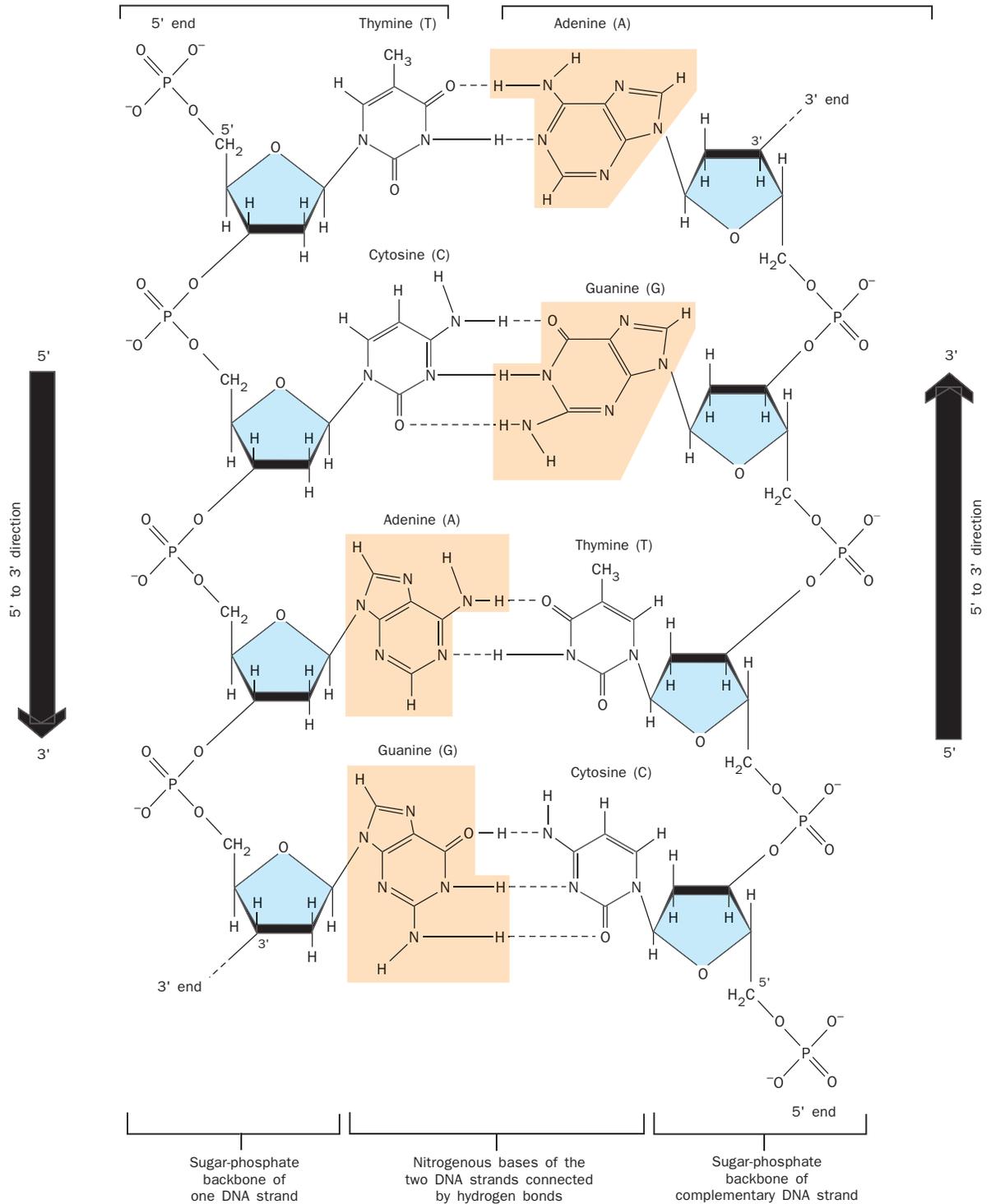
COMPARISON OF DNA AND RNA
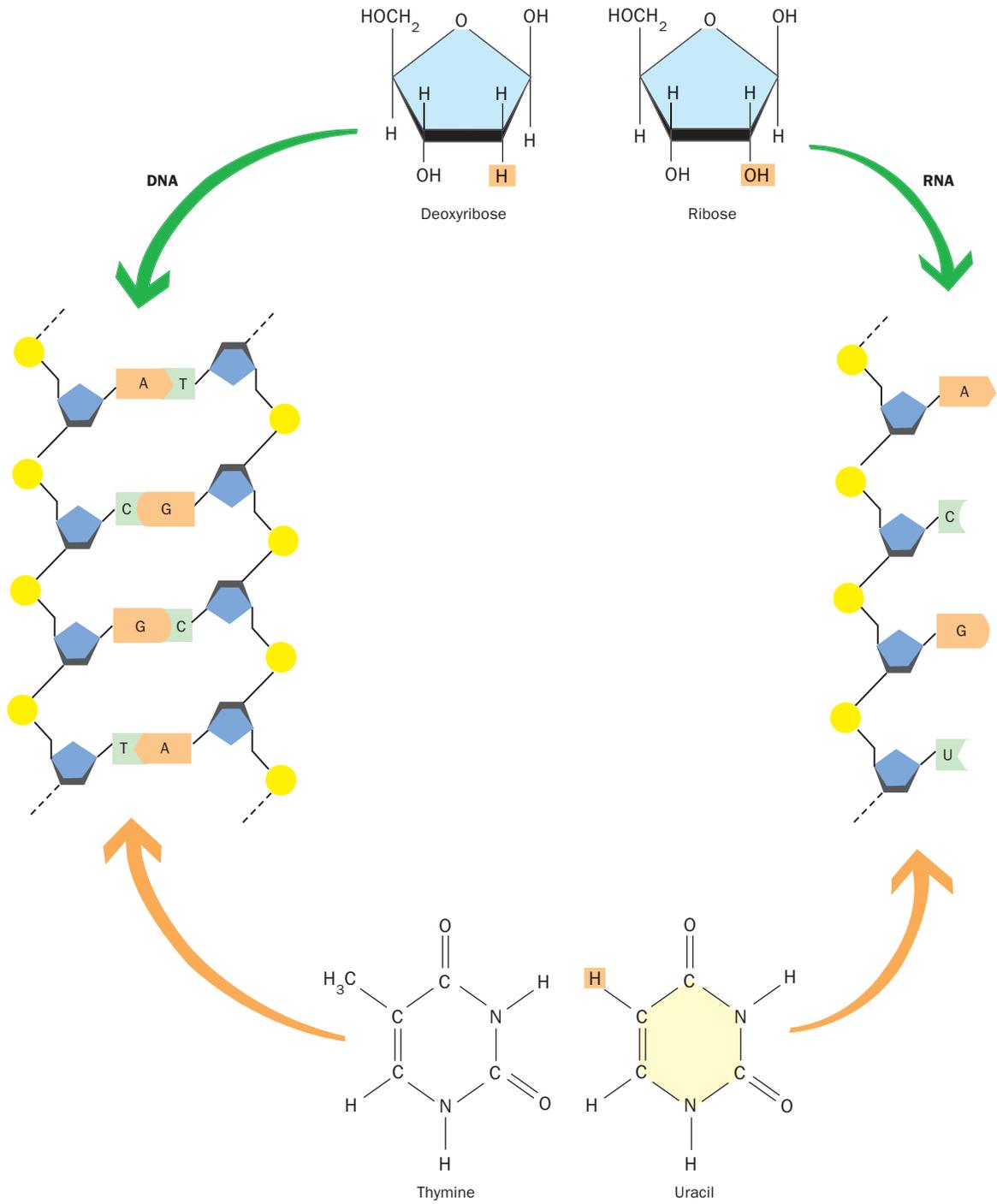
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Echinoderm

The echinoderms (*echino* means "spiny;" *derm* means "skin") are large, conspicuous, entirely marine invertebrates. Today, this group inhabits virtually every conceivable oceanic environment, from sandy beaches and coral reefs to the greatest depths of the sea. They are also common as fossils dating back 500 million years. These less-familiar fossil types are represented by a bizarre variety of animals, some of which reveal their relationship to the living echinoderms only at close inspection.

Diversity

The species living today are generally regarded as belonging to five subgroups: sea lilies and feather stars (Crinoidea, 650 species); starfish (Asteroidea, 1,500 species), brittlestars and basket stars (Ophiuroidea, 1,800 species), sea cucumbers (Holothuroidea, 1,200 species); and sea urchins and sand dollars (Echinoidea, 1,200 species).

Sea lilies have a central body, or calyx, surrounded by feathery, usually heavily branched arms. This whole arrangement sits at the end of a stem-like stalk attached to the sea bottom. The feather stars lack this stalk. Starfish (also called sea stars) have a central disk that is not marked off from the un-branched arms, of which there are usually five. Occasionally, one will encounter starfish species with more than five arms. Brittlestars also typically have five relatively long, flexible arms, but these are well differentiated from the central disk.

Sea cucumbers are soft-bodied and wormlike, with a cluster of tentacles around the mouth at one end. Sea urchins usually have a rigid body of joined plates upon which is mounted a dense forest of spines. The sea urchin body can be almost spherical, with long spines, or flattened to varying degrees with very short spines in types such as the sand dollars.

Anatomy and Physiology

In general, echinoderms are characterized by several unique features not found in any other animal **phylum**. They have a limestone (calcium carbonate) skeletal meshwork called "stereom" in their tissues, especially the body wall. The porous structure of stereom makes the skeleton light yet resistant to breakage. Echinoderms possess a special kind of ligament that can be stiffened or

phylum taxonomic level below kingdom, e.g., arthropod or chordate

1

Sea lily (crinoid)

Starfish (asteroid)

Brittlestar (ophiuroid)

Sea cucumber (holothuroid)

Sea urchin (echinoid)
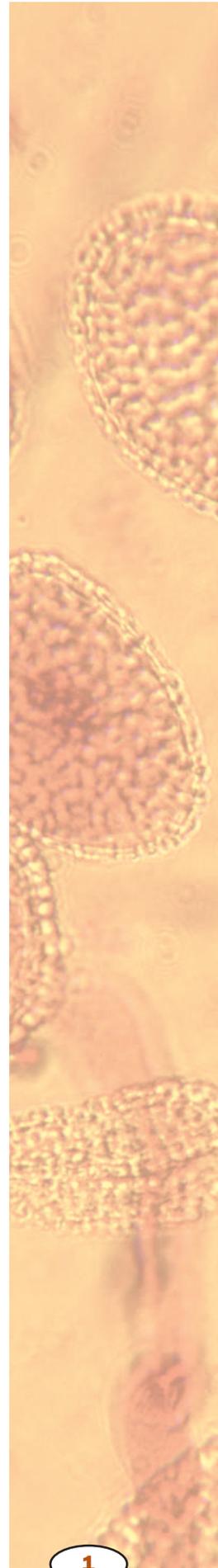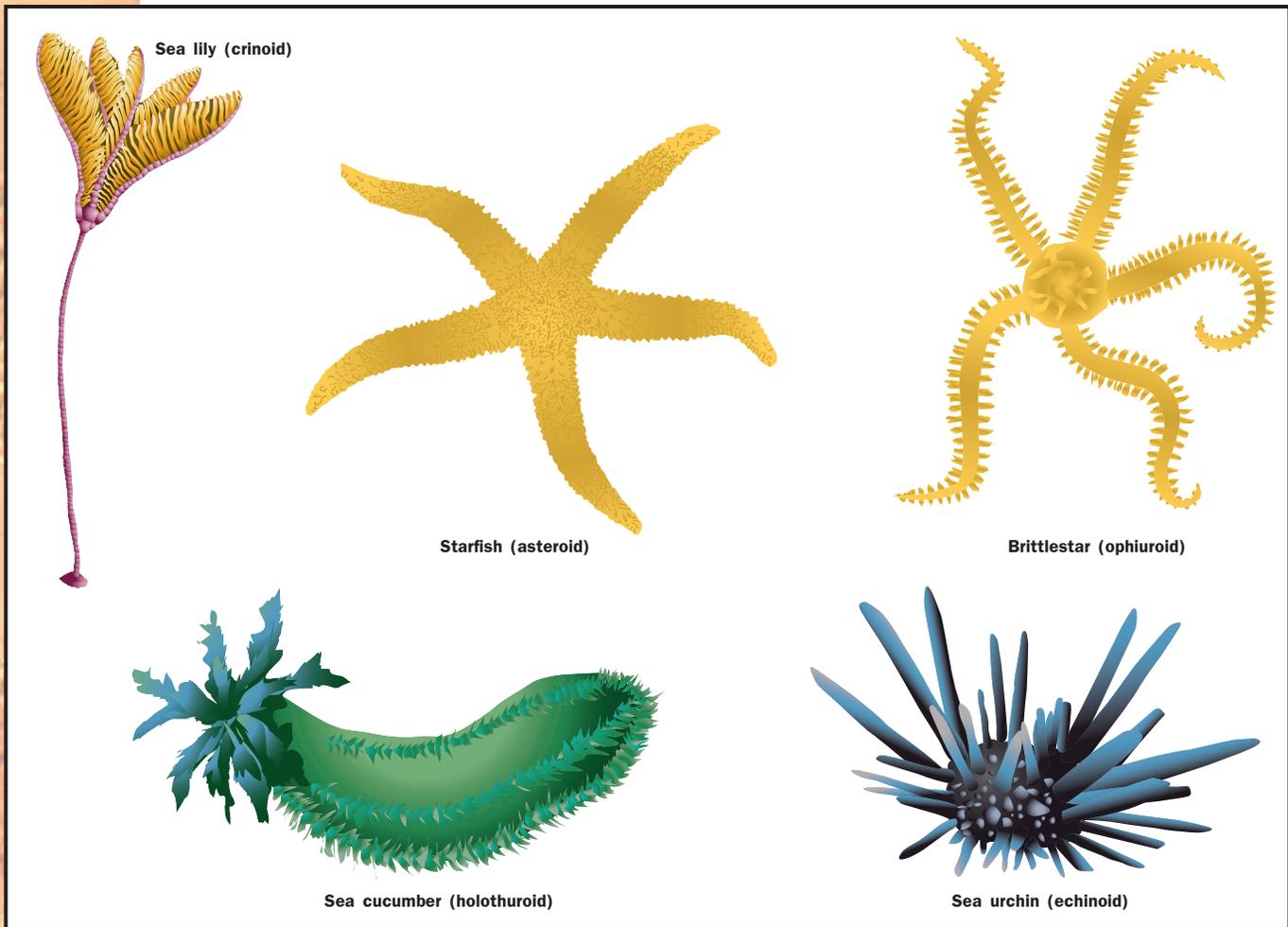
Echinoderms are marine invertebrates that inhabit every conceivable ocean environment. They are divided into five subgroups: Crinoidea, Asteroidea, Ophiuroidea, Holothuroidea, and Echinoidea.

bilaterally symmetric symmetric, or similar, across a central line

loosened at will so that these animals can maintain a posture without expending energy by muscular contraction. Echinoderms have an internal set of plumbing tubes, the "water vascular system" that manipulate flexible external tube feet. Tube feet are the "hands" and "feet" of echinoderms, and are involved in sensory, locomotory, feeding, and respiratory activities.

Males and females are separate, and fertilized eggs develop into a typically free-swimming larva that changes (or "metamorphoses") from a **bilaterally symmetric** form to an adult possessing a body structure with the five radiating rays that makes adult echinoderms so distinctive. Even the worm-like sea cucumbers and sea lilies show this five-part structure because the feeding tentacles and arms are usually present in multiples of five.

Echinoderms are relatives, although distant ones, of the vertebrates. Like vertebrates, and unlike other animal phyla, echinoderms are "denterostomes," meaning the mouth pore forms after the anal pore during early development. This makes them ideal subjects for studies that shed light on human development and evolution. In addition, the ecological importance of echinoderms, combined with their sensitivity to environmental degradation, gives them a key role to play in environmental research. SEE ALSO ANIMALIA; CORAL REEF; DEVELOPMENT

Richard Mooi

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Ecological Research, Long-Term

Many ecological studies last just one or a few years. There are many reasons for this. Sometimes people are doing the study as part of their research in graduate school and they want a project they can finish in a few years. Much ecological research is funded by various federal and state agencies, and these grants are normally for only one to three years. The problem with this approach is many important ecological processes occur over longer time frames than this. For example, droughts and fires play a very important role in determining what trees can grow in certain environments, such as **savannas**. If one studied a savanna for three years, and no drought or fire occurred during this time, one would never discover the importance of fire and drought in that habitat. Some animals such as snow shoe hares and ruffed grouse experience dramatic fluctuations in the size of their populations. If one conducted a study of just a few years on these species, one would never learn the fascinating fact that these populations experience regular population cycles approximately ten years in length.

savanna open grassland with sparse trees

Thus, although much important ecological information can be learned from short-term studies, long-term studies are essential to understanding many processes that occur over a longer period of time. Fortunately, organizations like the National Science Foundation (NSF), a federal agency that funds much ecological research, have recognized the need to support some long-term ecological studies. In 1980, the NSF instituted a special funding program called the Long Term Ecological Research (LTER) program. Instead of funding projects for just one to three years, this program funds research for at least five years and usually for much longer. Some projects have been funded for as long as twenty years, and funding is expected to continue for these projects into the future. More than twenty LTER research sites are located throughout North America in almost all the major habitats, including prairies, forests, deserts, mountains, tundra, freshwater lakes, and ocean coastal environments. This funding has enabled scientists to study such important issues as the long-term effects of acid rain on forests and aquatic organisms, the long-term effects of pollution on native prairie plants, and the possible impacts of rising atmospheric carbon dioxide levels on forest growth.

Ecologists are particularly interested in the possible ecological effects of global warming. Since this is a process that occurs over decades, and even centuries, very long studies are needed. Some of these studies are now underway and are expected to continue for decades. In other cases, ecologists have made use of data collected in the past to answer certain questions involving global warming. For example, century-old scientific notes and
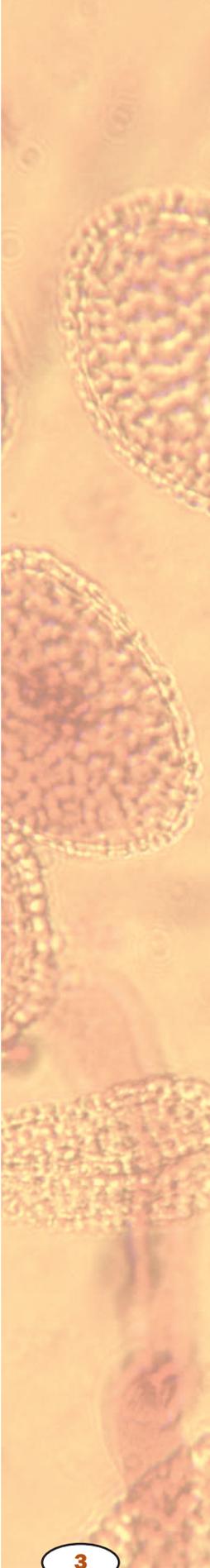
journals containing the spring arrival dates of migrating birds and blooming dates of wildflowers have shown that spring is occurring about ten days earlier in Europe and North America than it was 150 years ago. Some churches in Europe have recorded the dates of **ice-out** in nearby lakes for several hundred years. These continuous monitoring efforts represent some of the longest ecological data sets in existence. SEE ALSO COMMUNITY; ECOLOGY; ECOSYSTEM; FIRE ECOLOGY; GLOBAL CLIMATE CHANGE; LANDSCAPE ECOLOGY

Mark A. Davis

ice-out a thawing of ice covering a lake or other body of water

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Ecology

Ecology is the study of how plants, animals, and other organisms interact with each other and with their environment, or "home." The word "ecology" comes from the Greek word *oikos*, which means "home." Ecology is also the study of the abundance and distribution of organisms. An ecologist, for example, might try to find out why a species of frog that used to be common is now rare, or why fir trees are rare in a dry pine forest but common in a moister habitat.

Ecologists study living organisms in different ways. One might study a population, a group of individuals that can interbreed with each other; a community, the many species that inhabit an area; or an ecosystem, a community of organisms along with the nonliving parts of their environment. The nonliving parts, which ecologists refer to as "abiotic" components, include air, water, soil, and weather.

Population ecologists study what makes populations go extinct, what regulates populations at intermediate densities, and what makes populations increase in size. A major cause of extinction is loss of habitat or the break up of habitat into patches. Community ecologists study the relationships among different species; for instance, how groups of predators and prey affect one another.

The study of ecosystems means examining how all the parts fit together. An example of this is carbon in the atmosphere, which is taken up by plants during photosynthesis. Animals eat the plants, or eat the animals that ate the plants, and then exhale the carbon as carbon dioxide. The carbon cycles through networks of organisms, the atmosphere, and the Earth itself. Another example are shellfish, which make their shells from carbon. These shells drop to the bottom of the ocean to form thick sediments. Millions of years later, geological processes lift them up as mountains. The study of ecosystems is truly the study of life on the Earth. SEE ALSO COMMUNITY; ECOLOGY, HISTORY OF; ECOLOGICAL RESEARCH, LONG-TERM; ECOSYSTEM; PLANKTON; POPULATION DYNAMICS; THEORETICAL ECOLOGY

Jennie Dusheck

Founded in 1915, the Ecological Society of America is a non-profit organization of scientists that aims to promote ecological science, increase the resources available for the conduct of ecological science, and ensure the proper use of ecological science in environmental decision-making by improving communication between the ecological community and policy-makers.

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Ecology, History of

Ecology descended from a tradition of natural history beginning in antiquity. What has been called **protoecology** is seen in the writings of Carolus Linnaeus, a Swedish botanist, who, in the eighteenth century, wrote of interactions of plants and animals, which he called *The Economy of Nature.* In the early nineteenth century a German biogeographer, Alexander von Humboldt, stimulated the study of the distribution of vegetation as communities of plants and their environment that was pursued into the twentieth century by such European botanists as Oscar Drude and Eugene Warming. Edward Forbes, a British marine biologist, studied seashore communities early in the nineteenth century and was among the first to use quantitative methods for measuring water depth and counting individual organisms.

protoecology early ecology

Early Roots

The name *ecology*, however, was coined in 1866 by German biologist Ernst Haeckel, a prominent proponent of Darwinism. In 1870 Haeckel wrote, "Ecology is the study of all those complex interactions referred to by Darwin as the conditions of the struggle for existence." (Darwin himself figures prominently in protoecology.) Ecology emerged as a recognized science in the 1890s and early 1900s as a mix of oceanography, its freshwater counterpart limnology, and plant and animal ecology. It departed from the late-nineteenth-century emphasis on laboratory studies of physiology and genetics to return to the field emphasis of traditional natural history. Premier British animal ecologist Charles Elton defined ecology as scientific natural history.

In the United States, ecology flourished particularly in the Midwest. S. A. Forbes of the Illinois Laboratory of Natural History initiated studies of lakes and streams in the 1880s. In the 1890s Edward A. Birge pioneered lake studies at the University of Wisconsin. Frederic Clements initiated vegetation studies at the University of Nebraska and formulated ideas of ecological communities in the 1890s that dominated American ecology for fifty years. In the same decade Henry C. Cowles, from the University of Chicago, studied the vegetation of the dunes of Lake Michigan.

Clements and Cowles, among the first to earn advanced degrees in ecology, examined the changes of plant species populations, communities, and environments over time, a process they called **succession**, adapting the term from poet-naturalist Henry D. Thoreau. Clements's concept of succession, which dominated ecology until the 1950s, was of communities developing progressively to a relatively stable state, or climax, that he said had properties of a superorganism. Ecology became institutionalized in British and American ecological societies in 1913 and 1915, respectively.

succession series of changes seen in some plant communities over time, in which low-growing, rapidly reproducing species are replaced by taller and more slowly reproducing ones

Ernst Haeckel, the German biologist who coined the term "ecology."

Integration and Quantification

Charles Elton wrote the first book on animal ecology in 1927 and provided organizing ideas that served to integrate population and community ecology and remain as key concepts. These were:

1. Food chain or cycle (later called food web or trophic structure): the sequence by which nutrients and energy passed from plants to herbivores to predators then to various forms of decomposers and back to the inorganic environment.

2. Niche: Each species had adaptations that fitted it to a particular status in a community.

3. Pyramid of numbers: More small animals are required to support fewer large organisms in a food chain because some nutrients and energy are lost from the food chain.

The 1920s and 1930s also produced early developments in quantitative ecology and mathematical theory. Ecological studies increasingly used quantitative samples of populations and communities to assess the numbers and kinds of organisms in a habitat and to measure the physical environment. Theoretical, mathematical, population ecology was an attempt, particularly by a physicist, Alfred Lotka, and a mathematical biologist, Vito Volterra, to extend principles of physical chemistry into ecology in the form of a differential equation, the logistic, that describes the growth of a population over time.

Ecological theory flourished in the 1950s in the work of George Evelyn Hutchinson and Robert MacArthur, who formulated a niche theory of animal communities predicated on competition among species. Also in the 1950s, the long-ignored, individualistic concept of community of Henry A. Gleason, which held that organisms responded individualistically to the physical environment and other organisms, was resurrected and became widely accepted as alternative to the superorganism theory of Clements. Ecologists became increasingly aware of the significance of historical and chance events for developing ecological theory.

Ecosystems and Human Influences

British ecologist Sir Arthur Tansley recognized that it was not possible to consider organisms apart from their physical environment, as ecologists conventionally did, and in 1935 coined the term "ecosystem." Ecosystems are integrated systems of living organisms (biotic) and inorganic (abiotic) conditions. The ecosystem concept was integrated with the trophic concept and succession in 1942 by a young American limnologist, Raymond Lindeman. Ecosystem ecology focused on the movements of matter and energy through the food web. Partly through the influence of American ecologist Eugene Odum, ecosystem ecology became one of the principal forces in ecology in the 1960s and 1970s and the basis of a new theoretical ecology termed "systems ecology."

As ecology developed as a science it became evident that its concepts of population, community, environment, and ecosystem must incorporate human beings and their effects on Earth. This, too, had antecedents in nineteenth-century natural history. In 1864 George Perkins Marsh argued that

human actions have profound, reciprocal, and commonly destructive effects on the earth on which humanity depends. Early ecologists were acutely aware of the implications of ecology for human environments and worked on agricultural, fisheries, wildlife, disease, and conservation problems. This insight became widely evident to the American public and politicians with the recognition in the 1970s of the environmental crisis. In 1962 marine biologist Rachel Carson provided an early warning of the threat of herbicides and pesticides to the environment, a warning for which she was castigated by the chemical industry that produced them and the agricultural industry that used them injudiciously.

Aldo Leopold, an American forester turned animal ecologist, published the *Sand County Almanac* in 1949 as a plea for an ecological view of the earth and of humanity. Leopold wrote: "That land is a community is the basic concept of ecology, but that land is to be loved and respected is an extension of ethics." Leopold's ideas influenced conservationists and philosophers, especially ethicists, and extended ecological ideas to a concerned public. SEE ALSO BIOGEOCHEMICAL CYCLES; BIOGEOGRAPHY; CARSON, RACHEL; COMMUNITY; ECOLOGY; ECOSYSTEM; LINNAEUS, CAROLUS; THEORETICAL ECOLOGY; VON HUMBOLDT, ALEXANDER

Robert P. McIntosh

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Ecosystem

An ecosystem is all the living organisms in an area along with the nonliving, or abiotic, parts of their environment. The abiotic parts of an ecosystem include physical substances such as soil, air, and water; forces such as gravity and wind; and conditions such as temperature, light intensity, humidity, or salinity.

Components and Boundaries

Physical substances can include **organic** materials that were once alive, such as bits of wood from trees, rotting plant material, and animal wastes and dead organisms. The physical substance of an ecosystem also includes **inorganic** materials such as **minerals**, nitrogen, and water, as well as the overall landscape of mountains, plains, lakes, and rivers.

The organisms and the physical environment of an ecosystem interact with one another. The atmosphere, water, and soil allow life to flourish and limit what kind of life can survive. For example, a freshwater lake provides a home for certain fish and aquatic plants. Yet, the same lake would kill plants and animals adapted to a saltwater estuary.

organic composed of carbon, or derived from living organisms

inorganic not bonded to carbon

minerals iron, calcium, sodium, and other elements needed by living organisms

Just as the environment affects organisms, organisms affect their environment. Lichens break down rock. Trees block sunlight, change the acidity and moisture content of soil, and release oxygen into the atmosphere. Elephants may uproot whole trees in order to eat their leaves, beavers dam streams and create meadows, and rabbits nibble grasses right down to the ground.

Ecosystems are not closed; in fact, an ecosystem's boundaries are usually fuzzy. A pond, for example, blends little by little into marsh, and then into a mixture of open meadow and brush. A stream brings nutrients and organisms from a nearby forest and carries away materials to other ecosystems. Even large ecosystems interact with other ecosystems. Seeds blow from place to place, animals migrate, and flowing water and air carry organisms— and their products and remains—from ecosystem to ecosystem.

All ecosystems taken together make up the biosphere, all living organisms on the earth and their physical environment. The biosphere differs from other ecosystems in having fixed boundaries. The biosphere covers the whole surface of the earth. It begins underground and extends into the highest reaches of the atmosphere.

Feeding Relations

Ecologists divide the living, biotic part of an ecosystem into two groups of organisms: the autotrophs and the heterotrophs. Autotrophs, also called primary producers, are organisms that make their own food. The vast majority of autotrophs (literally self-nourishers) are either plants, algae, or bacteria that use sunlight to make sugars from carbon dioxide in the air through photosynthesis.

Heterotrophs (which means "nourished by others"), also called consumers, are organisms that consume other organisms. Heterotrophs include animals, protists, and bacteria, or fungi. Animals that eat plants, such as deer and caterpillars, are called herbivores. Animals that eat other animals, such as mountain lions and wasps, are called carnivores.

Decomposers are heterotrophs that feed from the carcasses of dead animals or dead plants. If they are animals, such as millipedes, lobsters, starfish, clams, and catfish, scientists sometimes call them scavengers. Many animals, including starfish, lions, hyenas, and humans, change from carnivore to scavenger and back, depending on what food source is available.

Some of the most important decomposers are nearly invisible. These are the detritivores: fungi, bacteria, and other organisms that feed on the remains of dead plants and other organisms. Each year, detritivores break down the remains of millions of tons of dead plant and animal material, recycling nutrients back into ecosystems around the world.

food web set of feeding relations in an ecosystem

Because animals eat one another, they can be linked in food chains, where, for example, a hawk eats a snake, which has eaten a ground squirrel, which has eaten a seed. Every ecosystem has numerous food chains that interlink to form a **food web**. A food web can change over time. In one year, a population explosion of oak moths means that insect predators focus on oak moth caterpillars. In another year, oak moths are rare, and predators eat a diversity of other herbivores.

trophic related to feeding

Ecologists assign the organisms in a food web to different **trophic** levels, depending on where they get their energy. Plants, which get their en-

A temperate rain forest. Rain forests have more organisms per square meter than any other ecosystem.

ergy directly from the sun, are in the first trophic level; caterpillars, which get their energy from plants, are in the second; birds that eat caterpillars are in the third. Predators that eat the birds would be in a fourth trophic level. Predators may eat at more than one level. (Humans are an example.)

Productivity and Nutrient Cycling

Every ecosystem is unique, yet similar ecosystems share fundamental characteristics, including climate, productivity, total mass of living organisms, and numbers of species. For example, tropical rain forests have higher species diversity than temperate forests.

In the same way, marshes all have high productivity and deserts all have low productivity. Primary productivity is the amount of energy captured by primary producers during photosynthesis on a square meter of land each year. One factor that determines productivity is latitude and its effect on sunshine. A square meter of land near the North Pole, for example, receives about 700,000 kcals (kilocalories) of sunshine per year, while the same area at the equator receives nearly 2.5 times that much sunshine. So all things
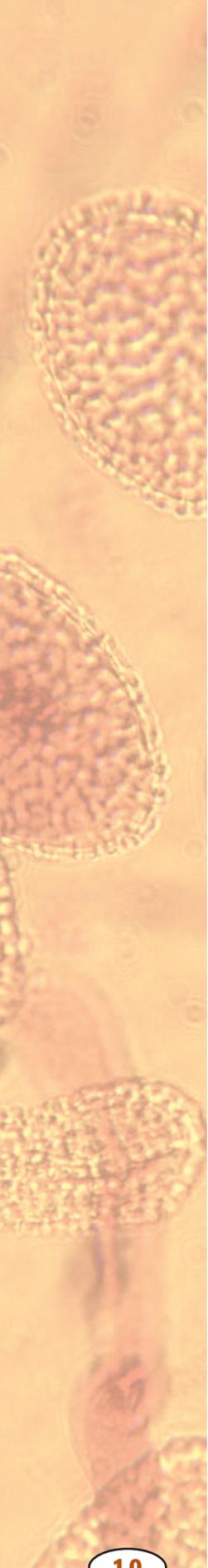
being equal, the tropical region has the potential for higher productivity. However, even in the same latitude, primary productivity varies enormously from ecosystem to ecosystem. A marsh, for example, is twice as productive as a temperate forest, four times as productive as a wheat field, and thirty-five times as productive as a desert.

Another important characteristic of ecosystems is total biomass, the dry weight of all the organisms living in it. Rain forests have more organisms per square meter and therefore more total biomass than other ecosystems, more even than the superproductive marshes.

On land, the biomass of plants is usually greater than the biomass of herbivores, which is greater than the biomass of carnivores. The reason for this is that every chemical process releases energy in the form of heat. So producers can use only part of the energy from the sun to build their bodies; the rest is lost as heat. In the same way, consumers can use only part of the energy in plants to build their own bodies; the rest is lost as heat. Each trophic level passes along only about 10 percent of the energy from the one below. This generalization is called the 10 percent law.

The 10 percent law explains why ecosystems have so few trophic levels and so few individuals at the highest trophic levels. If on a square meter of land, primary consumers store 15,000 kcal/year, herbivores will be able to consume only about 1,500 kcal/year from that meter, and herbivore-eating carnivores will only get 150 kcals, about as many calories as are in a cup of spaghetti. Carnivores must, therefore, roam over large areas to obtain enough to eat.

All sunlight energy eventually escapes from the biosphere in the form of heat. In contrast, the biosphere constantly recycles water, carbon, and other materials. As materials move from one trophic level to another, they may change form, but they rarely escape from the biosphere entirely. A single carbon atom in a fingernail may have been, at different times, part of an apple, part of a trilobite in the ocean, part of a mountain range, part of a dinosaur, or part of the oil in a Texas oil well. Carbon, oxygen, nitrogen, phosphorus, and other materials all pass through many forms—both biotic and abiotic—in a system called a biogeochemical cycle. The biogeochemical cycles of materials such as carbon and oxygen involve the whole biosphere. SEE ALSO BIOGEOCHEMICAL CYCLES; COMMUNITY; DESERT; ESTUARIES; FOREST, BOREAL; FOREST, TEMPERATE; FOREST, TROPICAL; LANDSCAPE ECOLOGY; PLANKTON; POPULATION DYNAMICS

Jennie Dusheck

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Electron Microscopy

The light microscope (LM) is limited in its resolution to about 0.25 micrometers. If two objects are closer together than that, they blur together

and cannot be distinguished by the LM. The electron microscope (EM) overcomes this limitation and achieves resolutions down to 0.2 **nanometers**, allowing useful magnifications of biological material up to several hundred thousand times, and even more for nonbiological specimens. The EM achieves this by using a beam of electrons instead of visible light. Resolution is governed by the wavelength of illumination, and an electron beam has a much shorter wavelength (about 0.005 nanometers) than visible light (about 400 to 750 nanometers). Electron microscopes can therefore resolve objects as small as individual **protein** and deoxyribonucleic acid (DNA) molecules and pores in cell membranes.

The electron beam of an EM is generated by a heated tungsten wire (cathode) and accelerated down an evacuated column by a charge difference of typically 60,000 to 100,000 volts between the cathode and a grounded, mushroom-shaped anode. After passing through a hole in the center of the anode, it is focused on the specimen by electromagnets, which take the place of the glass lenses of a light microscope.

The Transmission Electron Microscope

In the transmission electron microscope (TEM), the electron beam passes through ultrathin tissue sections or small specimens, such as viruses. After passing through the specimen, the electrons strike a fluorescent screen and produce an image. The image can also be captured on photographic film or with a camera that digitizes it for storage on a computer.

Specimens for the TEM are typically fixed with aldehyde and stained with heavy metals, such as osmium, that will absorb or scatter electrons. The specimen is then dehydrated and embedded in a plastic resin. When it hardens, the resin is cut into sections 60 to 90 nanometers thick with a glass or diamond knife. Very tiny particles such as viruses and purified cell **organelles** can be viewed without sectioning by depositing them on a thin membrane. This membrane is treated with a heavy metal "negative stain" so that the specimen stands out as a light image against a dark background.

Areas of a specimen that bind the most osmium absorb the most energy from an electron beam, and are called electron-dense regions. Areas that bind less of the stain allow electrons to pass through more freely and are described as electron-lucent regions. Electrons that pass through the lightly stained, electron-lucent regions lose relatively little energy and produce relatively bright spots of light when they strike the screen. The more heavily stained, electron-dense regions cause some electrons to lose energy and others to be deflected from the beam, and thus produce dimmer spots on the screen. TEM images are essentially shadows caused by accumulations of the heavy metal on cellular structures or, in the case of negative staining, on the supporting membrane.

The Scanning Electron Microscope

The scanning electron microscope (SEM) is used to examine a specimen coated with vaporized metal **ions** (usually gold or palladium). An electron beam sweeps across the specimen surface and discharges secondary electrons from the metal coating. These electrons produce an image on a monitor similar to a television screen. The image on the monitor can be

nanometer 10^{-9} meters; one-billionth of a meter

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

organelle membrane-bound cell compartment

ion an electrically charged particle
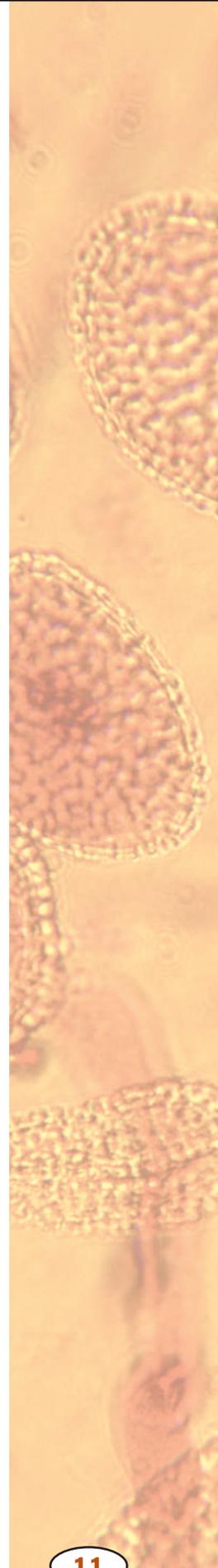
A scientist operating a scanning transmission electron microscope.
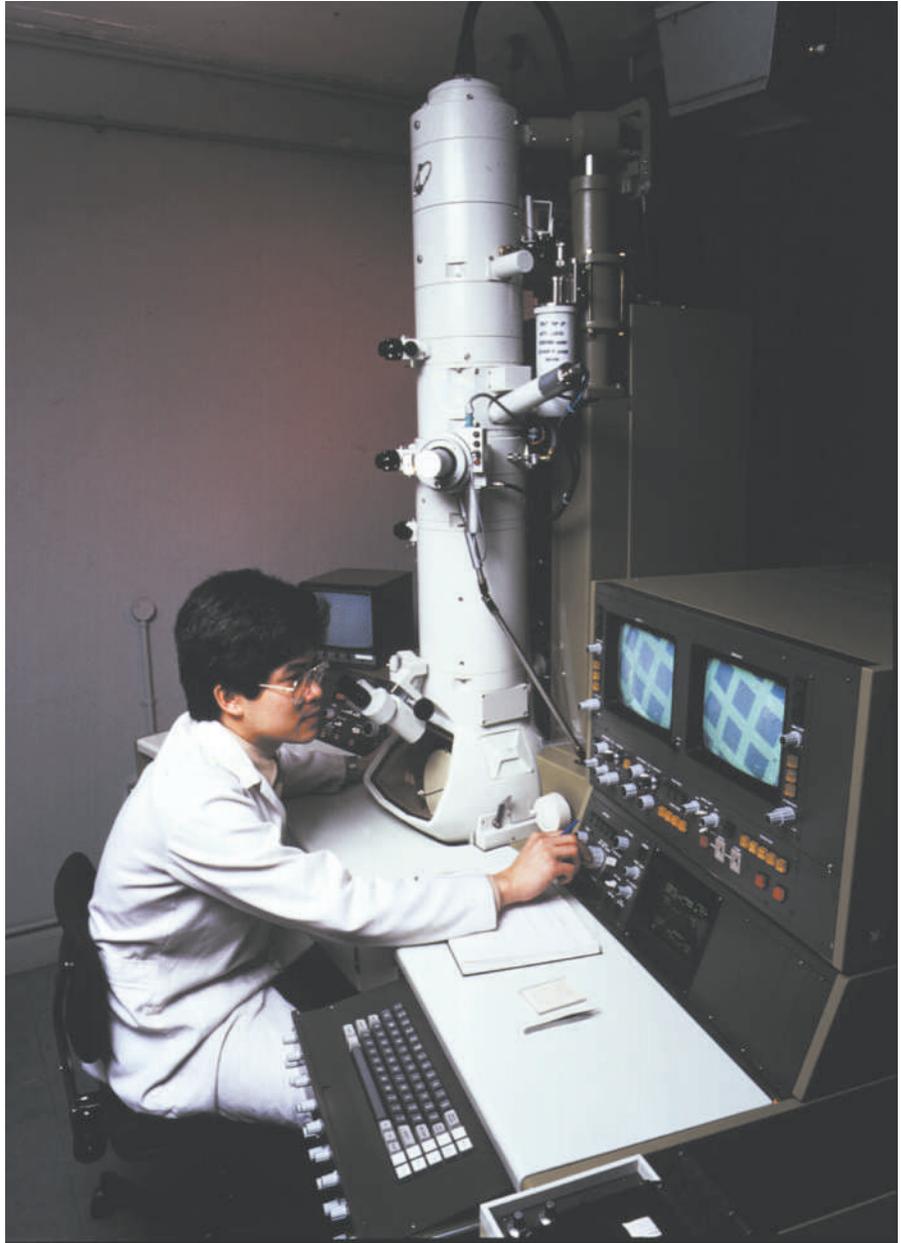
photographed or recorded with a digital camera. The SEM cannot see through a specimen as the TEM does, but can see only the surface where the metal coating is.

The SEM is capable of less resolution and useful magnification than the TEM. However, it produces dramatic three-dimensional images that can yield more information about surface topography than the flat images usually produced by TEM.

Other Variations in Electron Microscopy

Both SEMs and TEMs can be equipped with a detector that monitors X rays given off by a specimen when it is bombarded by electrons. Other types of microscopes irradiate the specimen with ions or X rays and record ions,

electrons, or X rays given off by the specimen. In both cases, the emitted particles and radiation yield information about the chemical composition of the specimen.

A scanning tunneling microscope measures the vertical movement of a tiny probe that is dragged over a specimen, producing a line representation of that movement. An atomic force microscope operates on a similar principle, but measures forces of attraction and repulsion between the specimen and the probe as the probe moves across the surface. In either case, multiple scan lines side by side produce images of the specimen surface, revealing details as small as the "atomic terrain" of individual molecules. SEE ALSO LIGHT MICROSCOPY; MICROSCOPIST

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Electrophoresis

Electrophoresis is one of the most important techniques used by molecular biologists. To name only a few applications, deoxyribonucleic acid (DNA) electrophoresis is used to map the order of **restriction fragments** within **chromosomes**, to analyze DNA variation within a population by restriction fragment length polymorphisms (RFLPs), and to determine the **nucleotide** sequence of a piece of DNA.

Electrophoresis refers to the migration of a charged molecule through a restrictive **matrix**, or gel, drawn by an electrical force. As the force drags the molecule through the gel, it encounters resistance from the strands of the gel, retarding its rate of migration. In gel electrophoresis, larger molecules migrate more slowly than smaller ones, and so the distance of migration within a gel can be used to determine a molecule's size.

Although it is possible to separate whole chromosomes using specialized electrophoresis techniques, DNA that is to be analyzed by electrophoresis is usually cut into smaller pieces using **restriction enzymes**. Fragments of DNA prepared by treatment with restriction enzymes are commonly separated from one another, and their sizes determined, using a gel of agarose electrophoresis, a **complex carbohydrate**. DNA is negatively charged due to the **phosphodiester** bonds that join the individual nucleotide building blocks. DNA will therefore electrophorese toward the positive electrode when placed in an electrical field. To visualize the results after electrophoresis, the gel is soaked in a solution that causes DNA to fluoresce when exposed to ultraviolet light.

restriction fragments fragments of DNA created by restriction enzymes

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

nucleotide the building block of RNA or DNA

The rate of migration is inversely proportional to the logarithm of a molecule's size.

matrix a network, usually of threadlike fibers

restriction enzyme enzyme that cuts DNA at a particular sequence

complex carbohydrate molecules formed by linking simpler carbohydrates such as sugars

phosphodiester the link between two nucleotides in DNA or RNA

An electrophoresis gel, which can be used to determine a molecule's size.

Treatment of the DNA sample with multiple restriction enzymes in various combinations enables the researcher to generate a restriction map of the original DNA fragment, which identifies the sites at the DNA where the restriction enzymes are.

Many research questions require a detailed analysis of one specific DNA fragment in a complex mixture. In such cases, a radioactive DNA probe can be used to identify the fragment based on its nucleotide sequence. The method, known as hybridization, is based on the rules of **complementary base pairing** (A bonds to T, G bonds to C). A probe is designed whose sequence is complementary to the piece of DNA to be detected. The gel-separated DNA is first transferred to a nylon membrane using a technique called a Southern blot.

During the blotting procedure, the strands within the DNA double helix are separated from each other, or denatured, by treatment with a base. Because double-stranded DNA is more stable than single-stranded, during the hybridization the single-stranded probe will locate and bind to the single-stranded gel-separated fragment with complementary sequence.

complementary matching opposite

base pair two nucleotides (either DNA or RNA) linked by weak bonds

Agarose, which is used to make electrophoresis gel, is derived from the seaweed agar.

Being fluorescent or radioactive, the position of the probe can be determined using photographic methods. The target sequence can then be removed by cutting at the piece of the gel that contains it.

The most common technique for determining DNA sequence is the Sanger method, which generates fragments that differ in length by a single nucleotide. High-resolution polyacrylamide gel electrophoresis is then used to separate the fragments and to allow the sequence to be determined.

Electrophoresis of ribonucleic acid (RNA) is an integral procedure in many studies of **gene expression**. RNA is isolated, separated by electrophoresis, and then the gel-separated RNA fragments are transferred to a nylon membrane using a technique called a Northern blot. Hybridization with a single-stranded DNA probe is then used to determine the position of a specific RNA fragment.

DNA and RNA are relatively simple in terms of structure and composition. **Proteins**, however, are composed of twenty different **amino acids** in various combinations, and proteins vary significantly in their three-dimensional structure. The composition of amino acids will affect the charge on the protein, which ultimately will affect its electrophoretic behavior. The shape of a protein similarly will affect its rate of migration. As a result, a specialized technique, SDS-polyacrylamide gel electrophoresis (SDS-PAGE), is usually used to analyze proteins. In this method, protein samples are heated and then treated with the detergent sodium dodecyl sulfate (SDS). Proteins treated in this way are unfolded, linear, and uniformly coated by negatively charged detergent molecules. The rate of migration of treated proteins is inversely proportional to the logarithm of molecular weight. Following electrophoresis, the protein in the gel can be stained to visualize all the proteins in a sample, or the proteins in the gel can be transferred to a nylon membrane (Western blot) and specific ones detected with the use of **enzyme**-linked antibodies.

Regardless of the macromolecule being studied, gel electrophoresis is a crucial technique to the molecular biologist. Many scientific questions can be answered using electrophoresis, and as a result an active molecular biology research lab will have several benches that are devoted to the required specialized reagents and equipment. SEE ALSO DNA SEQUENCING

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Emergency Medical Technician

An emergency medical technician (EMT) is a person who delivers the initial medical treatment to persons in crisis situations. Traditionally, EMTs are part of the medical team that travels by ambulance or helicopter to the site of the emergency situation. The most common medical crises to which EMTs are called include: injuries acquired during automobile accidents and roadway and home births; sudden myocardial infarctions (heart attacks); and wounds resulting from interpersonal violence (such as gun shots and stab wounds).

SANGER, FREDERICK (1918–)

English biochemist who received two Nobel Prizes in chemistry. The first came in 1958, for finding the amino sequence of insulin, the protein that helps regulate blood sugar levels, and the second, in 1980, for inventing a technique to sequence the nucleotides in a strand of deoxyribonucleic acid (DNA).

gene expression use of a gene to create the corresponding protein

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

amino acid a building block of protein

enzyme protein that controls a reaction in a cell

Emergency medical technicians must be trained and certified. There are five levels of EMT training, from First Responders, who are certified in basic emergency medical care, to EMT-4 (paramedics), who are certified to administer drugs, read electrocardiograms, and use other advanced equipment in providing prehospital care. The training process is progressive, starting with EMT 1 (which includes First Responder training), requiring approximately 120 hours of training, through the paramedic level, requiring up to two years of training. Hospitals, trauma centers, private ambulance companies, and fire and police departments employ emergency medical technicians. In fact, many firefighters are also certified EMTs.

In order to be well prepared for EMT training, a strong background in the sciences is important. High school courses such as biology, chemistry, mathematics, and physics are essential prerequisites for EMT training. A good driver's education class is crucial as well, since many EMTs are also ambulance drivers who must negotiate challenging roadway situations in order to reach the crisis scene quickly and safely.

A career in emergency medicine can be very challenging. EMTs must maintain the difficult balance between compassion and emotional fortitude. Strong leadership and interpersonal skills are a must for an emergency medical technician. However, despite the challenges, it is very rewarding to help people and save lives daily. SEE ALSO DOCTOR, FAMILY PRACTICE; DOCTOR, SPECIALIST; MEDICAL ASSISTANT, NURSE

Susan T. Rouse

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Endangered Species

Endangered species are species of plants or animals (or other life forms such as fungi) that are threatened with extinction. As well as being a biological term, "endangered" has a formal political meaning: nations, states, and other organizations evaluate the status of species and determine which are in the greatest danger of going extinct; these species are designated as endangered species. Other species that are declining rapidly in numbers, but are not yet believed to be on the brink of extinction, are designated as threatened species. In the United States, the Endangered Species Act protects such species.

Several factors can cause a species to become endangered. The most common cause is loss of habitat. Much of the world's forests, grasslands, and wetlands are being transformed into agricultural and urban areas, and many species that lived in those habitats are unable to adapt to the new environment. As a result, their numbers can drop greatly in a very short time. In some cases, human hunting or gathering of particular species can drive a species to the brink of extinction. This is the case of the rhinoceros, which has been killed in large numbers during the past century to meet market needs in certain areas of the world. The horn of the rhino is prized for dagger handles in the Middle East and for medicinal uses in parts of Asia. Tigers

A white tiger (*Panthera tigris*) in a zoo. For some species, the only feasible way to preserve the species is to bring all the remaining individuals into captivity.

and sun bears in Asia have likewise been driven to the brink of extinction due to the huge market for animal parts that are believed by many to have potent medicinal powers.

Protection and Reestablishment

There are several ways that people can try to protect endangered species and to keep them from going extinct. One important way is to set up special protected areas around some of the last remaining populations of a species. China has created such reserves for the giant panda. However, for these reserves to be successful, they need to have the support of the resident people that live around the reserve. In some cases, the reserves provide the local people with jobs, and in other cases, some agricultural and even hunting activities are permitted within the reserve.

For some species, their habitat has essentially disappeared, or the species has declined to only a few individuals. In these instances, the only feasible way to try to preserve the species is to bring all the remaining individuals into captivity. One important function of zoos today is to house such endangered species. In some cases, captive breeding programs are initiated to

increase the number of individuals of the endangered species. The ultimate goal of many of these captive breeding programs is to reintroduce the species back into the wild at some future date.

There are several ongoing reintroductions. In the 1980s, when the California condor had declined almost to the point of extinction, the few remaining individuals were captured and placed in captivity. A successful captive breeding program increased the numbers to several dozen individuals, and some have been released back into the wild. Reintroductions of endangered species are not always successful because the reintroduced animals usually have lived only in captivity. Thus, it is often necessary to prepare these animals for their new life in the wild by teaching them how to catch their food and to avoid predators.

Probably the greatest success story of the recovery of an endangered species involves the national bird of the United States, the bald eagle. The bald eagle, like many other birds of prey, fell victim to the heavy use of pesticides by farmers in the 1950s, including DDT. Much of the DDT that was sprayed onto agricultural fields ran off into streams and rivers and lakes when it rained. Small aquatic life consumed some of this DDT, and it remained in their body tissue. When a small fish ate these small aquatic organisms, DDT accumulated in their bodies too and was passed on when a larger fish ate the smaller fish. This process has been referred to as bioaccumulation, or biomagnification.

Thus, by the time the bald eagle ate the larger fish, it was eating contaminated food, and the eagles' own tissues accumulated high concentrations of DDT. One unfortunate consequence of these high concentrations of DDT was the severe weakening of the eggshell laid by the eagle. They were so weak they would often break during the normal parental brooding of the eggs. As a result, the birth rates of the eagles plummeted at the same time the death rates from DDT poisoning rose.

In response to environmentalists like Rachel Carson, who saw how the use of these sorts of chemicals was harming wildlife, the United States banned further use of DDT and provided the bald eagle with special protection under its endangered species status. The eagle populations responded slowly, but in the 1990s the populations began to increase at a rapid rate. In the early twenty-first century, the bald eagle is seen commonly in many parts of the United States and Canada, and its numbers have increased substantially enough that it is no longer considered an endangered species. SEE ALSO BIODIVERSITY; CARSON, RACHEL; EXTINCTION; POLLUTION AND BIOREMEDIATION

Mark A. Davis

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Endocrine System

hormone molecule released by one cell to influence another

The endocrine system is the interacting group of glands that secrete **hormones**, helping to control cells and organs throughout the body. How do cells and organs at different locations in the body communicate with each
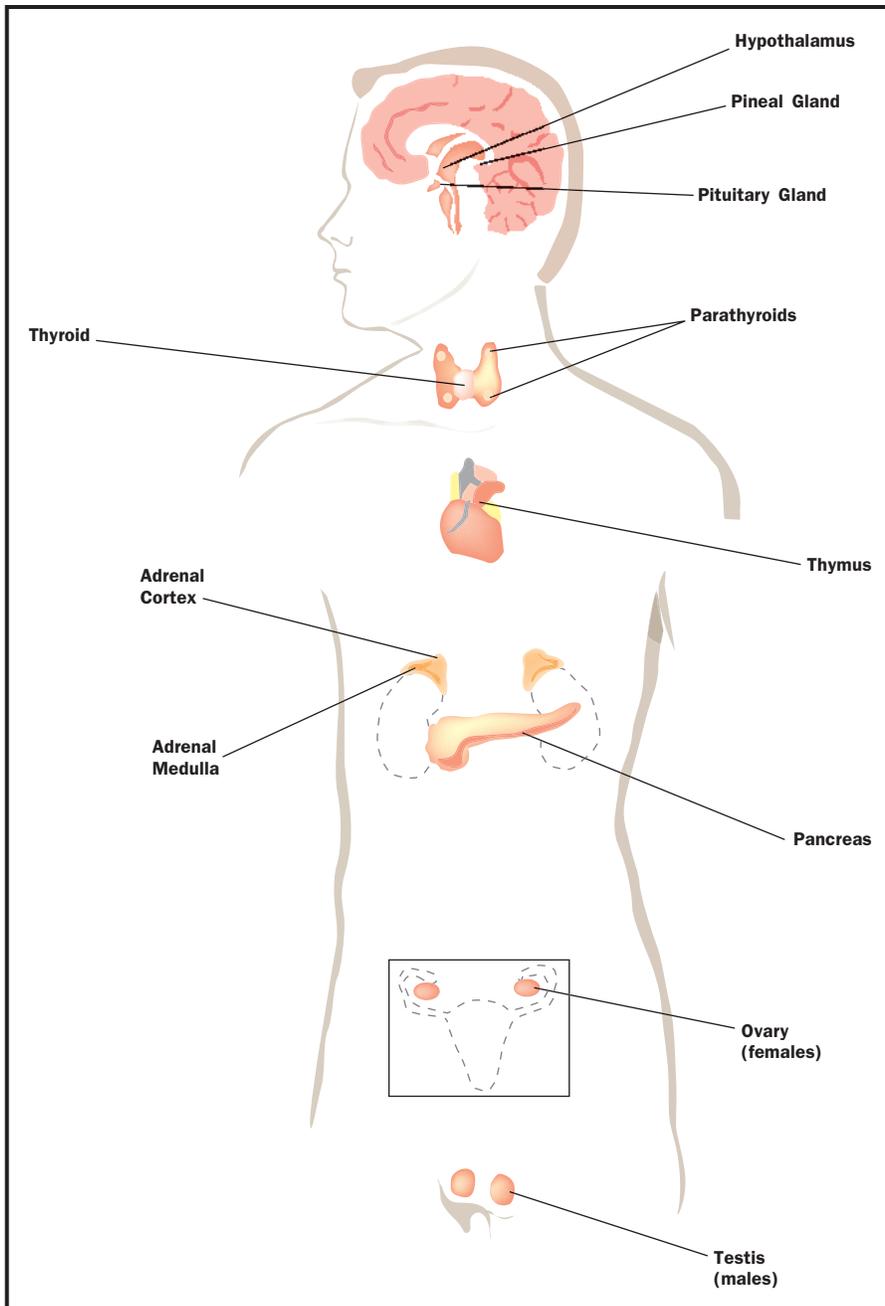
The endocrine organs in the human body.

Hypothalamus

Pineal Gland

Pituitary Gland

Parathyroids

Thyroid

Thymus

Adrenal Cortex

Adrenal Medulla

Pancreas

Ovary (females)

Testis (males)

other to maintain the physiology of healthy living organisms? What happens if organs do not communicate properly? These questions can be answered by understanding how organs of the nervous system and endocrine system function.

There are similarities and differences between how the human nervous system and endocrine system communicate with and control other organs. For example, the nervous system relies on electrical impulses and chemical **neurotransmitters**. Most endocrine organs do not transmit electrical information but instead secrete hormones (from the Greek, meaning "to arouse or excite"), which are molecules that act as chemical messengers.

neurotransmitters molecules released by one neuron to stimulate or inhibit another neuron or cell

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Hormones are released into the bloodstream whereby they travel to organs they affect, known as target organs.

Endocrine organs are located throughout the body, and they have diverse functions controlling events such as cell **metabolism**, blood sugar concentration, digestion, the menstrual cycle in females, and the production of male and female **gametes**. Primary endocrine organs include the hypothalamus, pituitary gland, pineal gland, thyroid and parathyroid glands, thymus, adrenal glands, pancreas, and male and female gonads, the testes and ovaries respectively. Other tissues serve endocrine functions through the hormones they produce. For example, the kidneys produce erythropoietin that stimulates formation of red blood cells, and the skin produces vitamin D, a steroid derivative required for calcium absorption by the small intestine.

Hormones

Hormones are "signaling" molecules because they influence the activity of other cells that may be far from where the hormone was produced. For a hormone to affect a target cell, it must attach to a receptor **protein** on the target cell membrane or inside the cell. Hormone binding to a receptor triggers an intricate set of biochemical interactions that can affect the target cell in myriad ways. For example, hormones can influence cell metabolism, cell division, electrical activity, ribonucleic acid (RNA) and protein synthesis, or cell **secretion**.

There are several different types of hormones that vary in their chemical organization and functions. The majority of hormones are peptides. These consist of short sequences of **amino acids**; examples include insulin and growth hormone. The class of hormones called **steroids** are synthesized from cholesterol—examples include male sex steroids such as testosterone and female sex steroids such as estrogen and progesterone.

Hormone production by an endocrine organ is regulated by complex interactions, called **feedback** loops, between the endocrine organ and its target organs. Feedback loops are two-way modes of communication in which a target organ also releases molecules that regulate the endocrine organ. Feedback loops are designed to maintain hormone concentration within a normal range. Endocrine disorders in which hormone concentration becomes abnormal can be difficult to diagnose and treat because of the complexity of feedback loops. One simple way to classify endocrine disorders is based on whether a condition is due to excess production (hypersecretion) or underproduction (hyposecretion) of hormone.

The Major Endocrine Glands

Located at the base of the brain, the pituitary gland produces many hormones that regulate other organs. Because of this, the pituitary is often referred to as the "master" endocrine gland, although the term "central" endocrine gland is more correct because hormone release by the pituitary is primarily regulated by a brain structure called the hypothalamus, which acts to connect the nervous system to the endocrine system. The hypothalamus produces hormones that stimulate or inhibit the release of pituitary hormones. The hypothalamus also produces antidiuretic hormone, which regulates water balance in the body by inhibiting urine formation by the

metabolism chemical reactions within a cell

gamete reproductive cell, such as sperm or egg

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

secretion material released from the cell

amino acid a building block of protein

steroids hormones such as testosterone or estrogens that control many aspects of physiology

feedback process in which the output or result influences the rate of the process

A frontal-view scintigram of a normal human thyroid. Part of the endocrine system, the thyroid controls basal metabolic rate.
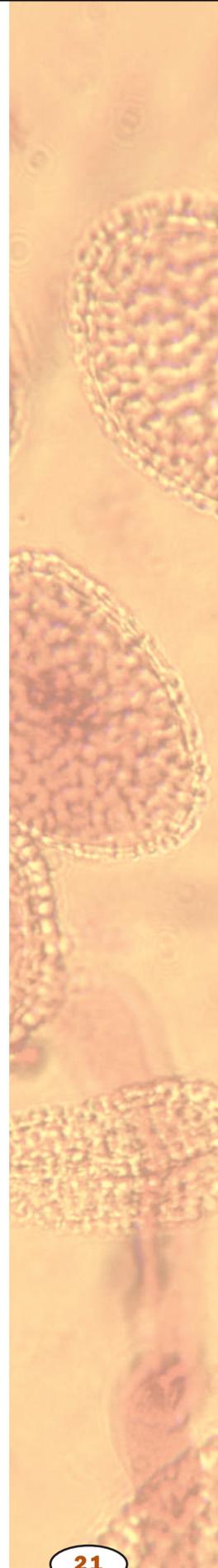
kidneys, and a hormone called oxytocin, which stimulates uterine contractions during childbirth and releases milk during breast-feeding.

Hormones released by the pituitary include growth hormone, which increases during childhood and stimulates the growth of muscle, bone, and other tissues. Sporadic bursts in growth hormone release often result in rapid growth "spurts" associated with adolescence. Hyposecretion of growth hormone can result in dwarfism, whereas hypersecretion of growth hormone can cause gigantism and other disorders. The pituitary also produces follicle-stimulating hormone and luteinizing hormone, which stimulate gamete production and sex steroid production in male and female reproductive organs, and prolactin, which stimulates milk formation in the mammary glands.

Located adjacent to the **larynx**, the thyroid gland primarily produces thyroxine and triiodothyronine, collectively referred to as thyroid hormone. Thyroid hormone stimulates growth of muscles and bones, carbohydrate metabolism, and basal metabolic rate. Its production requires iodine; the lack of dietary iodine causes goiter, a thyroid gland that is overly enlarged in an effort to compensate for the thyroid hormone deficiency.

larynx "voice box"; muscles at the top of the trachea that control pitch and loudness

Effects of thyroid disorders in children and adults can differ widely. For example, hyposecretion of thyroid hormone in infants causes **congenital** hypothyroidism, a disease characterized by mental retardation and poor body growth; hyposecretion in adults produces myxedema, with symptoms such as **lethargy**, weight gain, and dry skin. Conversely, hypersecretion of

congenital present at birth; inherited

lethargy lack of excitability; torpor

thyroid hormone in adults causes Graves' disease, a condition characterized by weight loss, nervousness, and dramatic increases in body metabolism. The thyroid also produces calcitonin, a hormone that regulates blood calcium concentration.

The adrenal glands are small organs on the apex of each kidney. The outer layers of cells in the adrenal gland, called the adrenal cortex, produce several hormones that affect reproductive development; mineral balance; fat, protein, and carbohydrate balance; and adaptation to stress. The inner part, called the adrenal medulla, secretes epinephrine and norepinephrine, which activate the **sympathetic nervous system** and stimulate the "fight-or-flight" response that helps the body cope with stressful situations, such as fear.

The pancreas produces insulin and glucagon, which function in opposing fashion to regulate blood sugar (glucose) concentration. When blood **glucose** level rises—for example, after eating a sugar-rich meal—insulin lowers it by stimulating glucose storage in liver and muscle cells as long chains of glucose called **glycogen**. Conversely, between meals, blood glucose level decreases. In response, the pancreas releases glucagon, which stimulates glycogen breakdown and subsequent release of glucose into the bloodstream. One of the most well characterized endocrine disorders is diabetes mellitus, resulting from hyposecretion of insulin or, more commonly, target cell insensitivity to it.

Endocrine functions of the gonads are addressed in articles on the male and female reproductive systems. The sex hormone testosterone regulates sperm production in males. Estrogen and progesterone influence egg maturation and release (ovulation) and control the uterine (menstrual) cycle in females.

Although the many hormones produced by human endocrine organs have a wide variety of actions, the common purpose of all hormones is to facilitate organ-to-organ communication necessary for body physiology. SEE ALSO ADRENAL GLAND; ANABOLIC STEROIDS; BLOOD SUGAR REGULATION; FEMALE REPRODUCTIVE SYSTEM; GROWTH; HOMEOSTASIS; HORMONES; HYPOTHALAMUS; NERVOUS SYSTEMS; PANCREAS; PITUITARY GLAND; STRESS RESPONSE; THYROID GLAND

Michael A. Palladino

sympathetic nervous system branch of the nervous system that promotes heightened awareness, increased nutrient consumption, and other changes associated with "fight or flight"

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

glycogen complex carbohydrate used as storage in animals and some other organisms

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Endocytosis

eukaryotic cell a cell with a nucleus

The ability to internalize material from outside the cell is important for several cellular processes including the ingestion of essential nutrients, removal of dead or damaged cells from the body, and defense against microorganisms. **Eukaryotic cells** internalize fluid, large and small molecules, and even other cells from their surroundings by a process called endocytosis. During endocytosis, the plasma membrane of the cell forms a pocket around the material to be internalized. The pocket closes and then separates from the
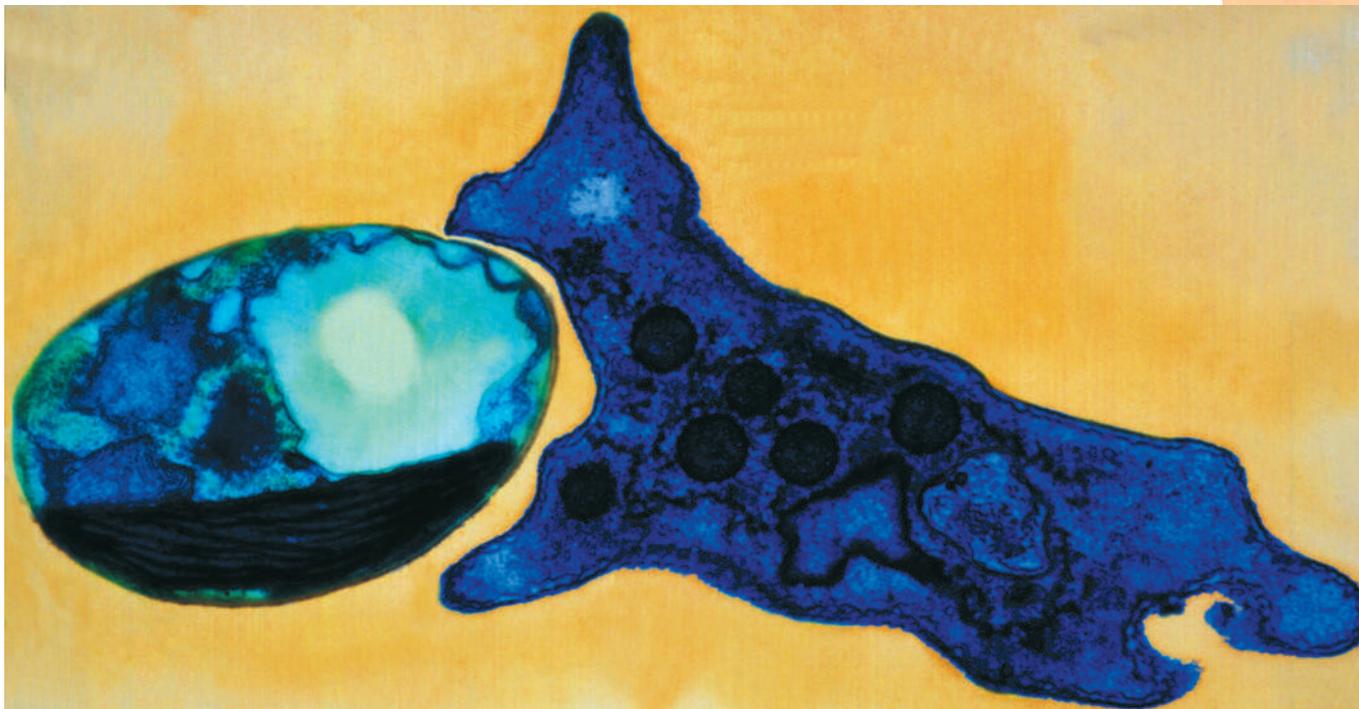
inside surface of the plasma membrane to form a membrane-enclosed bubble, or vesicle, containing the ingested material.

There are two main types of endocytosis that are distinguished by the size of the vesicle formed and the cellular machinery involved. Pinocytosis (cell drinking) describes the internalization of extracellular fluid and small **macromolecules** by means of small vesicles. **Phagocytosis** (cell eating) describes the ingestion of large particles such as cell debris and whole microorganisms by means of large vesicles. While all eukaryotic cells are continually ingesting fluid and molecules by pinocytosis, only specialized phagocytic cells ingest large particles.

Specialized Phagocytic Cells Engulf Large Particles

Phagocytosis begins with the extension of large, handlike projections from the plasma membrane. The projections surround the particle and fuse together so that the particle is completely engulfed in a large vesicle within the cell called a phagosome. Inside the cell, the phagosome fuses with another membranous **organelle** called a lysosome, forming a single membranous organelle and mixing their contents in the process. Lysosomes, acting as the "stomach" of the cell, carry digestive **enzymes** that break down all types of biological molecules. Consequently, after a phagosome fuses with a lysosome, the digestive enzymes break down the ingested material into small molecules that are transported into the **cytosol** and made available for cell use. Many single-celled organisms like **amoebas** and ciliates use phagocytosis as a means to acquire food. In multicellular animals, only specialized types of cells use phagocytosis. For example, in humans, specialized white blood cells called macrophages use phagocytosis to defend the body against infection by engulfing invading microorganisms and to remove cell debris from the body by ingesting damaged or old cells.

A color-enhanced transmission electron micrograph of an amoeba engulfing green algal cell for food. In phagocytosis, a type of endocytosis, large vesicles ingest whole microorganisms.

macromolecules large molecules such as proteins, carbohydrates, and nucleic acids

phagocytosis engulfing of cells or large fragments by another cell, including immune system cells

organelle membrane-bound cell compartment

enzyme protein that controls a reaction in a cell

cytosol fluid portion of a cell, not including the organelles

amoeba a single-celled protist that moves by crawling and can cause diarrhea

All Eukaryotic Cells Constantly Ingest Fluid and Molecules by Pinocytosis

pinocytosis introduction of fluids into a cell by enclosing it and pinching off of the plasma membrane

In contrast to phagocytosis, **pinocytosis** begins with small, convex pits on the cell surface that collect material or fluid to be internalized. The convex pits expand into the interior of the cell forming small vesicles that pinch from the inside of the plasma membrane. All eukaryotic cells have a continuous stream of vesicles budding from the plasma membrane. The constant removal of membrane from the plasma membrane would quickly deplete the plasma membrane if not for the balancing effects of another continual process called exocytosis. Exocytosis is the process by which vesicles from inside the cell fuse with the plasma membrane to secrete material and fluid. So, pinocytosis brings fluid and material into the cell and removes membrane from the plasma membrane, while exocytosis expels fluid and mate-rial from the cell while adding membrane to the plasma membrane. Thus, the two processes work together to continuously recycle the plasma membrane.

hormone molecule released by one cell to influence another

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

The most thoroughly understood form of pinocytosis is receptor-mediated endocytosis. Receptor-mediated endocytosis selectively internalizes specific molecules that are found in low concentrations in the extracellular space, such as **hormones**, growth factors, antibodies, iron, enzymes, vitamins, and cholesterol. The specific molecules to be internalized bind to **proteins** called receptors on the outside surface of the cell. Receptors are proteins that are embedded in the plasma membrane with portions of the protein extending outside the cell to form a binding site for a specific molecule. Once molecules bind to their receptors, the receptors move within the plasma membrane and become concentrated in small depressions called clathrin-coated pits. Clathrin-coated pits are formed when many clathrin protein molecules interact with each other to form a convex, basketlike structure on the inside of the plasma membrane that molds the membrane into a pit. The coated pits then progressively invaginate, or form inward, to form clathrin-coated vesicles that pinch off the plasma membrane into the **cytoplasm**. Hence, the clathrin-coated vesicles carry the receptor proteins taken from the plasma membrane and their bound molecules taken from the extracellular space.

cytoplasm material in a cell, excluding the nucleus

Once a clathrin-coated vesicle pinches from the inner surface of the plasma membrane, the clathrin coat is removed. The "uncoated" vesicle, still carrying receptor proteins and their bound cargo molecules, fuses with another membranous organelle called an endosome. Endosomes function as "sorting stations." In an endosome, molecules are sorted and packaged into new vesicles for transportation to various locations within the cell.

Receptors brought into the cell by receptor-mediated endocytosis have one of several fates after unloading their cargo and leaving the endosome: (1) they can be recycled back to the same area of plasma membrane from which they came; (2) they can be transported to another region of the plasma membrane; or (3) they can be transported to the lysosome where they are degraded. Thus, in contrast to phagocytosis, not all material brought into the cell by receptor-mediated endocytosis ends up in the lysosome for digestion.

Endocytosis of Cholesterol

Receptor-mediated endocytosis was discovered by Michael Brown and Joseph Goldstein, who were investigating the internalization of cholesterol by cells from the bloodstream. Brown and Goldstein won the Nobel Prize in medicine in 1985 for their discovery. Cholesterol, a type of **lipid**, is insoluble and is transported in the bloodstream bound to protein in particles called low-density **lipoproteins** (LDL). The LDL particles bind to LDL receptors on cell surfaces, and the LDL/receptor complexes are concentrated into clathrin-coated pits. The clathrin-coated pits develop into clathrin-coated vesicles that move into the interior of the cell, lose their clathrin coats, and fuse with an endosome. The **acidic** environment of the endosome causes the LDL particles to detach from the LDL receptors, and the two are sorted from each other. The LDL particles are transported to the lysosome where they are broken down by digestive enzymes; the cholesterol is released into the cytosol where it is used in the synthesis of new membrane. The LDL receptors are packaged into membrane vesicles that travel back to and fuse with the plasma membrane (via exocytosis) so that the receptors once again face the exterior of the cell and can pick up more LDL particles to start the cycle again. SEE ALSO EXOCYTOSIS; HORMONES; LIPIDS; LYSOSOMES; MEMBRANE PROTEINS

Cynthia K. Damer and Scott N. Daigle

lipid fat or waxlike molecule, insoluble in water

lipoprotein combination of protein and lipid, or fatlike molecule

acidic having an excess of H⁺ ions, and a low pH

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Endoplasmic Reticulum

The endoplasmic reticulum (ER) is a series of interconnected membranes or flattened sacs adjacent and connected to the nuclear membrane. The ER comes in two different morphological forms: smooth endoplasmic reticulum (sER) and rough endoplasmic reticulum (rER). The primary function of the sER is to serve as a platform for the synthesis of lipids (fats), carbohydrate (sugars) **metabolism**, and the detoxification of drugs and other toxins.

Tissues and organs that directly participate in these activities, such as the liver, are enriched in sER. Morphologically, the rER is studded with **ribosomes** that participate in **protein** synthesis giving its "rough" appearance when viewed with the electron microscope. The proteins synthesized on the ER are transported from the ER membranes by small **vesicles** that pinch off the surface and enter the Golgi membrane stack (cisternae). From the Golgi, the proteins are transported to the cell surface or to other **organelles**.

metabolism chemical reactions within a cell

ribosome protein-RNA complex in cells that synthesizes protein

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

vesicle membrane-bound sac

organelle membrane-bound cell compartment

nucleus membrane-bound portion of cell containing the chromosomes

The Rough Endoplasmic Reticulum (rER)

The rER is a series of stacked membranes closest to the **nucleus** that is the site for synthesis and maturation of proteins destined for the plasma

Rough endoplasmic reticulum in an animal cell. The ER membranes are seen running from the top to the bottom of the image. The small granules attached to the membrane of the ER are ribosomes.

transcribe creation of an RNA copy of a DNA gene

translation synthesis of protein using mRNA code

amino acid a building block of protein

carbohydrates sugars, starches, and other molecules combining carbon, hydrogen, and oxygen and serving as fuel or structural components

oligosaccharide chain of several sugar molecules

conformation three-dimensional shape

enzyme protein that controls a reaction in a cell

hydrophobic "water hating," such as oils

cytosol fluid portion of a cell, not including the organelles

membrane, secretory vesicles, or endocytic vesicles. Many ribosomes stud the cytoplasmic face of the rER, as well as populating the surrounding cytoplasm. Messenger ribonucleic acid (mRNA) **transcribed** in the nucleus leaves the nucleus via the nuclear pores and is transported into the cytoplasm. Docking sites on the head or "N-terminus" of the mRNA allow the ribosome to bind to it and initiate **translation**, decoding the linear sequences of bases in the RNA to an **amino acid** sequence that will constitute a protein.

Translocation into the Lumen. The first segment of the growing peptide consists of a "signal sequence" that binds to a pre-existing signal recognition particle (SRP) from the cytoplasm. The SRP is a small protein/RNA complex that acts as a targeting guide and is essential for protein **translocation** into the rER lumen (interior chamber). The cytoplasmic surface of the rER contains a protein called the SRP receptor that binds to the SRP, anchoring the ribosome with its growing peptide to the rER membrane. As translation proceeds, the peptide is fed into the lumen of the rER where the signal sequence is cut off and additional changes called post-translational modifications proceed immediately.

Glycosylation. Proteins are modified by the addition of **carbohydrates** (glycosylation) to specific amino acids in the peptide chain. One of the most common modifications is to attach an **oligosaccharide** (*oligo* means "few"; *saccharide* means "sugar" or "carbohydrate") to the growing peptide. The branched oligosaccharide is composed of a combination of three sugars: glucose, mannose, and N-acetylglucosamine that can be further modified in the rER and, later, in the Golgi complex. The oligosaccharide modifications on proteins assist in the correct folding of the protein and help stabilize it. The oligosaccharide may also assist in targeting the protein to the correct location in the cell.

Protein Folding. The ER lumen maintains a chemical environment that ensures that proteins are folded into the correct **conformation**. Misfolded proteins are useless and may cause problems if they are detected as "foreign structures" by the immune system of the body. How does the ER ensure that proteins are folded correctly? Newly synthesized proteins are quickly associated with ER "chaperone proteins" and folding **enzymes** that assist in the folding of the proteins into their correct conformations. A protein that is misfolded is retained by the ER and degraded. It is not known exactly how the ER recognizes misfolded proteins, but it may be able to recognize specific domains or segments on the proteins. For example, a **hydrophobic** domain (water-avoiding segment) should be tucked away inside the protein, but a misfolded protein may have this domain protruding outward. Such a protein would be retained and degraded.

Smooth Endoplasmic Reticulum (sER)

Lipid synthesis takes place at the interface of the sER membrane and the **cytosol**. The initial starting material is embedded in the membrane while cytosolic enzymes and building materials continually modify it until the lipid product is complete. How do these lipids, which are made in the sER, get to the plasma membrane or other organelle membranes? There are two models. According to the membrane budding model, a patch of membrane pinches off the ER and forms a vesicle that finds its way to its destination.

In the phospholipid exchange model, water-soluble proteins remove the lipid from the ER membrane and release it into the target membrane.

The ER is also involved in cell signaling by releasing stored calcium **ions** (Ca^{2+}) into the cytosol. This serves to amplify signals from molecules in very low concentrations, such as extracellular **hormones**, thus triggering a response in cells. Without amplification of the initial signal, the cells will not respond to the hormone. The chain of events can be summarized as follows: (1) a hormone binds to a specific receptor on the plasma membrane; (2) the receptor interacts with several other membrane-bound signaling proteins to produce a molecule called inositol 1,4,5-trisphosphate (IP_3), which is released into the cytoplasm; and (3) IP_3 interacts with its own receptor on the ER membrane and passes the signal on to a Ca^{2+} pump. Once the pump is activated, it releases a massive amount of calcium from the ER lumen into the cytoplasm. The Ca^{2+} ions act as "second messengers" that turn on several cellular systems ranging from cell motility to protein synthesis. SEE ALSO GOLGI; LIPIDS; NUCLEAR TRANSPORT; NUCLEUS; PROTEIN SYNTHESIS; RIBOSOME SIGNALING AND SIGNAL TRANSDUCTION

Edward Harris and James Cardelli

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ion an electrically charged particle

hormone molecule released by one cell to influence another

forensic related to legal proceedings

Entomologist

Entomologists study insects and their relatives and use their findings to help people, animals, and plants. Of the many branches of entomology, one of the most interesting is that related to **forensics**. Forensic entomologists help to solve crimes by identifying insects and insect remains at crime scenes. For example, some flies are found only in specific times and places. The police can use such information to determine where and when a crime occurred.

Other entomologists study insects that spread diseases in people. For example, malaria, an infectious disease that affects more people than any other, is spread by a mosquito. Entomologists' specialized knowledge has helped to trace the spread of West Nile virus and Lyme disease in North America.

Entomologists specializing in nervous systems test new brain drugs on cockroaches. Since their nerves work very similarly to those in humans, one can tell if a drug has potential to work on illnesses such as Parkinson's disease. Other entomologists use the existence of specific types of aquatic insects as indicators of water pollution. Many entomologists work in agriculture, helping prevent crop damage while minimizing the amount of pesticide used.

Most entomologists need to have at least a bachelor's degree in entomology. With this degree, a person can work for private companies or the

An entomologist sorts an insect collection from Guanacaste, Costa Rica, for the Institute for Biodiversity, which plans to inventory all living things in Costa Rica.

federal and state governments. Entomologists also work in sales and insecticide application. Usually an additional certification is needed for the latter.

If a student has done well academically while working for the bachelor's, then he or she may start work on the doctor of philosophy (Ph.D.) at any of a number of excellent universities worldwide. With this degree, the entomologist can get jobs as a director of research program or in college teaching. SEE ALSO AGRICULTURE; ARTHROPOD; EPIDEMIOLOGIST; INSECT

David L. Evans

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Environmental Health

congenital present at birth; inherited

pathogenic causing or capable of causing disease

communicable transmissible from person to person

Environmental health describes the effects of civilization, culture, personal habits, pollution, population growth, and travel on human health. It is a new science that measures a variety of factors leading to acquired and **congenital** diseases. Acquired diseases are illnesses people get from exposure to harmful chemicals, injurious activities, and **pathogenic** organisms. Congenital diseases are caused by genetic defects or factors that harm fetal development.

Throughout history people have witnessed the increase in human disease with the growth of agriculture and cities. It was not until the late nineteenth century that people had scientific explanations for the cause of the diseases. Urban growth and overpopulation are associated with higher incidences of **communicable** diseases spread by insects, rats, and humans. Agriculture also resulted in a host of new human diseases. A variety of diseases, such as influenza, measles, and smallpox, may have been developed from diseases originally found in agricultural animals.

The role of pollution and health was not well known to the public until the publication of *Silent Spring*, written by Rachel Carson in 1962. She alerted people to the health effects of pesticides and other pollutants on humans and wildlife. Many scientists supported her views, and this resulted in the formation of the Environmental Protection Agency by the U.S. government in 1970. The National Institutes of Health was later set up to look at other environmental health issues. This agency focuses on illnesses associated with household and work environments. In 1948 the World Health Organization was formed by the United Nations to deal with international environmental health problems.

Occupational health and wellness includes health issues related to the work environment. Some issues include injuries due to certain activities or illness due to handling certain chemicals. Ergonomics is a field of study that has linked conditions such as carpal tunnel syndrome to repetitive hand actions such as continuous typing on a keyboard or handling automobile parts on an assembly line.

Mental health is also a concern of public health agencies working in environmental health. Abuse, poverty, violence, and stressful work environ-

In the past twenty years, plastics have become the most popular material for manufacturing a variety of products including automobiles, household goods, and medical devices. Plastics have replaced many traditional uses of glass, metal, and wood. They have permitted the development of fuel-efficient automobiles, lightweight airplanes, durable furniture, and safer food containers. With all these benefits comes a high environmental cost. Many scientists are discovering that many plastics leak pollutants capable of altering the body's endocrine system, which is responsible for body maintenance, growth, and reproduction.

ments are associated with mental illnesses. Public health agencies seek ways of changing the social environment in attempts to reduce mental disease.

Today, scientists are continuously conducting research linking environmental factors to human illness. There are two types of environmental health research: experimental research and epidemiological research.

Environmental health experiments involve laboratory and field tests that show how an environmental factor can cause a particular disease. For example, animal experiments are showing that many types of water pollution will cause birth defects, cancer, and reproductive disorders. Epidemiological research techniques involve collecting data associating a particular illness to a certain activity or environmental factor. The data are gathered through surveys, public medical records, and field studies. Air pollution has been linked to increases in asthma and emphysema in epidemiology human studies. This was determined by comparing high rates of asthma and emphysema to increased levels of air pollution in an area.

Laws prohibiting smoking in many public areas are recent examples of government policy based on environmental health research. Food safety regulations controlling the amount of pesticides in foods are another example. The Environmental Protection Agency set laws that limit pollution to levels that do not cause illness to humans and wildlife. SEE ALSO CARSON, RACHEL; DISEASE; EPIDEMIOLOGIST

Brian R. Shmaefsky

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Enzymes

Enzymes are incredibly efficient and highly specific biological **catalysts**. In fact, the human body would not exist without enzymes because the chemical reactions required to maintain the body simply would not occur fast enough.

catalyst substance that aids in a reaction without being used up

Think about the soda you drank moments ago before hitting the books. The sugar in the soda was converted to CO_2, H_2O, and chemical energy within seconds of being absorbed by your cells, and this chemical energy enabled you to see, think, and move. However, the 2.2-kilogram (5-pound) bag of sugar in your kitchen cabinet can sit for years and still not be converted to CO_2 and H_2O. The net reaction (glucose $+ 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O$) is the same in both cases, and both pathways are thermodynamically favorable. However, the human body speeds the overall reaction through a series of enzyme-mediated steps. The key is in the catalytic power of enzymes to drive reactions on a time scale required to digest food, relay signals via the nervous system, and contract muscles.

How do enzymes do what they do? They create an environment to make the reaction energetically more favorable. This environment, the **active site**,

active site surface region of an enzyme where it catalyzes its reaction
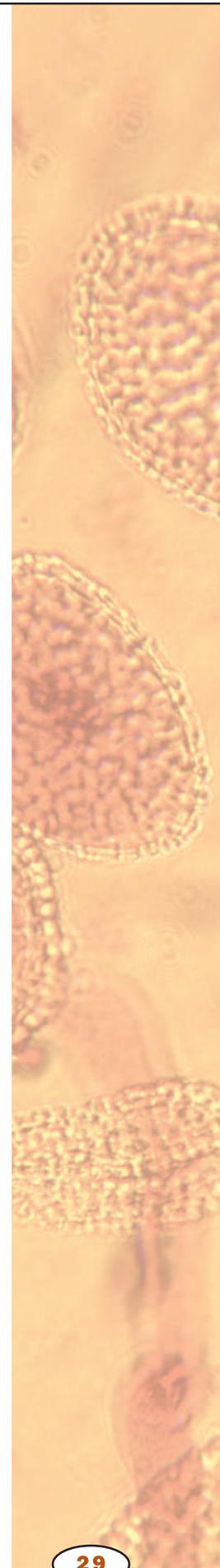
amino acid a building block of protein

substrate the molecule acted on by an enzyme

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

pH measure of acidity or alkalinity; numbers below 7 are acid, above are basic

Glucose

Hexokinase enzyme

Glucose in active site

Glucose-hexokinase complex
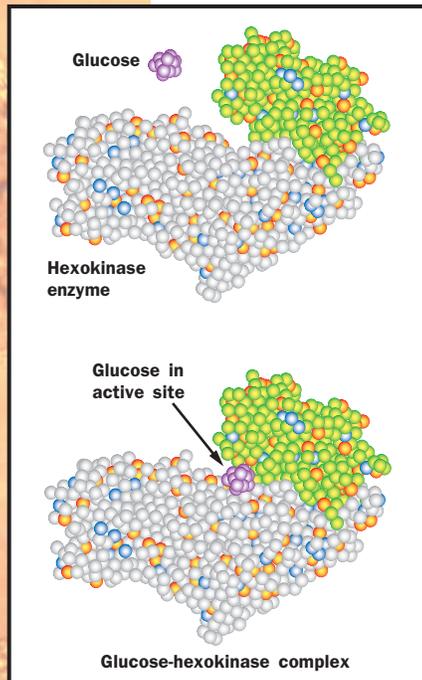
Figure 1. The active site is a groove or pocket on the enzyme surface, into which the substrate (here, a glucose molecule) binds and undergoes reaction.

catalyze aid in the reaction of

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

is typically a pocket or groove that is lined with **amino acids** whose side chains bind the **substrate** (such as sugar) and aid in its chemical transformation to products (see Figure 1). Therefore, the amino acids that form the active site provide the specificity of substrate binding and the proper chemical environment so that the reaction occurs more rapidly than it otherwise would.

Enzymes are central to every biochemical process that occurs in the body. Most enzymes are **proteins**. There are exceptions, however. For example, there are catalytic ribonucleic acid (RNA) molecules called ribozymes that are involved in RNA processing, and, in 1994, the first DNA enzyme was engineered. Although no naturally occurring deoxyribozymes have been identified, these laboratory-generated DNA enzymes are being developed as therapeutic agents to fight infectious disease and cancer.

All enzymes are characterized by having a high degree of specificity for their substrates, and they accelerate the rate of chemical reactions tremendously, often by a factor of a million times or more. Most enzymes function in the cellular environment at mild conditions of temperature, **pH**, and salt. There are few nonbiological catalysts that can be so efficient in this type of environment.

Enzymes play a critical role in everyday life. Many heritable genetic disorders (diabetes, Tay-Sachs disease) occur because there is a deficiency or total absence of one or more enzymes. Other disease conditions (cancer) result because there is an excessive activity of one or more enzymes. Routine medical tests monitor the activity of enzymes in the blood, and many of the prescription drugs (penicillin, methotrexate) exert their effects through interactions with enzymes. Enzymes and their inhibitors can be important tools in medicine, agriculture, and food science.

Four Common Features of Enzymes

Enzymes exhibit four fundamental characteristics. First, enzymes do not make a reaction occur that would not occur on its own, they just make it happen much faster. Second, the enzyme molecule is not permanently altered by the reaction. It may be changed transiently, but the enzyme at the end of the reaction is the same molecule it was at the beginning. Therefore, a single enzyme molecule can be used over and over to **catalyze** the same reaction. Third, an enzyme can catalyze both the forward and the reverse reaction. One direction may be more favorable than the other, but the unfavorable direction of the reaction can occur. Fourth, enzymes are highly specific for the substrates they bind, meaning they catalyze only one reaction.

How Enzymes Work

Take a look at Figure 2. Note that **glucose** ($C_6 H_{12} O_6$) in the presence of oxygen ($6 O_2$) will generate carbon dioxide ($6 CO_2$) and water ($6 H_2O$). The forward reaction from glucose to the top of the energy hill to carbon dioxide and water at the base is energetically favorable, as indicated by the "downhill" position of the products. Because energy is released, the forward reaction sequence is called exergonic. Conversely, to synthesize glucose from CO_2 and H_2O requires energy input to surmount the energy hill and drive the reaction in reverse; therefore, glucose synthesis is called endergonic.
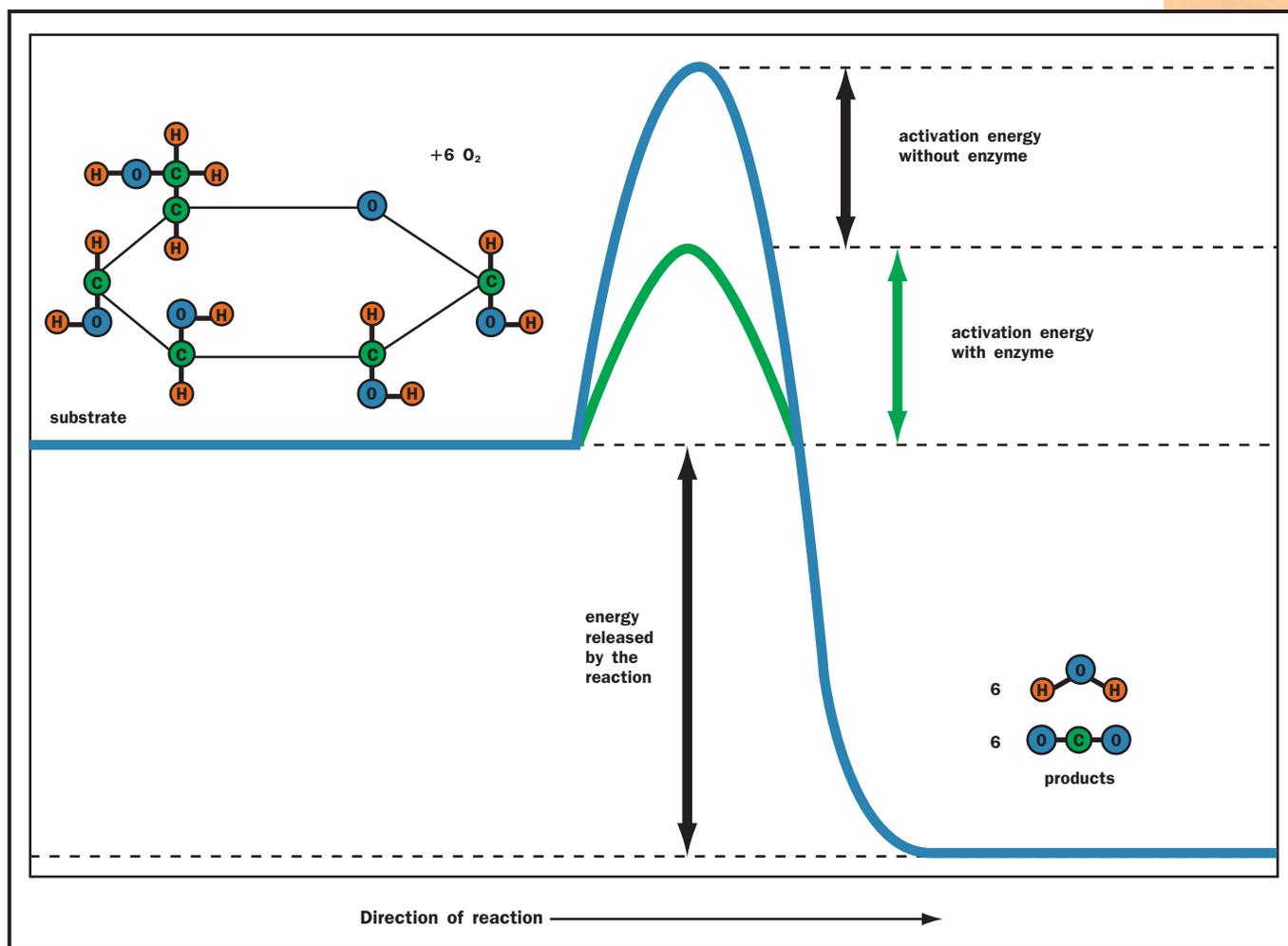
Every biochemical reaction involves both bond breaking and bond forming. The reactant molecules or substrates must absorb enough energy from their surroundings to start the reaction by breaking bonds in the reactant molecules. This initial energy investment is called the activation energy. The activation energy is represented by the uphill portion of the graph with the energy content of the reactants increasing. It is the height of this hilltop that is lowered by enzymes. At the top of the energetic hill, the reactants are in an unstable condition known as the transition state. At this fleeting moment, the molecules are energized and poised for the reaction to occur. As the molecules settle into their new bonding arrangements, energy is released to the surroundings (the downhill portion of the curve). At the summit of the energy hill, the reaction can occur in either the forward or the reverse direction.

Look again at Figure 2. The products CO_2 and H_2O can form spontaneously or through a series of enzyme-catalyzed reactions in the cell. What enzymes do to accelerate reactions is to lower the energy activation barrier (green) to allow the transition state to be reached more rapidly. What is so special about the active site that allows it to accomplish this goal? Several mechanisms are involved.

Figure 2. An energy profile for the glucose reaction. An enzyme (green) enhances the reaction rate by lowering the amount of activation energy required to boost the reactants to the transition state at the summit of the energy barrier.

Proximity Effect. Substrate molecules collide infrequently when their concentrations are low. The active site brings the reactants together for collision. The effective concentration of the reactants is increased significantly at the active site and favors transition state formation.

Orientation Effect. Substrate collisions in solution are random and are less likely to be the specific orientation that promotes the approach to the transition state. The amino acids that form the active site play a significant role in orienting the substrate. Substrate interaction with these specific amino acid side chains promotes strain such that some of the bonds are easier to break and thus the new bonds can form.

Promotion of Acid-Base Reactions. For many enzymes, the amino acids that form the active site have functional side chains that are poised to donate or accept hydrogen **ions** from the substrate. The loss or the addition of a portion (H^+) can destabilize the covalent bonds in the substrate to make it easier for the bonds to break. **Hydrolysis** and electron transfers also work by this mechanism.

Exclusion of Water. Most active sites are sequestered and somewhat **hydrophobic** to exclude water. This nonpolar environment can lower the activation energy for certain reactions. In addition, substrate binding to the enzyme is mediated by many weak noncovalent interactions. The presence of water with the substrate can actually disrupt these interactions in many cases.

Enzymes can use one or more of these mechanisms to produce the strain that is required to convert substrates to their transition state. Enzymes speed the rate of a reaction by lowering the amount of activation energy required to reach the transition state, which is always the most difficult step in a reaction.

Lock and Key or Induced Fit Model

The first ideas about substrate binding to the active site of an enzyme were based on a lock and key model, with the active site being the keyhole and the substrate being the key. When the right substrate entered the active site, **catalysis** occurred because the substrate was perfectly **complementary** to the active site. This model described some enzymes, but not all. For others, binding leads to conformational, or shape changes, in the enzyme active site to enhance the bond breakage and formation required to reach the transition state. In both models, the active site provides the tightest fit for the transition state, and the substrate is drawn into the transition state configuration as a result.

The Cellular Environment Affects Enzyme Activity

Temperature and pH. Enzymes are sensitive to their environmental conditions. Up to a point, the rate of the reaction will increase as a function of temperature because the substrates will collide more frequently with the enzyme active site. At extremes of pH or temperature, either high or low, the native structure of the enzyme will be compromised, and the molecule will become inactive (see Figure 3). Note that there is a sharp decrease in the temperature optimum for typical human enzymes at approximately 40 degrees Celsius (104 degrees Fahrenheit). At temperatures greater than 40

ion an electrically charged particle

hydrolysis splitting with water

hydrophobic "water hating," such as oils

catalysis aiding in the reaction of

complementary matching opposite
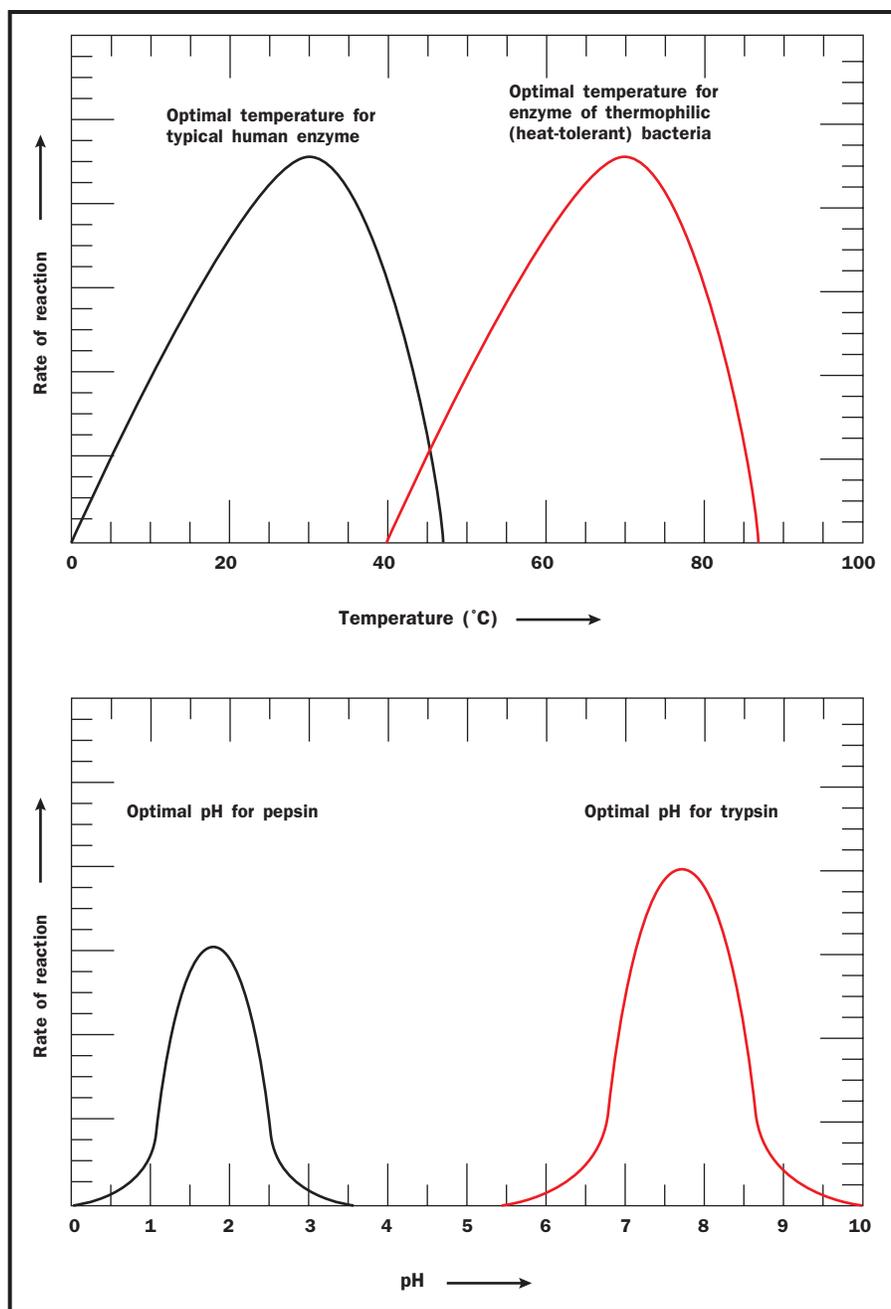
Figure 3. Temperature and pH profiles. Each enzyme has an optimal pH and temperature that favor the native conformation for maximum activity.
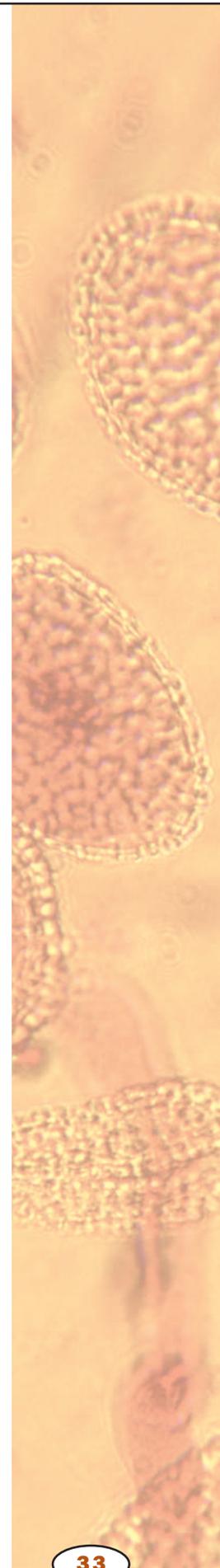
degrees Celsius, the enzyme degrades because the noncovalent interactions that stabilize the native conformation of the enzyme are disrupted. The enzyme in essence falls apart, and the active site is no longer able to function. In contrast, the optimal temperature for enzymes of the thermophilic bacteria (extremophiles) that live in hot springs is quite high at 70 degrees Celsius (158 degrees Fahrenheit), a temperature that would instantly scald skin.

Enzymes also show a pH range at which they are most active (see Figure 3). The pH effect results because of critical amino acids at the active site of the enzyme that participate in substrate binding and catalysis. The ionic or electric charge on the active site amino acids can enhance and stabilize interactions with the substrate. In addition, the ability of the substrate

and enzyme to donate or receive an H^+ is affected by pH. The pH optimum differs for different enzymes. For example, pepsin is a digestive enzyme in the stomach, and its pH optimum is pH 2. In contrast, trypsin is a digestive enzyme that works in the small intestine where the environment is much less **acidic**. Its pH optimum is pH 8.

Cofactors and Coenzymes.   Many enzymes require additional factors for catalytic activity. The cofactors are **inorganic** such as the metal atoms, zinc, iron, and copper. **Organic** molecules that function to assist an enzyme are referred to as coenzymes. Vitamins are the precursors of many essential coenzymes. Cofactors and coenzymes may remain at the active site of the enzyme in the absence of the substrate, or they may be present transiently during catalysis.

Allosteric Inhibitors and Activators.   In addition to the active site where the substrate binds, an enzyme may have separate sites, called allosteric sites, where specific molecules can bind to increase or decrease the activity of the enzyme. The allosteric inhibitors and activators bind the enzyme through weak, noncovalent interactions and exert their effects by changing the conformation of the enzyme, a change that is transmitted to the active site. Typically, the allosteric modulators regulate enzyme activity by affecting substrate binding at the active site.

Control of Metabolism

Although biochemical reactions are controlled in part by the specificity of substrate biding and by allosteric regulation, the human body could not function if all enzymes were present together and all operating maximally with no regulation. There would be biochemical chaos with substances being synthesized and degraded at the same time. Instead, the body tightly regulates enzymes through metabolic pathways and by controlling specific enzymes within a pathway. This approach allows an entire pathway to be turned on or off by simply regulating one or a few enzymes. Metabolic pathways can also be regulated by switching specific genes on or off.

Compartmentation.   One of the major characteristics of **eukaryotic cells** is the presence of membrane-bound **intracellular organelles**. These structures help to segregate specific enzymes and metabolic pathways, especially when the pathways are competing with each other. For example, the enzymes that catalyze synthesis of fatty acids (a type of **lipid**) are located in the **cytoplasm**, while the enzymes that breakdown fatty acids are located in the **mitochondria**.

Covalent Modification.   Enzymes can be activated or inactivated by covalent modification. A common example is **phosphorylation** of an enzyme (addition of a phosphate group to the amino acids serine, threonine, or tyrosine) mediated by another enzyme called a **kinase**. The phosphorylation is reversible, and other enzymes called phosphatases typically catalyze the removal of the phosphate group from the enzyme. The phosphorylated form of the enzyme is often, but not always, the active form. For some enzymes, the dephosphorylated form is active, and the phosphorylated state is inactive. Enzymes can also be activated by removing a fragment of the protein. Many of the digestive enzymes (trypsin, chymotrypsin) are synthesized and stored in the pancreas. They are secreted to the small intestine where
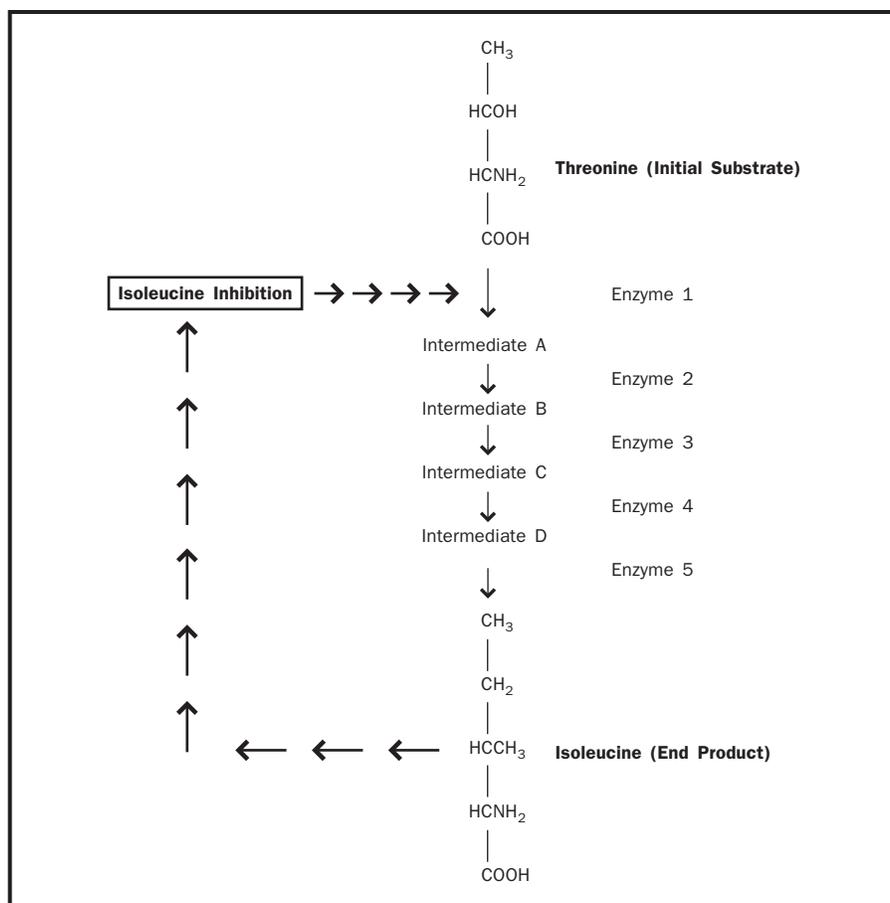
acidic having an excess of H^+ ions, and a low pH

inorganic not bonded to carbon

organic composed of carbon, or derived from living organisms

eukaryotic cell a cell with a nucleus

intracellular within a cell

organelle membrane-bound cell compartment

lipid fat or waxlike molecule, insoluble in water

cytoplasm material in a cell, excluding the nucleus

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

phosphorylation addition of the phosphate group PO_4^{3-}

kinase enzyme that adds a phosphate group to another molecule, usually a protein

they are activated by removing or cleaving off a small portion of the protein. This "proteolytic" cleavage to activate an enzyme is irreversible but serves an important function to prevent the digestive enzymes from digesting the pancreas.

Allosteric Regulation. Allosteric modulators can increase or decrease the activity of an entire metabolic pathway by altering the conformation of a single enzyme. Sometimes, the end product of the metabolic pathway acts as an allosteric inhibitor by binding to the enzyme at its allosteric site, causing a conformational change in the enzyme to decrease the activity of the enzyme. This type of regulation is called **feedback** inhibition (see Figure 4).

Cooperativity. Frequently, enzymes are multisubunit complexes with more than one active site. Binding of the first substrate molecule may lead to conformational changes that are communicated to the other subunit(s) such that the binding of each additional substrate molecule is enhanced. Positive cooperativity can amplify the response of enzymes to substrates and provides an additional mechanism to regulate enzyme activity.

feedback process in which the output or result influences the rate of the process

Molecular Motors

Finally, enzymes can be thought of as nanomachines, powering the reactions of the cell to enable the human body to be the entity it is. There is a special class of enzymes called molecular motors that drive all the movements that occur in the body, including muscle contraction (myosin/actin),

cilia short, hairlike cell extensions of the cell membrane formed by the cytoskeleton

vesicle membrane-bound sac

neuron nerve cell

flagella and **cilia** beating (dynein/microtubule), and **vesicle** movements in **neurons** (kinesin/microtubule). These molecular motors harness the energy from adenosine triphosphate (ATP) to drive actin-based or microtubule-based movements. SEE ALSO CELL MOTILITY; CONTROL MECHANISMS; CYTOSKELETON; GENETIC DISEASES; LIPIDS; MITOCHONDRION; VITAMINS AND COENZYMES

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Epidemiologist

An epidemiologist is a scientist who studies how diseases interact with populations. Most epidemiologists study the relationships between germs and people, but some investigate animal or plant diseases. These scientists study the factors involved in every aspect of a disease, including the start, spread, and treatment.

Three primary types of studies/reports are performed by epidemiologists: descriptive, analytical, and experimental. In descriptive studies epidemiologists determine the physical aspects of existing diseases. For example, they might record the number of cases of chicken pox in a given locale. Analytical studies report on the cause/effect relationships in a disease, such as the reasons behind increased numbers of cholera cases in a flood ravaged area or a decrease in influenza cases due to a mild winter. In experimental studies, epidemiologists test hypotheses about treatment of diseases such as the efficacy (success rate) of a hepatitis vaccine or testing experimental cures for HIV (human immunodeficiency virus) infections on animal models.

Epidemiologists work in a variety of settings, including the field (from urban health clinics to villages in Africa), the laboratory (testing vaccines), or the office (organizing and interpreting data).

In addition, epidemiologists work for a wide range of employers. Governmental services ranging from the Centers for Disease Control (CDC) to local city and county health departments employ many epidemiologists. International health centers such as the World Health Organization (WHO) track worldwide **pandemics** to localized **epidemics** across the globe. Hospitals often employ epidemiologists to assist them in disease control within the hospital. Epidemiologists also work in the private sector, often for pharmaceutical companies tracking the success rate of newly introduced drugs.

The degrees held by people working in epidemiology vary from associate degrees in health sciences to doctoral degrees specializing in epidemiology. Important secondary classes that could be taken to prepare for

pandemic disease spread throughout an entire population

epidemic rapid spread of disease through a population, or a disease that spreads in this manner

epidemiology training include microbiology, biology (advanced and general), medical terminology, biochemistry, and statistics. SEE ALSO BACTERIAL DISEASES; DOCTOR, SPECIALIST; HEALTH AND SAFETY OFFICER; SEXUALLY TRANSMITTED DISEASES; VIRAL DISEASES

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Epithelium

Epithelium is a tissue composed of sheets of cells that are joined together in one or more layers. Epithelia cover the body surface, line body cavities and hollow organs, and form glands. Epithelial tissue forms a barrier between the body and the external environment and plays important roles in protection, filtration, absorption, excretion, and sensation. The rapid regeneration of epithelial cells is important to their protective function. Impervious barriers between cells (tight junctions) allow some epithelia (as in the gut) to tightly regulate flow of materials across them. Glands typically contain clusters of epithelial cells that either secrete their products (such as **hormones**) into the bloodstream or secrete products (such as digestive **enzymes**) by way of ducts onto an epithelial surface, such as the epidermis or stomach lining.

Epithelia are classified on the basis of cell shape and number of layers: Squamous cells are thin and flat, cuboidal cells are cubical to round, and columnar cells are tall and cylindrical. A simple epithelium is composed of a single layer of cells, all of which contact a nonliving basement membrane below. A stratified epithelium is composed of two or more cell layers. Each of these classes has four types of epithelium (see table below).

Simple squamous epithelium is a single layer of flat cells, simple cuboidal epithelium has a single layer of cubical cells, and simple columnar epithelium has a single layer of columnar cells. Pseudostratified columnar epithelium is a simple epithelium that looks stratified because some of its cells are shorter than others and do not reach the free surface.

Stratified epithelia are named for the shape of the cells at the surface; the deeper cells may or may not have a different shape. In stratified

hormone molecule released by one cell to influence another

enzyme protein that controls a reaction in a cell

Type of Epithelium	Typical Locations	Typical Functions
Simple Squamous	lining of heart, blood vessels, and lungs	filtration and secretion
Simple Cuboidal	lining of kidney tubules and other ducts	secretion and absorption
Simple Columnar	lining of gastrointestinal tract	secretion and absorption
Stratified Squamous	epidermis of skin	protection
Stratified Cuboidal	lining of sweat gland ducts	protection
Stratified Columnar	lining of large ducts	protection
Transitional	lining of urinary bladder	elastic properties
Pseudostratified Columnar	lining of the upper respiratory tract	secretion and movement
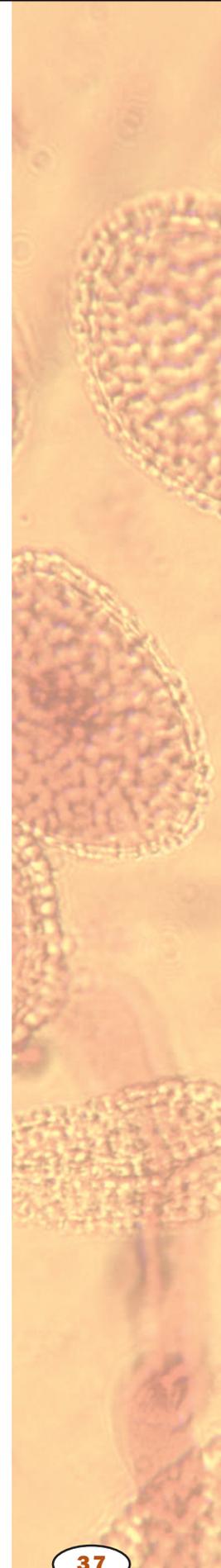
squamous epithelium, the surface cells are flat; in stratified cuboidal epithelium, the surface cells are cubical or round; and in stratified columnar epithelium, surface columnar cells rest on a **basal** layer of cuboidal cells. Transitional epithelium, a stratified type found only in the urinary tract, has cells that change shape and move across each other as an organ, such as the bladder, expands and contracts. SEE ALSO DIGESTIVE SYSTEM; GAS EXCHANGE; SKIN; TISSUE

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Estuaries

Estuaries are partially enclosed bodies of water that occur where the land meets the ocean. The world's largest estuaries are at the ocean ends of rivers that deliver freshwater from surrounding and sometimes remote upland areas. Estuaries may be configured as sounds, bays, lagoons, or networks of tidal creeks and marshes. Many estuaries are separated from the ocean by barrier islands and do not have major sources of freshwater inflow. Estuaries are more common on coasts with wide and shallow continental shelves than on coasts close to **tectonic plate** boundaries.

Estuaries are physically and chemically dynamic and complex **ecosystems**. Annual, seasonal, and daily fluctuations in freshwater input, tidal inundation, temperature, wind, and other hydrological and meteorological factors are responsible for the highly changeable character of estuaries. Due to variations in tidal height, currents, wave exposure, sediment types, salinity, and depth within estuaries, many different types of submerged and intertidal habitats exist. The diversity and interrelatedness of habitats contributes to the biological richness of estuaries.

Temperate and tropical estuaries are among the most biologically productive ecosystems on Earth. Salt marshes dominated by *Spartina* grasses can produce 5 to 10 tons of **organic** matter per acre per year, which is more than most agricultural crops. In tropical estuaries, mangroves are the dominant producers. Submerged seagrass beds, macroalgae ("seaweeds"), and **phytoplankton** also produce organic material that supports abundant and diverse populations of animals. Direct consumption of estuarine plants is important, but many small estuarine animals process decomposing plant material and associated microbes known as detritus. Rich populations of invertebrates living in the sediments and water provide food for shrimps, crabs, fishes, birds, and mammals.

Estuaries support large commercial and recreational fisheries. Crabs, clams, oysters, herrings, drums, striped bass, and other harvested species reproduce and grow within estuaries and rivers. In addition, major fishery species such as shrimps, flounders, mullets, and menhaden, which spawn in the ocean, rely on estuaries as nurseries for juveniles. At least 70 percent of the species harvested in the United States requires a period of estuarine res-

basal lowest level

tectonic plate large segment of Earth's crust that moves in relation to other similar plates

ecosystem an ecological community and its environment

organic composed of carbon, or derived from living organisms

phytoplankton microscopic floating creatures that photosynthesize

An aerial view of the sandy Ravenglass Estuary in Cumbria, England.
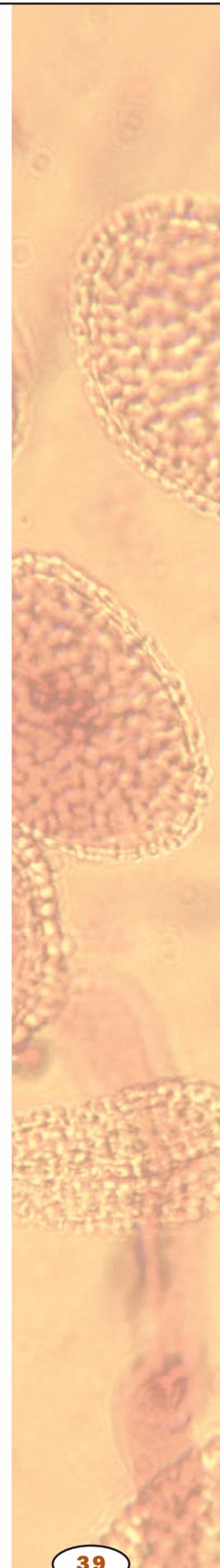
idency to complete their life cycles. Adult fish, marine mammal, and bird migrations are often timed to coincide with best conditions for reproduction and feeding in estuaries.

Coastal areas, especially estuaries, have always attracted and supported human populations. About 40 percent of the world's population lives within 60 miles of the coast, and 22 of the 32 largest cities are located on estuaries. Human impacts associated with agricultural, industrial, and residential development in coastal watersheds have resulted in changes in freshwater inflow, increases in nutrients, and the destruction of wetlands. Dredging, diversion, and damming have also altered estuarine habitats. Reductions in water and habitat quality and overharvesting have reduced resources and changed biological communities.

Healthy estuaries help to regulate flooding and decompose contaminants. Increasing awareness of impacts and advances in scientific knowledge and technology have led to some success in reducing impacts and restoring water quality. Education and long-term planning are keys to achieving a balance between sustaining economies and preserving the ecological

integrity of estuaries. SEE ALSO BIODIVERSITY; OCEAN ECOSYSTEMS: HARD BOTTOMS; OCEAN ECOSYSTEMS: SOFT BOTTOMS; PLANKTON; RIVERS AND STREAMS; WETLANDS

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Ethnobotany

Ethnobotany is a field of study that combines botany (the study of plants), anthropology (the study of human cultures), and medicine. Plants have been the original sources of many medicines used in all past and current societies. Many species of plants are biochemically quite complex, in part because they have had to evolve chemical defenses to deter herbivores and protect against attack from fungal, viral, and bacterial diseases. Thus, many of these same chemicals have been exploited by humans as treatment or prevention of diseases.

Ethnobotanists visit and learn from traditional healers in order to try to identify plants with valuable uses, particularly medicinal uses. Sometimes referred to as shamans, healers of every traditional culture are still using specific plants to treat specific health conditions based on generations of traditional knowledge and experience. In many cases, subsequent research by scientists has shown that the plant extracts used by the shamans contain chemical compounds that have natural healing or disease-fighting effects. In some cases, once the active chemical compound has been identified, scientists are able to synthesize, or create, it in the laboratory, and the plant is no longer needed. In other cases, the chemical or chemicals are too complex for easy synthesis, and the plant remains the raw material for the drug.

One controversial issue associated with ethnobotany is who should share the money that is produced when a plant compound, identified with the help of a traditional healer, is used by a major drug company to produce a very profitable drug. In many cases, the traditional peoples believe that they should receive some compensation since their knowledge was used by the drug companies for financial gain. In addition, sometimes the government of the country in which the plant grows believes that it should receive compensation since the plant species grows within their national boundaries. Compensation arrangements may be worked out in some cases. Another problem is that the culturally transmitted knowledge base of many traditional cultures is disappearing at a very rapid rate, as the traditional cultures themselves disappear or begin to adopt a more technology-based form of health care using manufactured medicines. Ethnobotanists may be in a race against time to preserve the knowledge of traditional healing systems before the practitioners die. SEE ALSO HERBAL MEDICINE; PHARMACOLOGIST

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Eubacteria

Bacteria are microscopic organisms that comprise the domain Eubacteria. A domain is the highest grouping of organisms, superseding the level of kingdom in the classical Linnaean system of biological classification. There are three domains, two of which, Eubacteria and Archaea, are composed entirely of **prokaryotic** organisms; the third domain, Eucarya, encompasses all other (**eukaryotic**) life forms, including the single-cell and multicellular protists, as well as animals, green plants, and fungi. Unlike eukaryotic cells, prokaryotic cells lack nuclei and other **organelles**, and tend to be less complex.

Eubacteria are differentiated from archaea primarily based on chemical composition of cellular constituents. For example, bacterial cell walls are composed of **peptidoglycan** (though there are examples of bacteria that lack cell walls) while archaeal cell walls are composed of a **protein**-carbohydrate molecule called pseudopeptidoglycan or other molecules. Bacterial cell membranes are composed of fatty acids joined to glycerol by ester bonds (COOC), while archaeal membranes are composed of isoprenoids rather than glycerol, linked to fatty acids by ether bonds (COC). In addition, the archaea have a more complex ribonucleic acid (RNA) polymerase than bacteria.

Life Cycle

Reproduction in bacteria involves duplicating the genetic material and dividing the cell into two daughter cells, a process known as binary fission. Under very favorable conditions, certain bacterial cells can divide as often as once every twenty minutes. Some bacteria, such as *Clostridium* and *Bacillus* species, possess the ability to form a resting state, or "spore," when unfavorable conditions are encountered. These spores are very resistant to heat, drying, radiation, and toxic chemicals. Bacterial spores have reportedly been reawakened from a 250-million-year-old salt crystal that existed before the time of the dinosaurs. Sterilization techniques used in medicine must overcome these resistant properties.

Size and Shape

Prokaryotes range in size from 0.2 micrometers to more than 50 micrometers, although the average prokaryote is around 1 to 3 micrometers in size. Eukaryotic cells are approximately one order of magnitude larger, ranging in size from 5 to 20 micrometers in diameter, with an average size of 20 micrometers.

The bacteria come in a number of distinct shapes as well. Common shapes include spherical (coccus), cylindrical (rod), and spiral forms (spirilla). While bacteria are generally regarded as unicellular organisms, there are also examples of bacteria that exist as multicellular colonies, aggregates, or filaments. In addition, bacteria can aggregate on surfaces. Called biofilms, these assemblages can consist of a single species or communities of microorganisms that can participate in metabolic cooperation.

Origin of Bacteria

It is not known whether the ancestor of bacteria originated on Earth or elsewhere. Some scientists believe that a life form existed extraterrestrially in
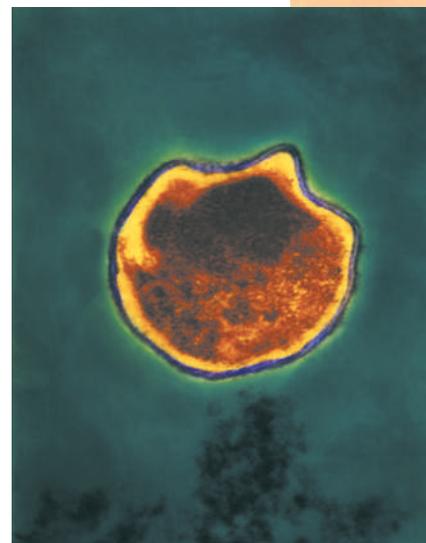
The spherical-shaped *Chlamydia pneumonia* bacteria.

prokaryotic without a nucleus

eukaryotic with a nucleus

organelle membrane-bound cell compartment

peptidoglycan polymer that is composed of polysaccharide and peptide chains

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions
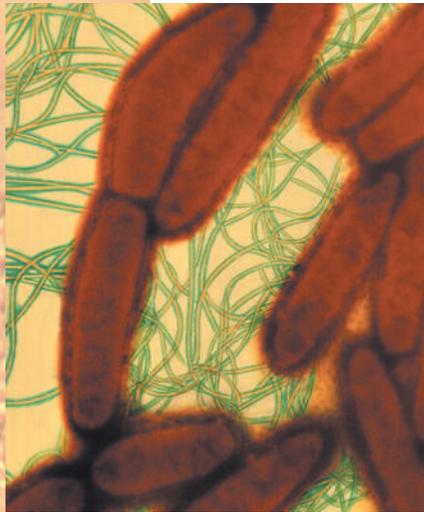
Colored transmission electron micrograph of the rod-shaped *E.coli* bacteria, showing its long flagellae.

organic composed of carbon, or derived from living organisms

inorganic not bonded to carbon

pH measure of acidity or alkalinity; numbers below 7 are acid, above are basic

obligate required or necessary, especially referring to a metabolic process or mode of nutrition

aerobe organism that needs oxygen

anaerobe organism not needing oxygen

α the Greek letter alpha

genome total genetic material in a cell or organism

the Martian meteorite ALH84001. Whether primitive life originated on Earth or elsewhere, current consensus is that bacteria were present on Earth 3.8 billion years ago.

Diversity

Bacteria show an incredible range of metabolic diversity. Some bacteria can get their energy from light (these are referred to as phototrophic organisms), **organic** compounds (organotrophic), or **inorganic** compounds such as hydrogen (H_2), sulfur compounds (H_2S), inorganic nitrogen compounds or ferrous iron compounds (chemolithotrophic). Some bacteria can make all of their organic compounds by fixing carbon (autotrophic), while others need to break down organic compounds to provide a carbon source (heterotrophic). Many bacteria are capable of fixing atmospheric nitrogen as a nitrogen source, in addition to organic and inorganic sources of nitrogen. Because of this metabolic diversity, bacteria play an important role in biogeochemical cycles such as the carbon, nitrogen, and phosphorous cycles.

This metabolic diversity also permits them to occupy a wide range of habitats. Bacteria can thrive in extremes of temperature, **pH**, salt, pressure, or toxic substances. Some bacteria can survive these conditions by spore formation, while other bacteria are able to multiply under extreme conditions. The most primitive bacteria extant today are theromophiles, leading to the consensus view that life arose under extreme conditions. Within and between these extremes, bacteria are found in marine, aquatic, terrestrial and subterranean environments. There are bacteria that are **obligate aerobes** and some that are obligate **anaerobes**, and many that fall somewhere in between.

In recent years, highly conserved genes such as the gene coding for the small subunit ribosomal RNA have been used as principal taxonomic characters. As bacteria evolve over time the sequence of this molecule changes, allowing taxonomic relationships between bacteria to be discerned.

Many divisions exist within the Bacteria. An example of this diversity is the subdivision **α**-proteobacteria, whose members are more diverse from each other than are plants from animals. More recently, full **genome** sequencing has revealed that genes can move between cells and even between species. Thus, bacterial genomes are in constant flux driven by gene acquisition from other species as well as evolutionary forces. The known bacterial tree of life is remarkable, but as 99 percent of bacterial life remains uncultured, this tree will undoubtedly expand greatly over time.

Associations

While most bacteria are free living at some point of their life cycles, many bacteria are capable of living in close associations with other organisms, including eukaryotes. Some of these so-called symbiotic associations are so highly evolved as to be obligate, while other associations are facultative, meaning the symbiotic partners can live apart from each other. In some symbioses, the eukaryotic host provides a highly specialized structure within which the bacteria reside, such as the nitrogen-fixing root nodules found on leguminous plants, such as clover, or the rumen possessed by some herbiv-

orous mammals. Looser symbiotic associations exist where the host provides no specialized structure for the symbiotic bacteria. Organisms that populate the root zone of plants can provide growth benefits; these bacteria are in turn making use of plant products exuded though the roots.

There are also bacteria that are very harmful or even fatal to eukaryotic hosts. An example of this is *Yersinia pestis*, causative agent of the bubonic plague. Not all associations between bacteria and their eukaryotic hosts have such a drastic result. Many bacteria exist in relatively benign associations with their hosts, such as the *Escherichia coli* bacteria in the human large intestine. Some resident bacteria can become pathogenic under certain circumstances. These **opportunistic** pathogens can cause serious infection in hosts whose defenses are compromised by age or previous illness.

Some association can be very intimate, occurring on the **intracellular** level. It is generally accepted that the eukaryotic chloroplasts and **mitochondria** arose from associations between bacteria and other cells. These organelles are similar in size to bacteria and contain remnants of bacterial genomes. SEE ALSO ARCHAEA; BACTERIAL DISEASES; BACTERIAL GENETICS; BIOGEOCHEMICAL CYCLES; CELL WALL; CHLOROPLAST; EXTREME COMMUNITIES; MITOCHONDRION; NITROGEN FIXATION; SYMBIOSIS

Marisa K. Chelius, Angela D. Kent, Anthony C. Yannarell, and Eric W. Triplett

opportunistic caused by a microorganism that is usually harmless but which causes an infection in an immunosuppressed person

intracellular within a cell

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

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Eudicots

The eudicots are the largest group of flowering plants (angiosperms). The term *eudicots* derives from the term "dicotyledons." Historically, **dicots** were the group of flowering plants characterized by having two seeds leaves upon germination, presence of woody or secondary growth, tap root system, reticulate (netlike) venation in the leaves, and flower parts in groups of four or five. Recent studies based on molecular **phylogenetic** evidence suggest that the dicotyledons are an evolutionarily natural, or **monophyletic**, group. However, a smaller, monophyletic, well-supported **lineage** termed the eudicots or "true dicots" contains the majority, but not all, of the former dicots.

There are approximately 319 families of plants within the eudicots, and these include about three-quarters of all flowering plant species. One of the most important defining morphological features of the eudicots is the presence of pollen grains having three, long, grooved apertures or openings, and in recognition of that fact, the eudicots are also known as the tricolpates.

dicot plant having two cotyledons, or seed leaves

phylogenetic related to phylogeny, the evolutionary development of a species

monophyletic a group that includes an ancestral species and all its descendants

lineage ancestral line
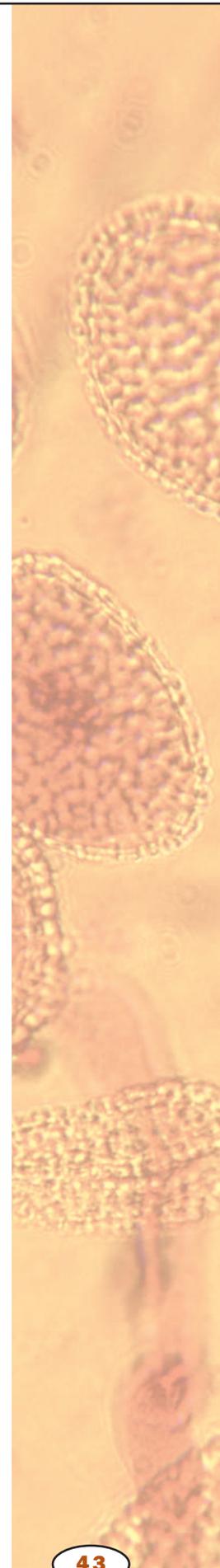
Some eudicots have evolved highly specialized associations with animal pollinators.

organelle membrane-bound cell compartment

sepals whorl of flower organs outside of the petals, usually green and serving to protect the flower before it opens

Many eudicots also exhibit a specific cell ultrastructure: The sieve elements (sap-conducting cells) contain **organelles** called plastids, which contain starch grains.

The eudicots are believed to represent one of the early radiations, or evolutionary expansions, of flowering plants, but the relationship of the eudicots to other flowering plant lineages is not well known. The eudicots include many familiar flowering plants. The earliest diverging lineage includes a group called the Ranunculales (including *Ranunculus*, the buttercups; *Podophyllum*, the mayapples; and *Papaver*, the poppies). Other groups within the eudicots include *Proteas* (grown as an ornamental) and related plants, the sycamore or plane tree family (Platanaceae), and the so-called "core eudicots." The core eudicots are the largest group of eudicots and include a number of diverse plant families, such as the following groups and their relatives: the carnations, sandalwoods, saxifrages, geraniums, roses, and asters. The eudicots include many economically important plants, such as *Nicotiana tabacum* (tobacco), *Brassica oleracea* (cabbage, kale, and broccoli), the legumes (which include beans, peas, lentils, chickpeas, peanuts, and soybeans, among other crops), and *Solanum tuberosum* (potato).

The eudicots are one of the most diverse groups of flowering plants in terms of floral and vegetative shape, growth form, habitat, and association with animals for pollination, seed dispersal, or nutrition. Some eudicots, for example many woody trees (oaks, maples, hickories, and birches in the Northern Hemisphere), are wind-pollinated and have very reduced petals and **sepals**, while producing copious amounts of pollen. Others have evolved highly specialized associations with animal pollinators including many species of insects (including bees, butterflies, and moths), birds (especially hummingbirds) and even bats (some species of cactus are pollinated by bats).

Floral modifications characteristic of some eudicots include fusion of sepal and petal parts, and zygomorphic (asymmetical) shape (for example, *Antirrhium*, the snapdragon and its relatives, and many flowers of the mint family). This trait often provides a "landing pad" projecting from the flower, and is often associated with insect pollination. The aster or composite family (for example, the common daisy, dandelion, and sunflower) has a unique type of inflorescence that is composed of many tiny flowers, some of which form the rays and look like petals, and others which form the disk flowers in the center of the composite head. SEE ALSO ANGIOSPERMS; FRUITS; MONOCOTS

Molly Neprokroeff

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Evolution

The remains of stadiums, temples, and aqueducts indicate as clearly as any ancient document that the Roman Empire once existed. Likewise, fossils

speak eloquently of a time when dinosaurs and not humans dominated Earth. Even without ancient ruins, similarities in appearance, language, customs, and genetic makeup show that the Italians, Spanish, English, and French all came from the same ancestral culture. Likewise, similarities in structure and genetic makeup persuade humankind that algae and plants, insects and crustaceans, chimpanzees and humans came from the same ancestral species.

Evolution, which can be defined as the natural change in the inherited characteristics of groups of organisms, is as well established as the Roman Empire or any other event that is accepted as fact. Unfortunately, the common phrase "theory of evolution" has misled many people into believing that evolution is "only" a theory. To biologists, "theory of evolution" refers to a proposal about *how* evolution occurs, not *whether* it occurs. There are, in fact, several theories of evolution. Like evolution itself, some of these theories are well supported by observations and experiments.

Development of Evolutionary Theory

Evolution is generally associated with Charles Darwin (1809–1882), but by the time he wrote about it in 1858, it had already been suggested by many people. In fact, Charles Darwin's grandfather, Erasmus Darwin (1731–1802), was one of many who suggested that living species had descended from different species that had lived in the past. His theory of how evolution occurred was similar to that of French biologist Jean-Baptiste Lamarck (1744–1829) and was based on the belief that characteristics that develop in an adult can be passed on to its offspring. Thus, for example, giraffes could have evolved because their short-necked ancestors stretched their necks to reach higher leaves and therefore had offspring with longer necks. Both Lamarck and Erasmus Darwin were ignored, scorned, and ridiculed for this idea.

Charles Darwin was well aware of the controversy over evolution. As a theology student at Cambridge University with a passion for biology, he heard his professors dismiss evolution as nonsense, and he saw no reason to doubt them. Between 1831 and 1836, however, while serving as naturalist on an around-the-world voyage of *The Beagle*, young Darwin made observations that convinced him that evolution had, in fact, occurred. He saw that the fossil animals in parts of South America were different from, but similar to, the animals still living there. This gave Darwin the idea that living organisms were descendants of extinct ones that had lived in the same place in the past.

Darwin also observed that regions isolated from each other often had different but similar species. He noted, for example, that each of the Galapagos Islands had distinct species of mockingbirds. This suggested that all were descendants of the same ancestral species, and each had taken its own evolutionary path after being separated from the others. Darwin was also influenced by reading *Principles of Geology* by Charles Lyell (1797–1875). Lyell argued convincingly that geological changes were not caused by sudden global catastrophes, as most geologists then thought, but by gradual processes like erosion. This made Darwin realize that evolution must also have been gradual, otherwise organisms could not have remained adapted to their changing environments.

While in the Galapagos, Darwin did not come up with any answers as to why the forms of life were so different in those remote islands from the rest of the world. But a couple of years later, in 1837, he wrote the following in his journal: "In July opened first notebook on transmutation of species. Had been greatly struck from about the month of previous March on character of South American fossils, and species on Galapagos Archipelago. These facts (especially the latter) are the origin of all my views."

A cactus finch in the Galapagos Islands, where Charles Darwin began to formulate his theory of evolution. Darwin observed that regions isolated from each other often had different but similar species.

Darwin eventually returned to England convinced of the reality of evolution. He knew, however, that no one else would believe it unless he could find a better theory to explain it than his grandfather and Lamarck had proposed. Since some of his relatives owned estates on which they had successfully altered domesticated animals by selective breeding, it occurred to Darwin that something like this artificial selection might explain evolution. But how could unconscious nature select which individuals would breed and which would not? Darwin studied agricultural journals, conducted breeding experiments, and pondered the question for months. Then one day in 1838 he decided to read ("for amusement," he says in his autobiography) the famous piece *Essay on the Principle of Population* (1798) by Thomas Malthus (1766–1834).

Natural Selection

The essential idea of this essay is now called the Malthusian Principle. It proposes that human population has a tendency to increase much faster than the food supply. Consequently, there will always be competition between those who can get food and those who cannot. Darwin saw in a

flash that the same principle applies to all organisms. Virtually all species have the natural ability to produce many more offspring than can survive with the available resources. Within any species there will be some individuals that are better able to compete for food, mates, and other resources, and they will be more likely than others to produce more offspring. Scientists would now say that they have a greater fitness. To the extent that their fitness is hereditary, their offspring will also be better able to compete, and so on, generation after generation. In this way the fitter individuals become increasingly numerous, and the species gradually evolves. Darwin gave his theoretical mechanism of evolution the name "natural selection."

Natural selection may be the simplest yet most powerful theory in science. With it one can immediately see that evolution is not only possible but, given enough time, inescapable. All that is required is that there be competition among individuals of the same species, and that individual organisms have inherited traits that make some better able than others to compete. Darwin must have realized the importance of his theory. Rather than risk his budding reputation with a hasty report to a scientific journal, however, he began to accumulate supporting evidence for a book. Twenty years later he was still at work on his book when a remarkable coincidence forced him to publish. In 1858 he received a manuscript from an English collector in the East Indies, Alfred Russel Wallace (1823–1913).

As Darwin read the manuscript he was stunned to see that Wallace had hit upon the same theory of natural selection that he had been laboring over for two decades. Darwin reluctantly agreed to publish an outline of his ideas along with Wallace's paper. (It was discovered later that the basic concept of evolution by natural selection had already been proposed almost thirty years earlier by a little-known Scotsman named Patrick Matthew [1790–1874]. Matthew had also been ignored.) Ultimately, what finally made the words "evolution" and "Darwinism" well known was Darwin's book, *On the Origin of Species by Means of Natural Selection*, which was published in 1859. Its vast documentation and powerful arguments soon convinced the majority of biologists that evolution is a fact, and natural selection is one of the reasons why it occurs.

Since the publication of *On the Origin of Species*, few biologists have doubted that evolution occurs. By the early twentieth century, however, natural selection appeared to be heading toward extinction. One criticism of natural selection was that any adaptation that made an individual only slightly more fit would be diluted when the individual mated. For example, if a giraffe ancestor with a slightly longer neck mated with a normal member of its species, their offspring would have necks with lengths between that of the two parents. This reduction in neck length would continue with each generation. Thus any adaptation would be blended out of the species before natural selection would have a chance to favor it. In addition, beginning in 1900, genetic mutation seemed to provide an alternative theory that was better than natural selection. The discovery of the work of Gregor Mendel and further research on genetics suggested that new species resulted from large mutations occurring within a single generation instead of small mutations being selected over many generations.

WALLACE, ALFRED RUSSEL (1823–1913)

English-born naturalist and explorer who helped formulate the principles of biological evolution and natural selection. Wallace traveled more than 14,000 miles in the area that is now known as Indonesia and Malaysia and catalogued more than 125,000 biological specimens.

Neo-Darwinism

By the middle of the twentieth century, however, biologists saw that Darwin's theory of natural selection was not really in conflict with genetics. They synthesized the two views, resulting in what is now called the neo-Darwinian or Synthetic Theory of Evolution. The neo-Darwinian theory was aided by a shift in thinking about the scale of evolution. Rather than conceiving of evolution as something that happened to entire species, biologists began to think of it as occurring within smaller groups of interbreeding organisms, called populations. Most species comprise many populations.

The neo-Darwinian Theory was also made possible by a mathematical proof called the Hardy-Weinberg equilibrium. The Hardy-Weinberg equilibrium showed that adaptations would not be blended out of populations, and it also showed that natural selection was indeed a possible cause of evolution. This proof, which was proposed in 1908 independently by English mathematician G. H. Hardy (1877–1947) and German physician Wilhelm Weinberg (1862–1937), shows that under certain conditions even rare mutations persist indefinitely. In modern terms, scientists would say that the Hardy-Weinberg equilibrium shows that the gene frequency—the proportion of a particular type of gene in a population—will remain constant if certain conditions occur. These conditions are as follows:

1. The size of the population is practically infinite.

2. Individuals in the population mate at random.

3. All individuals in the population have the same fitness, regardless of their genes.

4. There is no gain or loss of genes due to immigration into or emigration out of the population.

5. There is no new mutation in the population.

Violating any one of these conditions can lead to a change in gene frequency. This is important because changes in gene frequency can result in evolution. In fact, many biologists now define evolution as any change in gene frequency. As an example, suppose a genetic mutation had caused an ancestor of giraffes to have a slightly longer neck. A departure from the Hardy-Weinberg conditions could continually increase the frequency of that mutated gene in the population. Gradually the entire population would have longer necks. This process repeated over thousands of generations could cause that population to evolve into the giraffe. The Hardy-Weinberg equilibrium therefore amounts to a list of conditions that, if absent, can cause evolution. The potential causes of evolution include small population size, nonrandom mating, natural selection, immigration and emigration, and mutation.

Small Population Size. A change in gene frequency due to small population size is called genetic drift. Genetic drift is now recognized as one of the major causes of evolution, although its results are usually random rather than adaptive. Chance events operating in small populations can have huge effects on gene frequency. Imagine, for instance, an isolated population of a very rare, endangered species of mountain sheep, whose males have horns that are either curved or straight. If a severe snowstorm happened to kill

the few sheep with genes for curved horns, the proportion of sheep with straight horns would increase greatly in future generations.

A related phenomenon, called a population bottleneck, occurs when a large population is decimated by disease, predation, or habitat destruction. The few surviving members constitute the "bottleneck" through which the species passes. The genes of those few members dominate the gene pool of future generations. Similarly, a population of organisms could differ from others simply because the few founders of the population happened to have a gene frequency different from that of the species as a whole. This is called the founder effect. The wide differences in blood group frequencies between the Old Order Amish of Pennsylvania and other U.S. populations of European ancestry is due to the founder effect operating in the Amish population. The role of genetic drift in species formation is an important area of research in evolution.

Nonrandom Mating.   A second potential cause of evolution is nonrandom mating. Nonrandom mating usually occurs when individuals choose their mates. Animals often select mates on the basis of fitness, and the results of such sexual selection are indistinguishable from natural selection. On the other hand, mate selection can be based on characteristics that have nothing to do with fitness. For example, the tail feathers of the peacock or the bright coloration of the male pheasant are not thought to confer selective advantage in any arena other than mate selection. But because females choose the showier bird, the trait is selected for in males. This is called sexual selection.

Natural Selection.   Natural selection, which is due to hereditary differences in fitness, is a third potential cause of evolution, as Charles Darwin argued. Natural selection is now considered to be the main, if not the only, cause of the evolution of adaptations that increase fitness. For example, the speed of the gazelle and the cheetah that chases it are both due to natural selection.

Immigration and Emigration.   Immigration and emigration can bring in or remove particular genes. The global travel of human beings has increased the importance of these forces not only in human populations, but in many other species that travel with humans, such as Africanized honey bees. The so-called killer bees from Africa are currently changing the gene frequencies of bee populations in the southern United States.

Mutation.   Finally, mutation can obviously change the frequency of a gene. Mutation can be especially potent when combined with genetic drift in small populations.

Mutation

As noted earlier, many biologists once thought that mutation by itself was the major cause of evolution. In the 1920s, however, British biologist J. B. S. Haldane (1892–1964), British statistician Ronald A. Fisher (1890–1962), and American geneticist Sewall Wright (1889–1988) published three different mathematical proofs showing that mutation by itself is insufficient. They showed that a rate of mutation fast enough to cause evolution would also be fast enough to undo any evolution that had happened in the past. Scientists now know that mutations are too rare (about one per billion

The Africanized honey bee was first found in the United States near Brownsville, Texas, in 1990. Since that time, the bees have spread throughout the state. They've also been found in Arizona, California and New Mexico.

A petri dish culture of antibiotic-resistant *Staphylococcus aureus*. Resistance to antibiotics evolves when antibiotics are used improperly, allowing the survival of a few bacteria with mutated genes that confer resistance.

nucleotide the building block of RNA or DNA

nucleotides per human lifetime) to account for most evolutionary change without the help of natural selection. Also, contrary to what Erasmus Darwin and Lamarck thought, scientists know of no way that the efforts or experience of an organism can induce specific, adaptive mutations in its offspring.

For a time, many biologists thought that natural selection was so rigorous that it would eliminate most mutations since most mutations were presumed to be harmful. Starting in the 1950s, however, it was found that genetic variations resulting from past mutations are quite abundant in most species. Most mutations have little effect on fitness, and they can accumulate generation after generation with little selection against them. With increased competition or some change in the environment, however, some of these mutations may result in differences in fitness. Natural selection can then bring about evolution by increasing the frequency of the beneficial mutations. Natural selection therefore seldom has to sit and wait for just the right mutation to come along and make an individual more fit. The mutations are usually already present in most populations.

Microevolution and Macroevolution

Changes in gene frequency that occur within a population without producing a new species are called microevolution. As microevolution continues, a population may become so different that it is no longer able to reproduce with members of other populations. At that point, the population becomes a new species. As the new species continues to evolve, biologists might eventually consider it to be a new genus, order, family, or higher level of classification. Such evolution at the level of species or higher is called macroevolution.

Microevolution can occur very quickly; indeed, it is probably always occurring. For example, in less than half a century after the discovery of antibiotics, many bacteria evolved resistance to them. Resistance to antibiotics evolves when antibiotics are used improperly, allowing the survival of a few

bacteria with mutated genes that confer resistance. Natural selection then leads to the evolution of antibiotic-resistant strains. Pesticide-resistant insects and herbicide-resistant weeds are additional examples of rapid microevolution.

Macroevolution occurs over much longer periods and is seldom observed within the human life span. Occasionally, however, scientists do see evidence that new species have recently evolved. There are species of parasitic insects, for example, that are unable to reproduce except in domesticated plants that did not even exist a few centuries ago. The pace of evolution can be quite variable, with long periods in which there is little change being punctuated by relatively brief periods of tens of thousands of years in which most changes occur. This idea that the pace of evolution is not always slow and constant is referred to as **punctuated equilibrium**. It was first proposed by paleontologists Niles Eldredge and Stephen Jay Gould in 1979, and it is one of many examples of how scientists' views of evolution are continually changing.

Several possible mechanisms exist for rapid evolution. Chromosomal aberrations, such as breakages and rejoining of chromosomal parts, can introduce large changes in genes and the sequences that regulate them. This may lead to changes much larger than that brought about by simple point mutations.

Environmental catastrophes can set the stage for rapid evolution as well. It is thought that the extinction of the dinosaurs was triggered by a large comet impact. This rapid loss of the dominant fauna in many **ecosystems** opened up many new niches for mammals, which at the time were a small group of fairly unimportant creatures. The sudden appearance of many new opportunities led to rapid and widespread speciation, in a process called **adaptive radiation**.

Other areas of biology are also continually changing under the influence of evolution. For example, as Charles Darwin predicted in *The Origin of Species*, classification has become more than simply the grouping of organisms into species, genera, families, and so on based on how physically similar they are. Classification now aims to group species according to their evolutionary history. Thus two species that diverged recently from the same ancestor should be in the same genus, whereas species that shared a more distant common ancestor might be in different genera or higher taxonomic levels.

Until the 1980s, evolutionary history, or phylogeny, of organisms could only be inferred from anatomical similarities. Since that time, however, it has been possible to determine phylogeny from comparisons of molecules. Often this molecular phylogeny agrees with the phylogeny based on anatomy. For example, about 99 percent of the sequence of bases in the deoxyribonucleic acid (DNA) of chimpanzees and humans is identical. This finding confirms the conclusion from anatomy that chimpanzees and humans evolved from the same ancestor only a few million years ago. Such agreement between anatomical and molecular phylogeny would not be expected if each species were a totally different creation unrelated to other species, but it makes sense in light of evolution. It is one of many examples of the famous saying by the geneticist Theodosius Dobzhansky (1900–1975):

punctuated equilibrium pattern of evolution in which long periods of relatively little change are punctuated by rapid change

ecosystem an ecological community and its environment

adaptive radiation diversification of a group of organisms into several different forms that adapt to different environments

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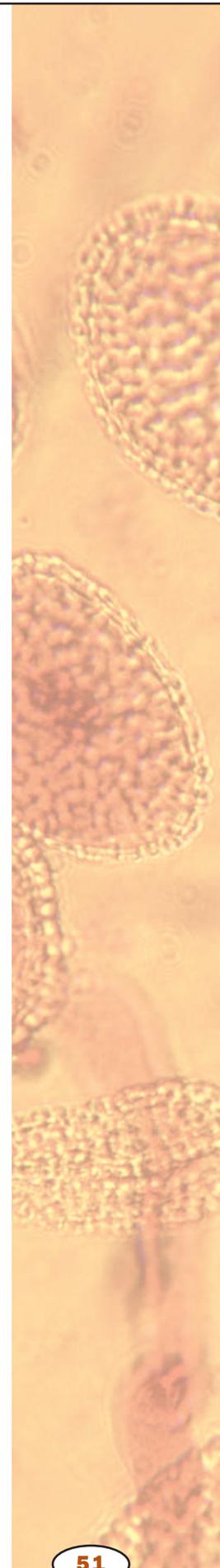
"Nothing in biology makes sense except in light of evolution." SEE ALSO ADAPTATION; BUFFON, COUNT (GEORGES-LOUIS LECLERC); CONVERGENT EVOLUTION; DARWIN, CHARLES; ENDANGERED SPECIES; EVOLUTION, EVIDENCE FOR; EXTINCTION; HARDY-WEINBERG EQUILIBRIUM; LAMARCK, JEAN-BAPTISTE; NATURAL SELECTION; SPECIATION

C. Leon Harris

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Evolution, Evidence for

Evolution is the unifying principle in biology. It explains the overwhelming diversity of life on Earth, as well as the constancy of molecular and morphological attributes observed in diverse assemblages of plants and animals. Charles Darwin's publication of *On the Origin of Species by Means of Natural Selection* in 1859 marks the beginning of scientific understanding of how evolution has molded the history of life.

Darwin, along with his contemporary Alfred Russel Wallace, provided convincing and abundant evidence that all organisms, living and fossil, have descended with modification from a common ancestor and that the chief agent of modification is **natural selection**. Shortly after the publication of *The Origin of Species*, nearly all biologists accepted the premise that organisms have changed over time. However, the exact mechanisms of natural selection and the rates at which evolutionary changes occur are still subject to scientific discussion.

Evidence from Living Organisms

Evidence for evolution comes in many forms, with some of the strongest derived from observations of living animals. First, there is the striking similarity among vertebrate embryos. Despite great variation in adult forms, early stages of embryonic development are virtually indistinguishable: the human embryo is not easily distinguished from the embryo of a fish or an elephant. This embryological similarity is consistent with a common ancestry among all vertebrates.

Second, there is the phenomenon of homology. Structures in two or more species are termed **homologous** if they can be traced back to a common origin. Clues to homology usually lie in the skeletal structure and its connections to surrounding parts, rather than to a similar function.

For instance, the forelimbs of a human, a seal, and a bird are all used for different types of locomotion, so one should not expect them to be identical. However, if one searches beyond the **superficial** structure of wings, fins, and arms and looks at the structural relationships of each bone, one will see that they are very similar. Each humerus is connected to a radius

natural selection process by which organisms best suited to their environments achieve greater reproductive success, thus creating more "fit" future generations

homologous similar in structure

superficial on the surface; not deep

and ulna, which are in turn connected to the bones of the hand. So, even though organs and bones may look drastically different and may serve very different functions, the fact that they can be identified as the same organ with modification supports evolution.

Finally, **vestigial** organs provide an indication of biological modification and change, in that they remain even when their original function is lost. For instance, whales are now fully marine organisms, but they evolved from terrestrial carnivores tens of millions of years ago. Whales retain remnants of pelvic elements situated near their "hips" that no longer have any clear function in hindlimb activity.

Additional evidence for evolution comes from the study of living populations. Some scientists take a macroscopic approach by documenting morphological and behavioral changes in natural laboratories. A good example of this type of work can be found in Jonathan Weiner's *The Beak of the Finch* (1994). In this account of evolution in action, scientists visit island populations where they measure morphological attributes of animals and plants (for example, the beak size of finches in the Galapagos) and correlate those changes to environmental changes. They can follow the breeding patterns of populations over many generations and record changes that are passed along, thus developing an hypothesis of adaptation and natural selection.

On a molecular level, some of the strongest support for evolution lies in the deoxyribonucleic acid (DNA) of organisms. New techniques allow

Fossil of a fish, *Xiphactinus (Portheus) molossus*. Evolution cannot be understood without studying the fossil record.

vestigial no longer functional

scientists to extract and replicate DNA sequences that can then be compared to sequences from other animals. Because DNA ultimately controls both morphological and behavioral features in organisms, similarities and differences among DNA sequences can clearly reveal the path of evolution.

Fossil Evidence

morphology related to shape and form

The distribution, **morphology**, and genetics of living populations all provide evidence for evolution, but the complete picture cannot be understood by the study of living populations alone. The origin of major new structures and body plans must be studied through the archive of evolution, the fossil record. In the sedimentary rocks deposited over the last several billion years of Earth's history the ancestry of living organisms can be traced, and the mysteries of species origination and extinction can be explored.

The 3.5-billion-year time frame for biologic evolution provided by the rock record is great enough for even the most improbable of events, such as rare mutations, to have occurred repeatedly. This archive of evolution was calibrated with the discovery of radioactive decay and the advent of radiometric dating in the mid-twentieth century. The absolute dates that define the modern geological time scale serve to guide scientific estimates of the time necessary for new genera and species to evolve by providing rates of change.

One of the main conceptual differences that continues to plague the scientific understanding of the evolutionary process is the question of evolutionary rates. Two main schools of thought have developed over the years. The traditional view is one of gradualism, with evolution proceeding slowly, through intermediate forms lost from the fossil record (missing links). There is some support for this view in the fossil record.

punctuated equilibrium pattern of evolution in which long periods of relatively little change are punctuated by rapid change

stasis state of no change

The alternative view of evolution is termed **punctuated equilibrium**, and it too is supported by patterns in the fossil record. Those who promote punctuated equilibrium hold that species evolution is driven largely by chance and occurs in pulses, whereas the maintenance of a species during its longevity is driven by selection and is viewed in the fossil record as relative **stasis**.

These ideas, both of which no doubt hold some credence, have revitalized debate extending across evolutionary topics, from the level of change within isolated populations to longer-term patterns. Most important, they have signified a general acceptance of the concept of evolution among biologists and have provided the impetus for paleontologists and biologists to probe deeper into the remaining mysteries of evolutionary pattern and process. SEE ALSO CONVERGENT EVOLUTION; CREATIONISM; DARWIN, CHARLES; EVOLUTION; PALEONTOLOGY; SPECIATION

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Evolution of Plants

Modern classification systems, based largely on molecular evidence, divide living organisms into three domains: Bacteria (also called Eubacteria), Archaea, and Eukarya. Plants are classified as a kingdom (Plantae) within the Eukarya; organisms that possess a **nucleus**, **mitochondria**, an internal **cytoskeleton**, and, in photosynthetic species, chloroplasts. Most scientists recognize three other eukaryotic kingdoms: Protista (most of which are single-celled organisms), Fungi, and Animalia (animals). The fungi, plants, and animals are thought to have evolved from different groups of protists.

Plants are multicellular organisms that have evolved the ability to live on land. The vast majority can carry out photosynthesis, but they are not the only organisms with this ability: many protists can photosynthesize too, as can several important groups of bacteria.

Algae in Plant Evolution

Photosynthetic protists (commonly called algae) are a diverse group of organisms and are divided into several phyla. Many are unicellular, including most euglenoids (phylum Euglenophyta) and dinoflagellates (Dinophyta), and some diatoms (Bacillariophyta) and green algae (Chlorophyta). These, along with the cyanobacteria (often misleadingly called blue-green algae), form the **phytoplankton** of aquatic **ecosystems**. Others, including all brown algae (Phaeophyta), most red algae (Rhodophyta), and many green algae are multicellular. The large marine forms of these phyla are usually called seaweeds.

Plants are thought to have evolved from a class of freshwater green algae called the charophytes. Two particular groups of charophyte, the Coleochaetales and the Charales, resemble the earliest land plants (bryophytes) in a variety of ways, including the structure of their chloroplasts and sperm cells, and the way their cells divide during **mitosis**.

The Importance of Vascular Tissue

Plants are classified into two main groups: the bryophytes (nonvascular plants) and the tracheophytes (vascular plants). Both groups have multicellular embryos, which indicates that they are closely related to each another and distinguishes them from the green algae. Indeed, true plants are often referred to as embryophytes because of this feature. The bryophytes consist of the liverworts, hornworts, and mosses, and as their name implies none of these plants possess vascular tissues.

All other plants, including the ferns, gymnosperms, and angiosperms, are classified as tracheophytes. These possess specialized vascular tissues—**phloem** and **xylem**—to transport sugars, water, and **minerals** throughout their bodies. The oldest known vascular plants appeared in the middle Silurian period (439–409 million years ago); the oldest known bryophytes appeared later, in the Devonian (409–354 million years ago). Despite this, most scientists believe that bryophytes evolved before vascular plants, and that the earliest bryophytes have not been found because they fossilize poorly. This belief is supported by a variety of evidence, including morphological traits, ultrastructural features visible under the electron microscope, and molecular information obtained from **gene** sequencing.

nucleus membrane-bound portion of cell containing the chromosomes

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

cytoskeleton internal scaffolding in a cell, composed of protein

phytoplankton microscopic floating creatures that photosynthesize

ecosystem an ecological community and its environment

mitosis separation of replicated chromosomes

phloem plant tissue that conducts sugars from leaves to roots and other tissues

xylem water-transporting system in plants

minerals iron, calcium, sodium, and other elements needed by living organisms

gene portion of DNA that codes for a protein or RNA molecule

Bryophytes

Since bryophytes are land plants, they need to support themselves in air. However, because they lack **lignified** vascular tissues, this support must be provided largely by the **turgor** pressure of their cells. Consequently, they cannot grow to be very tall, and most bryophytes are small and rather inconspicuous. An additional important feature of their lifestyle is their reproductive system. The male **gametes**, produced by reproductive structures called antheridia, are free-swimming sperm cells that need water to transport them to the female gametes, which are enclosed within structures called archegonia. Because of the need for water, bryophytes are especially common in wet habitats such as bogs, streambanks, and in moist forests. However, they are not restricted to these habitats, and some mosses thrive in deserts, above the treeline, and in the Arctic tundra.

Among the living bryophytes, liverworts are probably most closely related to the earliest land plants, since unlike hornworts, mosses, and all vascular plants they do not possess **stomata**. Indeed, the fact that stomata first appeared in hornworts and mosses is evidence that vascular plants evolved from one of these two groups. Vascular plants appear to be more closely related to mosses than to hornworts, because some mosses possess food-conducting cells (leptoids) and water-conducting cells (hydroids) that resemble the phloem and xylem of vascular plants.

Early Vascular Plants

The first detailed vascular plant fossils appear in rocks from middle Silurian, about 425 million years ago. The oldest of these, including a plant called *Aglaophyton*, appear to have possessed conducting cells similar to the hydroids of mosses. These ancient plants, which are sometimes called proto-tracheophytes, may have been an evolutionary link between the bryophytes and the true tracheophytes. Early vascular plants possessed two features that made them especially well adapted to life on land. First, their vascular tissues transported sugars, nutrients, and water far more efficiently than the conducting cells of mosses. Second, they evolved the ability to synthesize **lignin**, which made the cell walls of their vascular tissues rigid and supportive. Taken together, these features allowed them to grow much larger than their bryophyte ancestors and considerably reduced their dependence on moist habitats.

There are three major groups of tracheophytes: seedless vascular plants, gymnosperms, and angiosperms. Since the first appearance of tracheophytes in the Silurian, the fossil record shows three major evolutionary transitions, in each of which a group of plants that were predominant before the transition is largely replaced by a different group that becomes predominant afterward. The first such transition occurred in the late Devonian, approximately 375 million years ago. Prior to this time the most common plants were simple, seedless vascular plants in various phyla, several of which are now extinct. However, one **phylum** from this time, the Psilophyta, still has two living genera, including a greenhouse weed called *Psilotum*.

From the late Devonian until the end of the Carboniferous period (290 million years ago) larger, more complex seedless plants were predominant. The main phyla were the Lycophyta, the Sphenophyta, and the Pterophyta.

lignified hardened by impregnation with lignin, a compound formed in plants

turgor internal pressure

gamete reproductive cell, such as sperm or egg

stomata openings in leaves for gas exchange, surrounded and regulated by guard cells

lignin organic molecule used in plant cell walls to add stiffness to cellulose

phylum taxonomic level below kingdom, e.g., arthropod or chordate

All three groups contain living relatives, including club mosses (Lycopodiaceae) in the Lycophyta, *Equisetum* (the only living genus of sphenophytes), and ferns, which are pterophytes. Only the ferns, which have about 11,000 living species, are common today, but in the Carboniferous these three phyla comprised a large fraction of the vegetation on the planet. Many grew to the size of trees and dominated the tropical and subtropical swamps that covered much of the globe at this time.

The second major transition was the decline of the lycophytes, sphenophytes, and pterophytes at the end of the Carboniferous and their replacement by gymnosperms in the early Permian. Gymnosperms dominated the vegetation of the land for the next 200 million years until they themselves began to decline and were replaced by angiosperms in the middle of the Cretaceous. Although one group of gymnosperms (the conifers) is still abundant, the angiosperms have been the most diverse and widespread group of plants on Earth for the last 100 million years.

Gymnosperms

The gymnosperms probably evolved from an extinct phylum of seedless vascular plants, the progymnosperms, that appeared about 380 million years ago. The fossils of these plants, some of which were large trees, appear to form a link between the trimerophytes (another extinct phylum of seedless vascular plants) and true gymnosperms. Progymnosperms reproduced by means of spores like the former, but their vascular tissues were very similar to those of living conifers. The oldest true gymnosperms, which produce seeds rather than spores, first appeared about 365 million years ago. The evolution of seeds, with their hard, resilient coats, was almost certainly a key factor in the success of the group. A second factor was the evolution of pollen grains to protect and transport the male gametes. As a consequence of this, gymnosperms, unlike seedless vascular plants, were no longer dependent on water for successful **fertilization** and could broadcast their male gametes on the wind.

fertilization union of sperm and egg

Several early gymnosperm groups are now extinct, but there are four phyla with living representatives: the cycads, the gnetophytes, the conifers, and one phylum (Ginkgophyta) that has only a single living species, the ginkgo tree (*Ginkgo biloba*). Of these, the conifers are by far the most abundant and diverse, and many species are of considerable ecological and economic importance. Most conifers are well adapted to dry environments, particularly in their leaf **morphology**, and some can withstand severe cold. These features may have enabled them to thrive in the Permian, when Earth became much drier and colder than it had been in the Carboniferous.

morphology related to shape and form

Angiosperms

The angiosperms, or flowering plants, are all members of the phylum Anthophyta. There are at least 250,000 species, making the group easily the most diverse of all plant phyla. They share a number of features that distinguish them from other plant groups. The most obvious of these is the possession of flowers, highly modified shoots that carry the male and female reproductive structures. They also carry out a process called double fertilization, in which two male gametes (sperm nuclei) are released from the pollen tube into the **ovule**. One of these sperm nuclei fuses with an egg cell

ovule multicellular structure that develops into a seed after fertilization

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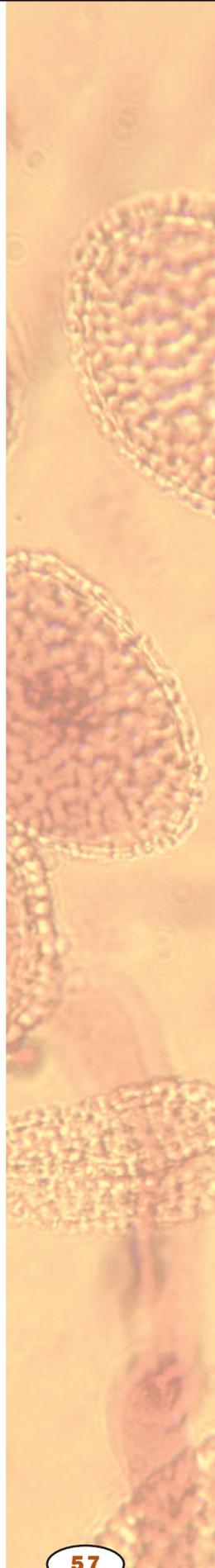
The ginkgo tree (*Ginkgo biloba*) is the only living species of the early gymnosperm phylum Ginkgophyta.

triploid possessing three sets of chromosomes

endosperm nutritive tissue within a seed

in a similar way to gymnosperms. The second nucleus (which degenerates in most gymnosperms) fertilizes other cells in the ovule called polar nuclei. Most commonly, two polar nuclei fuse with the sperm nucleus to form a **triploid endosperm** nucleus. The tissue that forms from this fusion is called endosperm, which in most angiosperms provides nutrients for the developing embryo.

A third feature that separates angiosperms from gymnosperms is that angiosperm embryos are protected by an ovary wall, which develops into a fruit after fertilization has taken place. In contrast, gymnosperm embryos are held relatively unprotected on the surfaces of ovule-bearing scales in the female cones.

Angiosperm Evolution

Angiosperms first appear in the fossil record about 130 million years ago, and by 90 million years ago they had become the predominant group of plants on the planet. English naturalist Charles Darwin considered the sudden appearance of angiosperms to be an "abominable mystery," and scien-

tists have debated about the origin of the group for many years. Comparative studies of living species suggest that angiosperms evolved from the gnetophytes, a group of gymnosperms with three living genera of rather strange plants: *Ephedra*, *Gnetum*, and *Welwitschia*. Double fertilization has been shown to occur in both *Ephedra* and *Gnetum*, and the reproductive structures (strobili) of all three genera are similar to the flowering stalks of some angiosperms. Some gene sequencing studies also indicate that gnetophytes and angiosperms are closely related to each other and to an extinct group of gymnosperms called the Bennettitales. However, more recent molecular studies suggest that gnetophytes are more closely related to conifers than they are to angiosperms.

In 1998, the discovery of an angiosperm-like fossil called *Archaefructus*, which apparently existed 145 million years ago, also cast some doubt on the idea that angiosperms descended from gnetophytes or Bennettitales. Although a great deal of information has been obtained since the time of Darwin, the origin of angiosperms is still something of a mystery.

Early Angiosperms, Monocots, and Eudicots

The oldest known angiosperms were a diverse group of plants called magnoliids. Some of these were herbs with simple flowers; others were woody plants with more complex flowers that were very similar to living magnolias. Magnoliids, probably those with small, inconspicuous flowers, gave rise to the two main groups of angiosperms, **monocots** and **eudicots**, although a few angiosperm families, including the water lilies, may have evolved earlier.

These plants possessed a number of adaptations that were probably crucial to their eventual success. Their vascular tissues were particularly efficient, their embryos were enclosed in a protective seed coat, their leaves were resistant to **desiccation**, and they were pollinated by insects, rather than by the wind. This last feature made pollen transfer much more efficient and was almost certainly a key innovation in the diversification of the group, as coevolution of plants and their pollinators, particularly bees, gave rise to increasing specialization of both flowers and insects.

The orchid family contains some of the most specialized insect-pollinated flowers of all and has more species (at least 24,000) than any other plant family. Other groups of angiosperms re-evolved the ability to be pollinated by wind. One of these groups—the grasses—appeared about 50 million years ago, diversified rapidly, and became the dominant plants over many regions of the planet. They still thrive and are crucial to human well-being. Approximately 54 percent of the food eaten by people is provided by grain (seed) from cultivated varieties of just three grasses: rice, wheat, and corn. SEE ALSO ALGAE; ANGIOSPERMS; ARCHAEA; BRYOPHYTES; CONIFERS; CYANOBACTERIA; EUBACTERIA; EUDICOTS; FRUITS; FUNGI; GYMNOSPERMS; MONOCOTS; PHOTOSYNTHESIS; PLANT; PROTISTA; PTERIDOPHYTES; SEEDLESS VASCULAR PLANTS; SEEDS

Simon K. Emms

monocot plants having a single cotyledon, or leaf, in the embryo

eudicot "true dicot"; plants with two seed leaves that originated from the earliest of flowering plants

desiccation drying out

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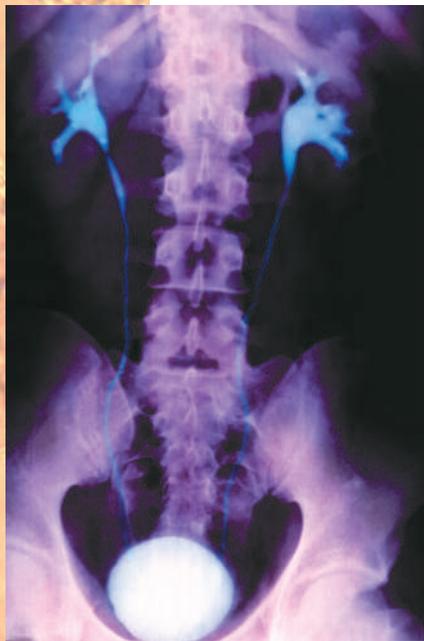
Excretory Systems

Most animals require some system to **excrete** the waste products of **metabolism** from the body fluids. Kidneys are the major organs of the excretory systems of humans and other vertebrates, but several other kinds of excretory organs occur in other kinds of animals.

Functions and Principles

Besides metabolic wastes, kidneys and other excretory organs also eliminate excess water, **ions**, or other substances that are taken in with food. Moreover, although they are referred to as excretory systems, what they retain in the body fluids is just as important as what they excrete. They are best viewed as systems that maintain a constant, or homeostatic, composition of the body fluids.

Water and ions are among the important components of the body fluids that must be maintained homeostatically. Cells will shrink if placed in a fluid that has too high an ion concentration because water will be drawn out of the cell by **osmosis**. Cells will swell in a fluid that is too dilute because water will be drawn into them by osmosis. Maintaining a balance of water and ions—osmoregulation—is another major homeostatic function of the excretory organs of most animals.

With few exceptions, the osmoregulatory and excretory functions are combined in the same organ, which generally works in two stages. First the organ filters blood or another body fluid into a tubule. Then as the **filtrate** passes through the tubule, needed molecules are pumped out of it and back into the body fluid. At the same time, metabolic wastes and excess water and other molecules in the body fluids are pumped into the filtrate by active transport. The resulting fluid, called urine, is eliminated through the open end of the tubule outside the body.

Variety in the Animal Kingdom

In flatworms and a few kinds of invertebrates the excretory/osmoregulatory organ is a protonephridium. By definition, the protonephridium has a tubule that is open only at the end leading outside the body. The other end of the protonephridium has **cilia** or a flagellum that draws body fluid in to form

A color-enhanced normal intravenous pyelogram X ray displaying the drainage of urine from the kidneys through the ureter toward the bladder.

excrete deposit outside of

metabolism chemical reactions within a cell

ion an electrically charged particle

osmosis passage of water through a membrane in response to concentration differences
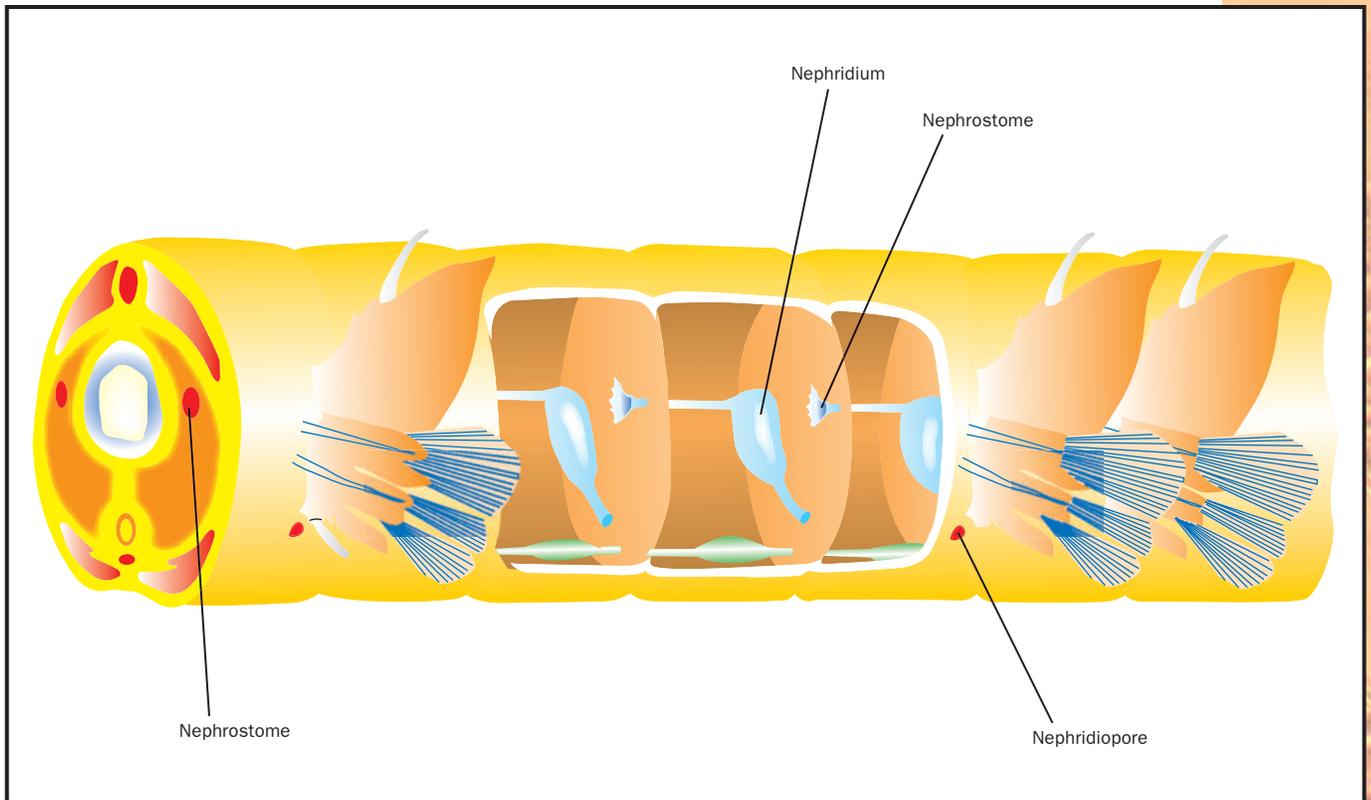
the filtrate. In most kinds of invertebrates, including earthworms, the organ is called the metanephridium (or sometimes simply nephridium). In the metanephridium the tubule is open at both ends, and the pressure of the body fluid forces the filtrate into the tubule.

Insects, crustaceans, spiders, and other **arthropods** have different types of excretory/osmoregulatory organs, but they too operate by filtration and active transport. In insects and spiders the main organs are Malpighian (pronounced mal-PIG-ee-yan) tubules, which are attached to the gut. For these terrestrial animals the problem is to conserve water, rather than eliminate it. Water, containing metabolic wastes and excess ions, is filtered into the Malpighian tubules and then joins the feces in the hind part of the gut. As the feces passes through the rectum, the water is pumped back into the body fluid.

In vertebrates the excretory/osmoregulatory organ is the kidney. The vertebrate kidney contains thousands or even millions of tubules, called **nephrons**, each one of which uses the same principles of filtration and active transport. One difference between kidneys and most other excretory/osmoregulatory organs is that kidneys filter blood rather than some other body fluid. Nephrons form a filtrate consisting of water, nutrients, ions, and other components of blood except cells and very large molecules. As the filtrate passes along the nephron tubule, nutrients, water, and other needed molecules are transported back into the bloodstream. Ions, metabolic wastes, and other excess molecules go into the resulting fluid. Finally, more water is removed from the fluid, transforming it into urine.

Metanephridia, the excretory organ in most invertebrates, including earthworms.

filtrate material passing through a filter

cilia short, hairlike cell extensions of the cell membrane formed by the cytoskeleton

arthropods organisms with jointed appendages and exoskeletons, including insects, spiders, and crustaceans

nephron functional unit of the kidney that performs filtration, reabsorption, and excretion

Flame cell

Cilia

Excretory pore (nephridiopore)

Execretory canal
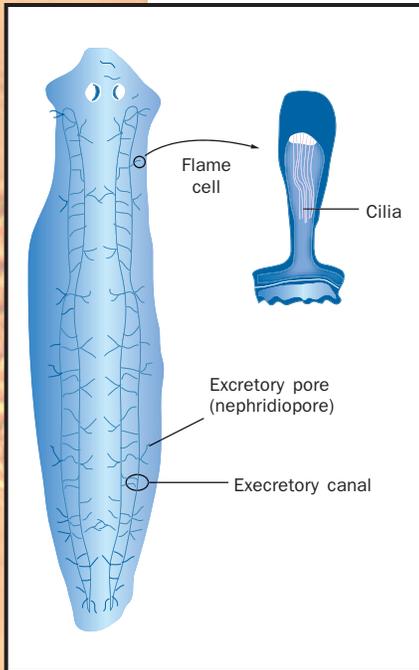
A protonephridia, the excretory organ of flatworms and some invertebrates.

Exceptions

There are two exceptions to the generalization that excretion and osmoregulation are performed by the same systems. The first exception occurs in animals that spend their entire lives in the fairly constant environment of the ocean. For them, osmoregulation is not needed because the balance of water and ions in the oceans is osmotically suitable for cells. (This is not surprising, considering that life most likely evolved in the oceans.) A starfish, for example, does not have or normally need an osmoregulatory system. If a starfish is placed in water with a higher concentration of salts than in the ocean, however, water will be drawn out of it by osmosis, and it will shrink. Conversely, if the starfish is placed in fresh water, it will swell and burst as water is drawn into the more concentrated body fluids.

The second exception to the rule that osmoregulation and excretion are performed by the same system occurs in some sponges and other relatively simple animals that live in fresh water. These animals osmoregulate by collecting excess water in each cell within a chamber called the contractile vacuole. When full, the contractile vacuole contracts and expels the water through the plasma membrane of the cell. The contractile vacuole is also called the water expulsion vesicle. SEE ALSO INSECT; KIDNEY; OSMOREGULATION; PORIFERA

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Exocytosis

intracellular within a cell

vesicle membrane-bound sac

cytoplasm material in a cell, excluding the nucleus

constitutive at a constant rate or continually

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

endoplasmic reticulum network of membranes within the cell

Exocytosis is the cellular process in which **intracellular vesicles** in the **cytoplasm** fuse with the plasma membrane and release or "secrete" their contents into the extracellular space. Exocytosis can be **constitutive** (occurring all the time) or regulated. Constitutive exocytosis is important in transporting **proteins** like receptors that function in the plasma membrane. Regulated exocytosis is triggered when a cell receives a signal from the outside.

Many of the products that cells secrete function specifically for the tissue type in which the cells reside or are transmitted to more distant parts of the body. Most of these products are proteins that have gone through rigorous quality control and modification processes in the **endoplasmic reticulum** and Golgi membranes. It is in the *trans*-Golgi network, the "downstream" end of the Golgi apparatus, where cellular products are sorted and accumulate in exocytic vesicles.

Mechanisms

The mechanisms controlling regulated exocytosis were largely discovered in the 1990s. Contrary to early ideas, membranes normally do not fuse together spontaneously. This is due to the negative charges associated with

the phospholipids that make up the **lipid bilayer** of the membranes of vesicles and **organelles**.

Membrane fusion requires energy and the interaction of special "adaptor" molecules present on both the vesicle and plasma membrane. The adapter molecules are highly selective and only allow vesicles to fuse with membranes of particular organelles, thus preventing harm to the cell. Once the appropriate adapter molecules bind to each other (docking), energy stored and released by **ATP** forms a fusion pore between the vesicle membranes and plasma membrane. The contents of the vesicle are released to the exterior of the cell (or the interior of an organelle) as the fusion pore widens. The vesicle ultimately becomes part of the plasma membrane or is recycled back to the cytoplasm.

Purpose of Exocytosis

Many cells in the body use exocytosis to release **enzymes** or other proteins that act in other areas of the body, or to release molecules that help cells communicate with one another. For instance, clusters of **α**-and **β**-cells in the islets of Langerhans in the pancreas secrete the **hormones** glucagon and insulin, respectively. These enzymes regulate **glucose** levels throughout the body. As the level of glucose rises in the blood, the β-cells are stimulated to produce and secrete more insulin by exocytosis. When insulin binds to liver or muscle, it stimulates uptake of glucose by those cells. Exocytosis from other cells in the pancreas also releases digestive enzymes into the gut.

Cells also communicate with each other more directly through the products that they secrete. For instance, a **neuron** cell relays an electrical pulse through the use of **neurotransmitters**. The neurotransmitters are stored in vesicles and lie next to the cytoplasmic face of the plasma membrane. When the appropriate signal is given, the vesicles holding the neurotransmitters must make contact with the plasma membrane and secrete their contents into the synaptic junction, the space between two neurons, for the other neuron to receive those neurotransmitters.

Components of the vesicle and extra neurotransmitter molecules are quickly taken up and recycled by the neuron to form new vesicles that are ready to send another pulse to an adjacent neuron. Neurons need to send many signals each second, which indicates how tight the controls are that regulate exocytosis.

The immune system also uses exocytosis to communicate information between cells. An immune cell can tell a virally infected cell that it must destroy itself to preserve other cells around it. A cell that is infected with a virus displays viral by-products on its surface, which is equivalent to the cell turning on red warning lights to attract immune cells.

Immune cells, such as the killer **T cells** that wander throughout the body, recognize the viral by-products and position themselves very close to the infected cell so that there is very little space between their plasma membranes. In a rapid succession, the killer T cells mobilize secretory vesicles filled with enzymes like perforin and granzyme B adjacent to the inner side of their plasma membranes. In response to a signal, the vesicles undergo exocytosis and release their contents. These enzymes then punch holes in the

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lipid fat or waxlike molecule, insoluble in water

bilayer composed of two layers

organelle membrane-bound cell compartment

ATP adenosine triphosphate, a high-energy nucleotide used by cells to power most energy-requiring reactions

enzyme protein that controls a reaction in a cell

α the Greek letter alpha

β the Greek letter beta

hormone molecule released by one cell to influence another

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

neuron nerve cell

neurotransmitters molecules released by one neuron to stimulate or inhibit another neuron or cell

Botulinum toxin, responsible for botulism poisoning, paralyzes muscles by disabling one of the adapter proteins in nerve cells.

T cell white blood cell that controls the immune response

plasma membrane of the infected cell. This causes the cell to undergo self-destruction or apoptosis, also known as programmed cell death, to prevent further spread of the virus. SEE ALSO BLOOD SUGAR REGULATION; ENDOCYTOSIS; ENDOPLASMIC RETICULUM; GOLGI; PROTEIN TARGETING

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Extinction

lineage ancestral line

Extinction is the termination of evolutionary **lineage**. The most common extinction event is the loss of a species. There are many reasons why a species might die out. Human intervention (either directly or indirectly) has become the leading cause of species extinction (possibly for the last fifteen thousand years).

Species and Populations

An important distinction must be made between true extinction and extirpation. Extirpation is the loss of a population, or loss of a species from a particular geographic region. A famous twentieth-century example is the extirpation of wolves from the Yellowstone region of Wyoming. The park service reintroduced wolves to Yellowstone in the 1990s, and these predators appear to be adapting well to their new home. True extinction must also be differentiated from pseudoextinction. Biologists studying the changes that take place in a lineage over time often designate distinct morphological stages as separate species. The extinction of a species in this context is not the result of the termination of a lineage, but rather the transformation into a new form.

A clear understanding of the definition of a species is necessary in order to discuss extinction. This is not a simple question, but one view defines a species as a population of potentially interbreeding individuals that is reproductively isolated from other such populations. By this definition the relatively common mating between coyotes and domestic dogs raises the question of the validity of their separate species status.

Environmental Change

Species go extinct primarily because they are unable to adapt to a changing environment. Animals with specialized food or habitat requirements, such as the giant panda (which feeds almost exclusively on bamboo), are particularly susceptible to environmental changes. Generalist species that feed on many types of food and live in a variety of settings are much more able to survive in a changing environment. For example, raccoons are common city dwellers, where they forage from trash cans instead of from streams. In addition, species with long generation times that produce few offspring are often vulnerable to extinction. If a population of animals is very small, it is subject to extinction from a variety of factors, such as disturbances and dis-

The giant panda actually has a carnivorous digestive system, so it must eat voraciously for 10 to 12 hours to consume enough bamboo (up to 66 pounds [30 kilograms]) each day.

A dinosaur skeleton on display at the Royal Terrell Museum in Dinosaur Provincial Park in Alberta, Canada.

eases. Organisms with short generation times that produce a lot of offspring, for example, many rodents and insect species, are often capable of increasing their populations quickly and therefore become less vulnerable to extinction. However, animals such as the rhinoceros or Siberian tiger take several years to mature and when they do reproduce only give birth to one or two offspring. Thus, species such as these cannot rebound from low populations quickly and thus are more likely to go extinct.

A firm grasp of ecological principles is crucial to an understanding of how species interactions can lead to extinction. Two species with significantly overlapping niches are unlikely to coexist over time unless some mechanism prevents either species from reaching its carrying capacity (the maximum number of individuals the habitat can sustain). Typically the species that is better adapted will drive the other species to extinction. This phenomenon is particularly important because of the widespread introduction of exotic species by humans. Many studies have shown the impact of domestic cats and dogs on native prey species. Less obvious, however, is their competitive impact on native predators.

placental related to mammals that nourish the fetus with a placenta, an exchange organ in the uterus

marsupial kangaroos and other mammals that gestate young in an external pouch

adaptive radiation diversification of a group of organisms into several different forms that adapt to different environments

The extinction of the Tasmanian wolf in the twentieth century is probably the best-known example of this negative impact on biodiversity. Typically whenever there is considerable overlap between the niches of a **placental** and a **marsupial** the placental will win out. The reasons for placental superiority are not entirely clear (relatively greater intelligence and reproductive physiology are possibilities), but this fact probably accounts for the existence of only one successful species of marsupial in North America, the opossum, a broad generalist with a very high reproductive rate.

Mass Extinctions

Mass extinction events have occurred periodically in Earth's history. Three of these events are particularly relevant to mammalian history. The first was the Cretaceous-Tertiary extinction 65 million years ago that led to the demise of the dinosaurs. Mammals and dinosaurs coexisted for approximately 140 million years, during which time dinosaurs dominated the majority of large terrestrial vertebrate niches. This extinction most likely was the result of a large meteor impact that eliminated over half of all species on the planet. Mammals survived that extinction event relatively well, probably because the majority of Mesozoic mammals were species with short generation times and large litters. During the Tertiary period, mammals underwent a rapid **adaptive radiation**, filling niches similar to those vacated by dinosaurs.

A second major extinction event occurred during the Eocene-Oligocene period, 30 to 35 million years ago. This extinction was the result of global cooling due to changes in ocean current patterns. Prior to this period modern families of mammals comprised only about 15 percent of the mammalian fauna; after cooling modern mammals made up more than 50 percent of the fauna at the family level.

The third mass extinction event began around 15,000 years ago and is still ongoing. Large species (mammoths, ground sloths, horses, camels, and lions) were more adversely impacted by the most recent extinction event than other taxa. In the twenty-first century, there are only about a dozen species of large mammals (over 100 pounds) in North America. As recently as 11,000 years ago there may have been three times that number.

There is controversy about what caused the extinction of these large mammals. Three possibilities include global warming at the end of the last major glaciation, overkill by early North American humans, and contagious diseases. The timing of each of these events correlates with the time of extinction, therefore determining which hypothesis is most likely must be based on the merits of each argument. Reduction in size of suitable habitat is the most likely factor if the extinction is due to climatic change. Much of North America was covered by a grassland habitat during the last glacial period. As this habitat declined the largest species may have been unable to adapt to the new conditions. Migration of humans into North America is the causative agent for the other two hypotheses. According to these models, the megafauna went extinct either directly through predation by a highly efficient hunter or indirectly by the introduction of exotic, infectious organisms.

Carolina parakeets collected in 1870 and housed in the British Museum of Natural History in Tring, England. Many of these birds were shot becaue they were eating fruit crops. Within a few decades, the species was extinct.

In the late twentieth and early twenty-first centuries, large-scale habitat destruction in tropical forests and elsewhere has caused extinction of significant numbers of species, many not fully identified. Pressures from population increase, agricultural expansion, and forest cleaning threaten many thousands of species throughout the world. SEE ALSO BIODIVERSITY; CONSERVATION; ENDANGERED SPECIES; EVOLUTION; FOREST, TROPICAL; POPULATION DYNAMICS; SPECIES

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Extracellular Matrix

The extracellular matrix is a meshwork of **proteins** and **carbohydrates** that binds cells together or divides one tissue from another. The extracellular matrix is the product principally of **connective tissue**, one of the four fundamental tissue types, but may also be produced by other cell types, including those in epithelial tissues. In the connective tissue, matrix is secreted by connective tissue cells into the space surrounding them, where it serves to bind cells together. The extracellular matrix forms the **basal** lamina, a complex sheet of extracellular matrix molecules that separates different tissue types, such as binding the epithelial tissue of the outer layer of skin to the underlying dermis, which is connective tissue. Cartilage is a connective tissue type that is principally composed of matrix, with relatively few cells.

Collagens

Collagens are the principal proteins of the extracellular matrix. They are structural proteins that provide tissues with strength and flexibility, and serve other essential roles as well. They are the most abundant proteins found in many vertebrates. There are at least nineteen collagen family members whose subunits, termed **α** chains, are encoded by at least twenty-five **genes**. The primary protein sequence of all collagen subunits contains repeating sequences of three **amino acids**, the first being glycine with the second and third being any amino acid residue (sometimes referred to as a GLY–X–Y motif).

Most, if not all, collagens assemble as **trimers**, with three α subunits coming together to form a tightly coiled helix that confers rigidity on each collagen molecule. Assembly of the collagen trimer occurs in the cell by a self-assembly process, which is mediated by short amino acid sequences at both ends of each α subunit, called propeptides. Some collagens, most notably collagen types I, II, III, and V, assemble into large, ropelike macrofibrils once they are secreted into the extracellular matrix. In these cases, the propeptides are cleaved off following **secretion**, permitting the trimeric molecules to undergo further self-assembly into fibrils. In the electron microscope each of these macrofibrils has a characteristic banded appearance and can be very large (up to 300 **nanometers** in diameter).

Type IV collagen, which is found in the basal lamina, does not assemble into a fibril since its α subunits retain their propeptides following secretion from a cell. Its triple helix has a series of interruptions in the GLY–X–Y repeating motif, preventing the subunits from binding quite as tightly, and giving the molecule more flexibility. Type IV collagen forms a scaffold around which other basal lamina molecules assemble. In contrast to the fibril-forming collagens and type IV collagen, type XVII collagen is membrane-spanning protein. It is a component of a cell/matrix junction called the hemidesmosome.

The fibrillar collagens are also associated with a class of collagen molecules that themselves do not form fibrils but that appear to play an important role in organizing the highly ordered arrays of collagen fibrils that occur in some connective tissues. Examples of this collagen class include type IX and type XII collagen.

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

carbohydrates sugars, starches, and other molecules combining carbon, hydrogen, and oxygen and serving as fuel or structural components

connective tissue one of four types of body tissue, characterized by few cells and extensive extracellular material

basal lowest level

α the Greek letter alpha

gene portion of DNA that codes for a protein or RNA molecule

amino acid a building block of protein

trimer a structure composed of three parts

secretion material released from the cell

nanometer 10^{-9} meters; one-billionth of a meter

Collagens do not simply provide filler for tissues. Both fibrillar and basal lamina collagens interact with other extracellular matrix proteins and play important roles in regulating the activities of the cells with which they interact. Cells associate with collagen via cell surface receptors, and through such interactions collagens may have a profound impact on cell proliferation, migration, and differentiation. Fibers and meshworks of collagen molecules also act as a repository of growth factors and matrix-degrading **enzymes**. These are often present in inactive form and become activated in order for tissues to undergo remodeling, for example in development, during cyclical changes in the female reproductive system, and in **pathological** conditions such as cancer. SEE ALSO Amino Acid; Connective Tissue; Epithelium; Protein Structure

Jonathan Jones

enzyme protein that controls a reaction in a cell

pathologic related to disease

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Extreme Communities

The environments of Earth include conditions in which physical and chemical extremes make it very difficult for organisms to survive. Conditions that can destroy living cells and biomolecules include high and low temperatures; low amounts of oxygen and water; and high levels of salinity, acidity, alkalinity, and radiation. Examples of extreme environments on Earth are hot geysers and oceanic thermal vents, Antarctic sea ice, and oxygen-depleted rivers and lakes. Organisms that have evolved special adaptations that permit them to live in extreme conditions are called "extremophiles."

Cellular Adaptations

Some organisms survive in extreme environments by keeping the extreme environment outside their cell walls. For example, organisms that live at the extremes of **pH** are often able to do so by maintaining their **cytoplasm** at near-neutral levels of pH, thus eliminating the need for other adaptive physiology. Where it is impossible to keep the extreme environmental conditions outside the cells, in very hot environments, for example, extremeophiles have evolved special physiological mechanisms and repair abilities.

pH measure of acidity or alkalinity; numbers below 7 are acid, above are basic

cytoplasm material in a cell, excluding the nucleus

High temperatures increase the fluidity of membranes, whereas low temperatures decrease membrane fluidity. To counter these changes, some extremeophile organisms change the ration of unsaturated to saturated fatty acids. As temperatures decrease, the proportion of unsaturated fatty acids in the membrane increases. The increase in the proportion of unsaturated fatty acids is also often a response to increased pressure, which also reduces the fluidity of cell membranes. To withstand below-freezing temperatures, some organisms protect cell fluids from freezing by producing chemicals that act like antifreeze, lowering the temperature at which the cell fluids will freeze (crystallize) to as low as -40 degrees Celsius. Other organisms are freeze tolerant, permitting freezing of up to 65 percent of their body water, as in the case of the wood frog.

A hydrothermal vent on the East Pacific Rise. Life forms ranging from microbes to invertebrates have adapted to the extreme conditions around these underwater geysers.
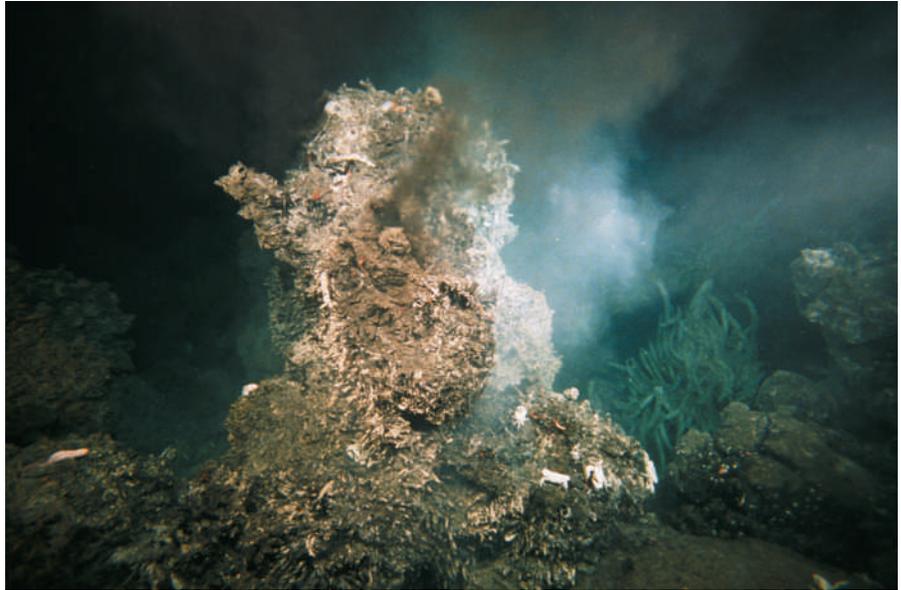
protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

enzyme protein that controls a reaction in a cell

oxidative characterized by oxidation, or loss of electrons

antioxidant substance that prevents damage from oxidation

ion an electrically charged particle

amino acid a building block of protein

cytosol fluid portion of a cell, not including the organelles

desiccation drying out

prokaryote single-celled organism without a nucleus

High temperatures destroy the delicate **proteins** of unadapted organisms. Extremeophiles have protein structures stabilized against the disruptive effects of heat. One Archean thermophile, *Thermus aquaticus*, which lives in hot springs, is the source of the heat-stable deoxyribonucleic acid (DNA) polymerase **enzyme** used in polymerase chain reaction (PCR). PCR forms part of the foundation of much of the biotechnology industry.

Radiation and **oxidative** damage have always been common on Earth. Mechanisms evolved to cope with these conditions include the production of **antioxidants** and detoxifying enzymes and the ability to repair damage to cells. Many microorganisms respond to increases in osmolarity (concentration of dissolved substances in the environment) by accumulating osmotica (**ions**, **amino acids**, or other small molecules) in their **cytosol** to protect them from dehydration and **desiccation**. With the exception of the Halobacteriaceae, which use K^t (potassium ion) as their osmoticum, glycine-betaine is the most common effective osmoticum in most **prokaryotes**. During desiccation, osmotic concentration increases, and thus responses are similar to those in a cell in a saline environment.

Examples of Extreme Communities

Deep Sea. The deep sea environment has high pressure and cold temperatures (1 to 2 degrees Celsius [33.8 to 35.6 degrees Fahrenheit]), except in the vicinity of hydrothermal vents, which are a part of the sea floor that is spreading, creating cracks in the earth's crust that release heat and chemicals into the deep sea environment and create underwater geysers. In these vents, the temperature may be as high as 400 degrees Celsius (752 degrees Fahrenheit), but water remains liquid owing to the high pressure. Hydrothermal vents have a pH range from about 3 to 8 and unusual chemistry. In 1977, the submarine *Alvin* found life 2.6 kilometers (1.6 miles) deep near vents along the East Pacific Rise. Life forms ranged from microbes to invertebrates that were adapted to these extreme conditions. Deep sea environments are home to psychrophiles (organisms that like cold tempera-

tures), hyperthermophiles (organisms that like very high temperatures), and piezophiles (organisms adapted to high pressures).

Hypersaline Environments.   Hypersaline environments are high in salt concentration and include salt flats, evaporation ponds, natural lakes (for example, Great Salt Lake), and deep sea hypersaline basins. Communities living in these environments are often dominated by halophilic (salt-loving) organisms, including bacteria, algae, diatoms, and protozoa. There are also halophilic yeasts and other fungi, but these normally cannot tolerate environments as saline as other taxa.

Deserts.   Deserts can be hot or cold, but they are always dry. The Atacoma desert in Chile is one of the oldest, driest hot deserts, sometimes existing for decades without any precipitation at all. The coldest, driest places are the Antarctic Dry Valleys, where primary inhabitants are cyanobacteria, algae, and fungi that live a few millimeters beneath the sandstone rock surface. Although these endolithic (living in rocks) communities are based on photosynthesis, the organisms have had to adapt to long periods of darkness and extremely dry conditions. Light dustings of snow that may melt in the Antarctic summer are often the only sources of water for these organisms.

Ice, Permafrost, and Snow.   From high-altitude glaciers, often colored pink from red-colored algae, to the polar permafrost, life has evolved to use frozen water as a habitat. In some instances, the organisms, such as bacteria, protozoa, and algae, are actually living in liquid brine (very salty water) that is contained in pockets of the ice. In other cases, microorganisms found living on or in ice are not so much ice lovers as much as ice survivors. These organisms may have been trapped in the ice and simply possessed sufficient adaptations to enable them to persist.

Atmosphere.   The ability for an organism to survive in the atmosphere depends greatly on its ability to withstand desiccation and exposure to ultraviolet radiation. Although microorganisms can be found in the upper layers of the atmosphere, it is unclear whether these constitute a functional **ecosystem** or simply an aerial suspension of live but largely inactive organisms and their spores.

ecosystem an ecological community and its environment

Outer Space.   The study of extremeophiles and the ability of some to survive exposure to the conditions of outer space has raised the possibility that life might be found elsewhere in the universe and the possibility that simple life forms may be capable of traveling through space, for example from one planet to another. SEE ALSO ARCHAEA; EUBACTERIA; POLYMERASE CHAIN REACTION

Rocco L. Mancinelli and Lynn J. Rothchild

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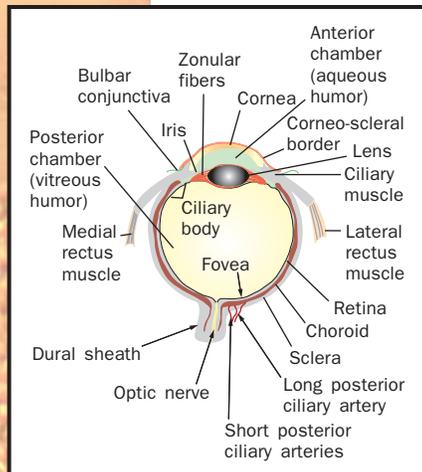
Structure of the human eye.

Eye

The human eye is an amazing instrument. It is the body's camera, capturing images of the world with striking clarity in a virtual instant. The eye and the typical camera share many of the same structural features. A camera needs an operator, a housing (box) to hold onto and to contain the working parts and film, an aperture to let the light in (preferably one that allows for different light conditions), a lens for focusing the image, and film for capturing the image. Then the film must be developed (or the digital images downloaded). The following description illustrates how the eye performs these same functions.

Anatomy of the Eye

The eye consists mainly of three layers, or tunics. The bulk of the outermost layer (fibrous tunic) is the white of the eye, or sclera. Like a camera's housing, the sclera is the eye's skeleton, giving structure to the eye and protecting the internal components; it also provides an attachment site for the eye muscles that position the eye under the control of the brain. In the very front of the eye, where the light must pass through, the fibrous tunic is a transparent structure called the cornea. The cornea is responsible for approximately 70 percent of the focusing power of the eye; without a cornea, vision would be impossible. (One can, however, see without a lens, just not very keenly.) Because it must be transparent, there are no blood vessels in the cornea. The tissue must get all of its oxygen and nutrients by diffusion; the cornea actually "breathes" across its surface (hence "gas-permeable" contact lenses can be worn for longer periods than "hard contacts").

The middle layer (vascular tunic) mostly provides for internal maintenance functions, as well as for aperture and fine focusing control. In the posterior two-thirds, the vascular tunic consists of the choroid, a layer of nutritive and supporting tissue. Toward the front, it forms the ciliary body and the iris.

The ciliary body contains the smooth muscles that pull on suspensory ligaments attached to the lens, changing its shape and thus adjusting its focusing power. (Sometimes the **proteins** that make up the lens become cloudy, a condition called a cataract.) The ciliary body also secretes **aqueous** humor, the watery fluid that fills the space between the cornea and lens (anterior cavity). This fluid provides a sort of circulatory system for the front of the eye. When excess fluid accumulation causes excess **intraocular** pressure, the vision-threatening condition known as glaucoma occurs.

The iris, the colored portion of the eye surrounding the dark opening (pupil), sits in front of the lens. The iris is made of two sets of smooth muscle that contract to produce pupil **dilation** or constriction; this brainstem reflex controls the intensity of the light reaching the innermost sensory layer, the retina.

The retina makes up the inner layer, or **neural** tunic, and occupies only the posterior two-thirds of the eye. The retina consists of several layers of cells, including the rods and cones, the sensory cells that respond to light. The tips of the rods and cones are embedded in a pigmented layer of cells on the very back of the retina. The pigment helps prevent light from scattering in the back of the eye. (Some **nocturnal** animals have a reflective

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

aqueous watery or water-based

intraocular within the eyeball

dilation expansion or swelling

neural related to nerve cells or the nervous system

nocturnal characterized by activity at night, or related to the night

layer instead of pigment, called the tapetum lucidum, which increases their sensitivity to low light and makes their eyes "shine" when a bright light strikes them.) When light strikes a rod or cone cell, it passes the signal to a bipolar cell, which passes it on to the ganglion cells, which perform the first level of information processing. The **axons** of the ganglion cells also form the "cables" that make up the optic nerve, carrying visual information to the brain. (There are no rods and cones where the optic nerve leaves the eye; this is called the "blind spot.") The retina is pressed flat against the inner wall of the eye by a thick, gel-like substance called vitreous humor, which fills the space behind the lens (posterior cavity).

Accessory Structures

There are accessory structures associated with the eye. The eye is protected by being located in the orbit of the skull. Eyelashes help prevent foreign matter from reaching the sensitive surface. The eyelids help protect the exposed **anterior** part of the eye. The eyelids have glands that produce lubricating **secretions**. Infection of the glands at the base of the eyelash produces a painful localized swelling called a sty. A thin membrane called the **conjunctiva** lines the inside of both eyelids and covers the exposed eye surface (except the cornea); when this membrane gets irritated, blood vessels beneath it become dilated, resulting in a condition called conjunctivitis ("pinkeye").

Tear (lacrimal) glands located on the upper lateral (outside) region of the eye provide secretions (tears) that lubricate the surface, remove debris, help prevent bacterial infection, and deliver oxygen and nutrients to the conjunctiva; blinking of the eyelids provides a wiping action across the surface that keeps the eye "polished" and distributes the tears. These tears then drain into the tear ducts in the lower inner corner of the eye, draining into the nasal cavity. Another gland, the lacrimal caruncle (the pinkish blob in the inner corner), produces thick secretions that sometimes accumulate during sleep (the "sand" from the "sandman").

Most vertebrate animals have eyes that are essentially the same as the human eye. Among invertebrates, there is a wide variety of eyes. Some have simple eyespots that do not form images, detecting only the presence of light. Others, like the cephalopod mollusks (octopus, squid), have a camera eye very similar to that of vertebrates. Perhaps the most unusual eye is the compound eye found in **arthropods** such as insects and crustaceans. These eyes actually consist of hundreds of individual eye units, called ommatidia (up to thirty thousand in dragonflies). Each ommatidium has its own lens and set of receptor and supporting cells; each forms its own tiny picture of only a small part of the visual field. The insect's brain thus receives a mosaic of hundreds of individual images that it uses to make a somewhat "grainy" composite image of the entire visual field. SEE ALSO VISION

Harold J. Grau

A colored scanning electron micrograph of rod cells (blue and purple) in the retina of a human eye.

axon long extension of a nerve cell down which information flows

anterior toward the front

secretion material released from the cell

conjunctiva eye membrane that helps seal the eye socket

arthropods organisms with jointed appendages and exoskeletons, including insects, spiders, and crustaceans

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F

organic composed of carbon, or derived from living organisms

Feeding Strategies

All animals are heterotrophic, meaning they must eat other organisms, living or dead, to acquire **organic** nutrients. A large percentage of an animal's life is occupied with acquiring food. Almost every living species is eaten by something else, but food varies in its spatial distribution, seasonal availability, predictability, how well hidden or easily detected it is, how much competition for it exists, and whether or not it can resist being eaten. Consequently, animals have a variety of feeding strategies to meet these challenges.

Some animals are food generalists (euryphagous); that is, they eat a wide variety of foods. Coyotes, opossums, and humans are good examples. Others are food specialists (stenophagous), feeding on a narrow range of foods. For example, the Everglades kite (a small hawk) feeds on just one species of snail, and many feather mites can survive on just one species of bird.

Behavioral ecologists who study feeding strategies are often concerned with theories of optimal foraging. Obviously, animals must gain more energy from their food than they expend in searching for it, capturing it, and consuming it. In addition to energy, they must acquire specific nutrients, such as certain salts, which provide no energy but are crucial for survival. Thus, theories of feeding are concerned with such issues as food choice, prey switching, sensory mechanisms for recognizing and locating food, optimal search strategies, overcoming the defenses of food organisms, and how to compromise between finding food and not carelessly falling prey to some other hunter.

Following are some of the basic methods that animals use to acquire food. Many animals use mixed strategies, shifting from one method to another as different kinds of food become available, or using combinations of methods simultaneously.

Grazing

Grazers crop grasses and other ground plants on land or scrape algae and other organisms from surfaces in the water. They include animals as diverse as snails, grasshoppers, geese, rodents, kangaroos, and hoofed mammals. Grass and algae are palatable foods that offer little or no resistance to being eaten, but are adapted to survive grazing and quickly replace the lost biomass. A disadvantage of such food, however, is that it is nutrient poor. Grazers therefore must consume a large quantity of it and spend a larger percentage of their time eating than predators do. While eating, they are vulnerable to attack. To eat without being eaten requires alertness and quick escape responses. Grazing mammals tend to form herds: There is safety in numbers, and the abundance of grass supports the high population density of grazing herds.

Browsing

Terrestrial browsers nip foliage from trees and shrubs. They include caterpillars, tortoises, grouse, giraffes, goats, antelopes, deer, pandas, koalas, and monkeys. In aquatic habitats, browsers feed on algae, aquatic plants, and corals, and include sea slugs, sea urchins, parrot fish, ducks,

and manatees. Browsers depend on food that is less abundant and widespread than grass, so they tend to form smaller groups or to be solitary and secretive.

Eating Nectar, Fruits, Pollen, and Seeds

Plants provide an abundance of food other than foliage, some of it for the purpose of rewarding animals. Sweet nectar rewards bees, flies, moths, butterflies, and bats that spread pollen from one flower to another, and sugary fruits entice birds, monkeys, fruit bats, bears, elephants, and humans to eat them and spread the indigestible seeds throughout the countryside. Pollen and seeds, being a plant's reproductive capital, are not meant to be eaten, but many bees, flies, and beetles nevertheless consume pollen, while birds, squirrels, and harvester ants take their toll on the seed crop.

Burrowing

Some animals burrow into their food, eating a tunnel as they go. These include many herbivores such as bark beetles, fly and moth larvae called leaf miners, and wood-boring termites. In the sea, unusual clams and crustaceans called shipworms and gribbles, respectively, burrow through wooden piers and ships, causing enormous destruction. Earthworms and many marine worms burrow in soil and sediment, eating indiscriminately as they go, digesting the organic matter and defecating the indigestible sand and other particles. Burrowing animals not only have the benefit of being surrounded by food, but also are less exposed to predators.

Filter-feeding

Filter-feeding is a common strategy in aquatic habitats, especially the ocean. It uses anatomical devices that act as strainers to remove small food items from the water. **Sessile** filter-feeders, such as barnacles, oysters, fanworms, brachiopods, and tunicates sit in one place, pumping sea water and straining **plankton** from it. Other filter-feeders are mobile. Herring swim with their mouths open, letting water flow through the gill rakers, which strain small particles of food from it. Flamingoes take in mouthfuls of water and mud, then force the water through the fringed edges of their bills, which serve as strainers that retain food such as brine shrimp, aquatic insects, and plankton in the mouth. Small and even microscopic food in the water may not seem very abundant, yet the largest animals on Earth—the basking sharks, whale sharks, manta rays, and baleen whales, including the largest species alive today, the great blue whale—nourish themselves entirely in this way. Filter-feeding is more common in the ocean than in fresh water, because plankton is less concentrated in fresh water.

Suspension and Deposit Feeding

Another form of small particulate food in aquatic habitats is the steady "rain" of organic matter that settles to the bottom: living and dead plankton and bits of dead animal, plant, and algal tissue. Suspension feeders pick this material from the water as it falls and deposit feeders consume it after it settles on the bottom. Many sea anemones, corals, marine worms, and crinoids, for example, spread out an array of tentacles and capture whatever settles

Fruit bats consume both fruit and flowers. They normally suck on the flowers and fruit, then swallow the nectar or juice and spit out the rest. Because fruit bats disperse seeds and pollinate the flowers of many plants, many of the fruits and vegetables we eat every day would not exist without these bats.

sessile attached and remaining in one place

plankton microscopic floating organisms

substrate surface for attachment

ciliated possessing cilia, short, hairlike extensions of the cell membrane

on them. Other worms, some bivalves, brittle stars, and sea cucumbers spread sticky palps, arms, or tentacles over the **substrate**, picking up the organic matter that has settled there. The feeding arms or tentacles of many of these animals have **ciliated**, sticky grooves. Food becomes caught in mucus, and cilia steadily propel the mucus strand toward the mouth. Sea cucumbers, however, reach out and pick up sediment on their sticky tentacles, then draw the tentacles into their mouths and remove the food, like licking jam off one's fingers.

Predation

Predators are animals that depend on killing other animals outright. Since the other animals have evolved defenses against predation—hard shells, toxins, the ability to fight back, or simply running or flying away—predators have evolved a wide range of strategies for capturing their prey. Some hunt in packs (wolves), some collaborate to ambush prey (lions), some are stalkers (solitary cats), some use lures to attract unsuspecting prey (snapping turtles and angler fish), some employ camouflage so their prey does not notice them until it is too late (praying mantids), and some use snares (spiders, jellyfish).

Symbiosis

Symbionts are animals that live in a close physical relationship with another animal, the host, from which they benefit. Unlike predators, symbionts do not benefit from the death of their hosts; ideally, they steal food or consume host tissue at a rate that the host can tolerate, allowing the host to survive. Symbiosis includes mutually beneficial relationships (mutualism); relationships in which one partner benefits, typically by stealing food from the host or eating its tissues, but the host is neither benefited nor harmed (commensalism); and relationships in which the host is harmed, usually because the symbiont consumes nutrients or tissue faster than the host can replace it (parasitism). The host is often both food and shelter for its symbiont.

Scavenging

Finally, and fortunately for the planet's "hygiene," many animals belong to a community of scavengers that feed on organic refuse such as manure (dung beetles, flies), leaf litter (snails, millipedes, earthworms), and dead animals (blowflies, vultures, hyenas, storks). The family name of the vultures, Cathartidae, is from the Greek *katharos*, meaning "to cleanse." Disgusting as some people may find their habits, we would be infinitely more disgusted with an environment from which such scavengers were lacking. SEE ALSO ECOSYSTEM; HERBIVORY AND PLANT DEFENSES; OCEAN ECOSYSTEMS: HARD BOTTOMS; OCEAN ECOSYSTEMS: OPEN OCEAN; OCEAN ECOSYSTEMS: SOFT BOTTOMS; PARASITIC DISEASES; PREDATION AND DEFENSE; PROTOZOAN DISEASES; SYMBIOSIS

Kenneth S. Saladin

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Female Reproductive System

Like the male reproductive system, a primary function of the female reproductive system is to make **gametes**, the specialized cells that contribute half of the total genetic material of a new person. The female reproductive system has several additional functions: to be the location for joining of the male and female gametes, to protect and nourish the new human during the period of **gestation**, and to nourish the newborn infant for some time after birth, though **lactation** and nursing.

Basic Anatomy

The parts of the female reproductive tract normally include two ovaries, two uterine tubes (also called **fallopian tubes**), a single pear-shaped uterus, and a single vagina. Gamete production is the responsibility of the ovaries, whereas protection and nourishment of the growing embryo and fetus before birth are functions of the uterus. The two uterine tubes, one from each ovary, provide pathways for the female gametes (eggs) to get from the ovaries to the uterus.

The portion of the reproductive tract called the vagina is between the narrow uterine cervix and the outside of the body. In female humans there is a second opening where the urethra from the urinary bladder connects to the outside of the body. The urethral opening is normally separate from, and in front of, the vagina. Both the urethra and the vagina are located between two outer folds of skin called the labia majora and two inner folds, the labia minora. The structure called the clitoris is located where the two folds of the labia minora join each other at the front. The organs of the female reproductive tract are kept in place internally by ligaments that attach the ovaries and uterus to the body wall and by the peritoneal membrane that lines the body cavity containing the intestines and other digestive organs.

gamete reproductive cell, such as sperm or egg

gestation period of fetal development within the mother

lactation production of milk by the mammary glands

fallopian tubes tubes through which eggs pass to the uterus
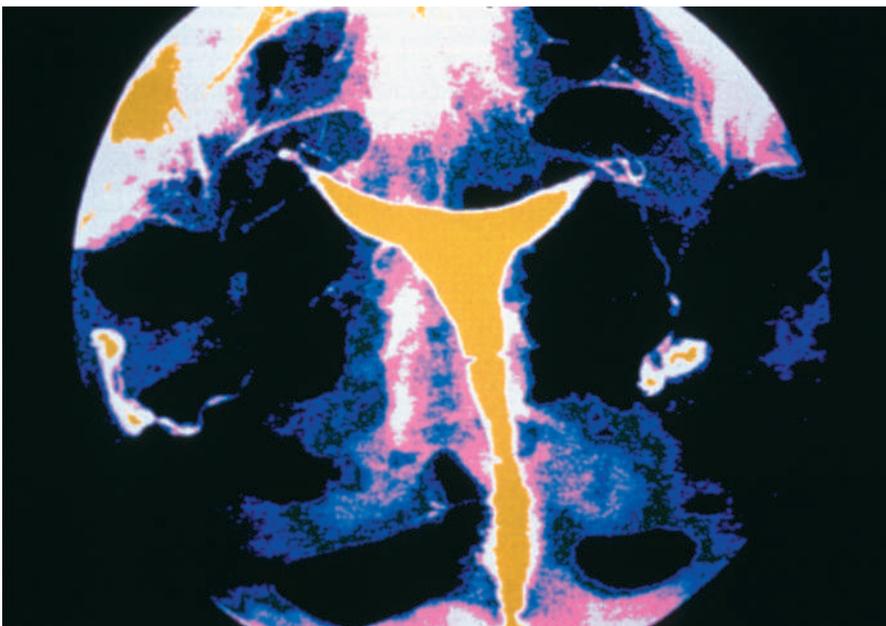
A hysterosalpinograph (X ray) of a normal human uterus and fallopian tubes.

Clavicle

Intercostal muscle

Pectoralis major

Alveolus and acini

Ductule

Lactiferous duct

Lactiferous sinus

Nipple pores

Suspensory ligaments of Cooper
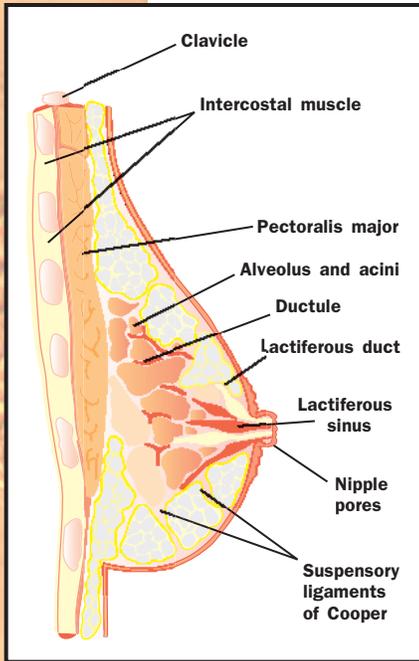
A cross-section of a breast showing the structure of the mammary gland and its placement on the surface muscles of the chest.

follicle a vesicle that contains a developing egg surrounded by a covering of cells

hormone molecule released by one cell to influence another

fertilization union of sperm and egg

The mammary glands are not part of the female reproductive tract but are important secondary reproductive organs. The mammary glands develop in the tissue underneath the skin but on top of the muscles of the chest. Both males and females start with the same tissues, but normally only females generate the correct hormonal signals to promote development of the mammary glands at puberty. The full ability of mammary glands to synthesize and secrete milk does not occur unless a woman is exposed to the hormonal changes of pregnancy.

The Menstrual Cycle

The primary **follicles** located in the ovary contain the only cells in the female that can complete the special form of cell division (meiosis) that produces gametes. In females the mature gametes are called egg cells or ova. The production of mature ova is not continuous. Each twenty-eight days or so, one primary follicle (containing one ovum) matures under the influence of **hormones** from the anterior pituitary, hypothalamus, and the ovary itself. The process of release of a mature ovum from a mature follicle is called ovulation.

While the follicle and ovum are maturing, the follicle secretes hormones that prepare the uterine lining (the endometrium). The endometrium gets thicker and is well supplied with blood vessels. If there are no viable sperm present in the uterine tube as the ovum moves along from the ovary to the uterus, then the ovum will not be fertilized. If **fertilization** does not occur, or for any other reason a blastocyst (future embryo) fails to implant within the endometrium, the built-up endometrial lining degenerates and is shed. Some bleeding accompanies this process, and the menstrual flow that leaves the woman's body through her vagina is made of blood and the cells that lined the uterus. Following menstruation, the cycle normally begins again with maturation of a new ovum and buildup of the uterine lining once more.

Women do not have menstrual cycles their entire lives. The first menstrual flow (the menarche) actually means that a female's first menstrual cycle has just been completed; the first menstrual flow is one commonly used outward sign that a female has entered the transition time called puberty. During puberty, a reproductively immature "girl" becomes a reproductively capable "woman." With an adequate diet and general good health, puberty typically begins early in a girl's second decade of life; a first menstrual cycle at eleven or twelve years of age is not unusual. Women also eventually stop having menstrual cycles sometime in their fifth or sixth decade (forty-five to fifty-five years of age). The last menstrual period that a woman experiences is referred to as her menopause. The exact time of menarche and menopause varies significantly from one woman to another.

Hormonal Control of Female Reproduction

Hormones typically coordinate functions in several different organs at the same time. Considerable coordination among the organs of the female reproductive tract is required. Reproduction will not be successful unless ovulation at the ovary occurs near the time when the uterus is prepared to receive the pre-embryo and, soon thereafter, begin forming the placenta. Without a functional placenta the pregnancy will not continue very long after implantation of the blastocyst.

Female Reproductive System

Follicular cells

Proliferation of granulosa cells

Zona pellucida

Differentiation of surrounding ovarian connective tissue into thecal cells

Primary oocyte

Primary follicles (40μm)

Primary oocyte

Single layer of granulosa cells

Mature follicle

Primary follicle

Corpus luteum

Beginning of formation of antrum

Degenerating corpus luteum

Corpus luteum

Thecal cells

Granulosa cells

Antrum

Developing secondary follicle

Zona pellucida
Ovum (primary oocyte)

Ovulated ovum (secondary oocyte)

Corona radiata

Follicular remnant

Ovarian surface
Ovum (secondary oocyte)

Zona pellucida

Developing corpus luteum

Mature follicle (12 - 16mm)

The ovarian cycle.

A suite of hormones begin preparing the uterus to receive a fertilized egg and control the development of the next ovum. The ovaries, the anterior pituitary, and the hypothalamus all have **endocrine secretions** involved in the control of female reproduction.

At puberty, the hypothalamus begins its first cyclic release of the peptide hormone gonadotropin releasing hormone (GnRH), which increases the secretion of peptide hormones called luteinizing hormone (LH) and

endocrine related to the system of hormones and glands that regulate body function

secretion material released from the cell

79

Hormonal profiles throughout the ovarian and uterine cycles with basal body temerature.
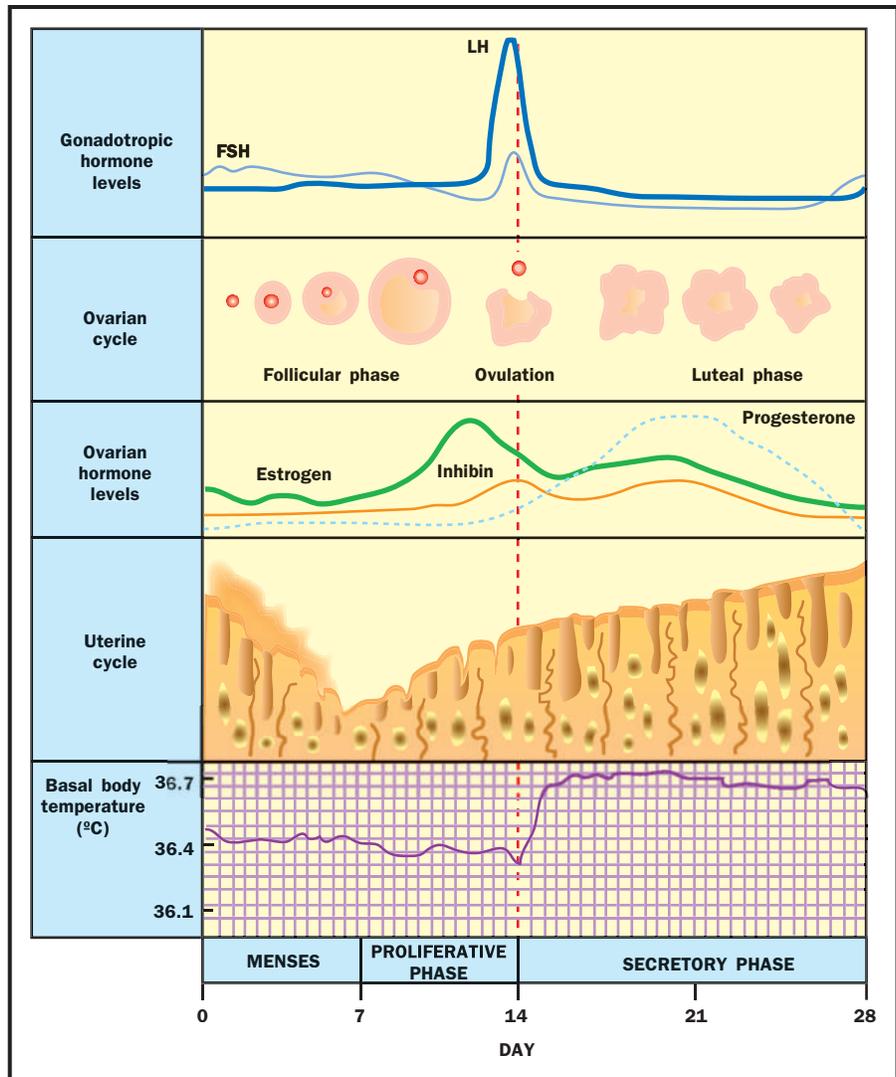
steroids hormones such as testosterone or estrogens that control many aspects of physiology

follicle stimulating hormone (FSH) from the anterior pituitary. More FSH and LH are then in the blood flowing through the ovaries. The ovarian cells making up follicles respond to FSH by maturing an ovum. Some of these follicular cells also begin producing their own hormonal signals that prevent other follicles from maturing (the **steroids** called estrogens) and inhibit the further release of FSH from the anterior pituitary (low levels of estrogens and the peptide hormone inhibin).

About halfway through the cycle on average, fourteen days since the last menstrual flow began, there is a measurable decrease in the woman's basal body temperature followed by a rapid increase in temperature and in her blood level of LH. This LH surge appears to be the biochemical signal for starting ovulation. Following ovulation, the follicular cells that remain in the ovary become the corpus luteum. The cells of the corpus luteum secrete steroid hormones (progesterone and estrogen). If fertilization and implantation are not successful, the corpus luteum begins to degenerate within ten days of being formed. The decreased levels of progesterone then allow the degeneration and shedding of the endometrium and the next menstrual flow.

Changes Associated with Conception and Pregnancy

In a normal menstrual cycle, only one fertilizable ovum is released. It remains capable of being fertilized for only about twenty-four hours following ovulation, whereas sperm cells may remain capable of fertilizing an ovum for as long as seventy-two hours after they have been deposited into the woman's reproductive tract by sexual intercourse. Once deposited, the male's gametes must swim upward through the fluids within the vagina and uterus to arrive at a freshly ovulated ovum in the uterine tube.

A fertilized ovum divides by **mitosis**, and in about a week produces the blastocyst that implants into the endometrium. If the blastocyst successfully implants in the uterine lining, then a pregnancy occurs. At the start of pregnancy, the corpus luteum continues secreting progesterone under the influence of human chorionic gonadotropin (HCG) secreted by the implanted embryo. The continuous secretion of progesterone maintains the endometrial lining. As the pregnancy continues, the placenta gradually takes over the reproductive endocrine functions that were performed in the nonpregnant woman by the ovaries. In addition to its endocrine function, the placenta is vitally important in providing nourishment and waste removal for the growing embryo/fetus throughout gestation.

mitosis separation of replicated chromosomes

Mammary Glands and Lactation

Newborn infants are not able to feed themselves. The same hormones that are responsible for the changes in the ovaries and uterus during the pregnancy also alter the internal function of the woman's mammary glands. The synthesis of mother's milk begins after the delivery of the newborn. An additional peptide hormone called prolactin is secreted from the anterior pituitary. Prolactin helps maintain the secretory capability of the mammary glands for as long as the baby continues to suckle. SEE ALSO DEVELOPMENT; HORMONES; HYPOTHALAMUS; LIFE CYCLE, HUMAN; MALE REPRODUCTIVE SYSTEM; PITUITARY GLAND; SEXUAL REPRODUCTION

Margaret A. Weck

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Fetal Development, Human

The miracle of the renewal of human life takes place in well-defined stages, from the union of the egg and sperm to the birth of the baby. Fetal development is the longest and clinically the most important phase of this process.

embryology development of the embryo

nucleus membrane-bound portion of cell containing the chromosomes

meiosis cell division that forms eggs or sperm

haploid having single, non-paired chromosomes in the nucleus

diploid having pairs of chromosomes in the nucleus

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

gestation period of fetal development within the mother

Early Development

Early human development may be summarized by the following four phases: (1) fertilization; (2) implantation; (3) gastrulation; and (4) embryogenesis.

Fertilization. This stage takes place during the first week of human **embryology**. Fertilization occurs when the cell membrane of a sperm fuses with the cell membrane of the oocyte (egg), injecting its **nucleus**. The egg then undergoes its second division of **meiosis**, and the resulting **haploid** nucleus fuses with the haploid sperm nucleus to re-form the **diploid** number of **chromosomes**. These events occur in the oviduct, or fallopian tube. The fertilized egg, now termed a "zygote," continues to move down the oviduct to the uterus, where it lodges in the wall.

Implantation. After the conceptus is implanted in the uterine wall, the cells that will form the embryo proper divide and organize themselves into a bilaminar (two-layered) disc. This disc is surrounded by an outer ring of cells, the trophoblast, which does not contribute to the new organism's tissues. After implantation, trophoblast cells multiply rapidly and invade the endometrium (uterine wall). Together, the trophoblast and endometrium form the placenta, through which all the nutrition for the developing embryo will pass. This rich mass of tissue is filled with blood vessels, allowing rapid exchange of nutrients and waste. Another group of cells separates from the developing embryo near this time, and these cells also do not form part of the new organism. Instead, they develop into the amnion, the membrane that will surround the fetus to form the embryonic sac. This fluid-filled sac helps to cushion the fetus during later development. This phase begins during the second week of development.

Gastrulation. During the third week, the embryo undergoes the process of gastrulation, forming a trilaminar (three-layered) disc. Gastrulation establishes the three germ layers—the endoderm, ectoderm, and centrally placed mesoderm—all of which will give rise to the various organ systems. Mesoderm also combines with trophoblast tissue to form the umbilical cord, which transports nutrients and wastes between the fetal circulation and the placenta.

Embryogenesis. At this point, the developing human enters the actual embryonic phase, which lasts from the third week through the eighth week after conception. The organ systems differentiate at greatly varying rates during this phase. For example, the circulatory system is largely functional at the end of this period, whereas the nervous system is still engaged in massive cell division and only beginning to establish functional connections. Most embryological malformations occur during this embryonic phase.

The remainder of human development, from weeks nine to thirty-eight, is called the fetal period, the time during which the embryo first acquires human appearance. (The medical definition of the fetal period extends to forty weeks because it is measured not from conception but from the onset of the woman's last menstrual period, usually two weeks earlier.) Fertilization takes place around the middle of the average four-week cycle, hence the two week discrepancy between the biological and medical **gestation** period.

A human fetus at ten weeks.

The Fetal Period

The fetal period is characterized by two processes. The first is rapid growth (increase in size and cell number) and the second is continued tissue and organ differentiation (specialization of cells to perform distinct functions).

Rapid growth. Fetal growth rate is greatest at the beginning of the fetal period (through week sixteen), during which time the fetus increases twenty-five-fold in weight. The largest increase in absolute weight gain, however, takes place during the final month of gestation. In these four weeks the fetus gains as much weight (500 grams [a little over 1 pound]) as it does during its first twenty weeks of development. Normal full-term babies weigh about 3,500 grams (7.7 pounds). Newborns weighing 500 grams or less rarely survive, although medical advances are improving their chances. Infants weighing between 500 and 1,000 grams (2.2 pounds) are classified as immature and those between 1,000 and 2,500 grams (5.5 pounds) are premature.

Besides weight, the length of the fetus is also used to estimate age and survivability. Specifically, the obstetrician can use ultrasonic probes to determine fetal crown-rump length, the distance from the top of the head to the bottom of the rump.

Many factors affect fetal growth, including the nutritional state and social habits (e.g., smoking, drug use) of the mother, the state of **placental** function, and the genetic makeup of the fetus. Perinatology is the medical subspecialty concerned with the mother and fetus from the time of **viability** outside the uterus, generally the last three months of normal gestation (the third trimester) to about one month after birth. A perinatologist uses a variety of methods to assess the fetus. Amniocentesis is the technique by which amniotic fluid is withdrawn by a needle inserted through the mother's abdomen into the amniotic sac. The fluid itself can be analyzed for various **metabolites**, and fetal cells that have been shed into the fluid can be isolated and grown in culture for **chromosomal analysis**.

The fetus itself can be visualized by two general methods. **Ultrasonography** is noninvasive. An instrument emitting ultrasonic waves is placed on the mother's abdomen and the reflected signals are rendered into images of the fetus by computer enhancement. Fetoscopy is an invasive technique in which a fiber-optic probe is inserted like an amniocentesis needle into the amnion. Fetoscopy can be used to both directly visualize the fetus and take a sample (biopsy) of specific fetal tissues.

Tissue and organ development.   Early in fetal development the head dominates the body, constituting half its length. The face is broad and flat, eyes are still wide apart, and ears are low. The intestines temporarily protrude through the abdominal wall until the tenth week, and the external **genitalia** appear similar between the sexes. The fetus also starts to **excrete** urine into the amniotic cavity. By the end of the fourth month, the rest of the body has caught up to the head and the limbs have grown to give the fetus proportions more nearly like those of a newborn. The fifth month is marked by the first fetal movements perceived by the mother, known as quickening. The skin of the fetus secretes a **lipid**-rich covering substance, the vernix caseosa. It also exhibits a temporary covering of fine hair, the lanugo.

By the sixth month, the fetus acquires the capacity for independent existence because the lungs have finally matured to the point where the fetus can breathe. This depends on the **secretion** from specific lung cells of a **protein**-lipid complex known as surfactant. Surfactant lowers the surface tension in the lungs at the air-liquid interface thereby aiding gas exchange. Without adequate surfactant, infants born prematurely succumb to hyaline membrane disease (respiratory distress syndrome). Modern medicine has had some success in saving such babies by providing them with an external source of surfactant.

During the seventh month the nervous system develops many basic reflex responses, including the constriction of the pupils in response to light. Other reflexes controlling breathing, swallowing, and general movement can be detected much earlier, around the middle of the third month, although the effective coordination of such movements requires several more months *in utero*.

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placental related to the placenta, an exchange organ in the uterus

viability ability to live

metabolite molecule involved in a metabolic pathway

chromosomal analysis staining, banding, and other techniques for detection of chromosomal abnormalities

ultrasonography use of sound waves to produce an image

genitalia reproductive organs

excrete deposit outside of

lipid fat or waxlike molecule, insoluble in water

secretion material released from the cell

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

in utero inside the uterus

The cardiovascular system undergoes dramatic changes at the time of birth. Because the placenta provides for gaseous exchange *in utero*, blood flow to the lungs is largely bypassed through a hole known as the foramen ovale within the wall between the left and right **atria**. In addition, a shunt (bypass) called the ductus arteriosus occurs between the aorta and pulmonary artery. Upon birth, the foramen ovale is functionally closed by the higher blood pressure on the left side of the heart. This is in part caused by the closure of the ductus arteriosus, which becomes a fibrous remnant, the ligamentum arteriosum. The umbilical arteries and vein also degenerate after birth to become ligamentous structures on the inside of the abdominal wall.

atria two upper chambers of the heart (singular, atrium)

As the fetus approaches term, substantial adipose (fat) tissue is deposited. The circumference of the abdomen slightly exceeds that of the head. Passage of the head through the birth canal is facilitated by the fact that the flat bones of the skull are widely separated by **connective tissue** called fontanelles. This allows a degree of compression of the head at birth, called molding. The often misshapen head of the newborn quickly returns to normal. The process of birth, or parturition (labor), occurs in three stages. The first is the **dilation** of the cervix, the second is the actual delivery of the fetus, and the third ends with the expulsion of the placenta. The entire process may take from only a few hours to well over a day to complete. SEE ALSO AMNIOTE EGG; DEVELOPMENT; FEMALE REPRODUCTIVE SYSTEM; HEART AND CIRCULATION; MALE REPRODUCTIVE SYSTEM; MEIOSIS

connective tissue one of four types of body tissue, characterized by few cells and extensive extracellular material

dilation expansion or swelling

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Field Studies in Animal Behavior

Field studies of animals help scientists understand the complexities and causes of animal behavior. Wild animals interact with their physical surroundings and the biological world while breeding, eating, and moving within their habitat. Although some behavioral studies are conducted in laboratories or zoos, many of the behaviors that animals exhibit in the wild are closely interconnected with the plants and animals around them and can only be observed during field studies.

Charles Darwin, an English naturalist, presented his theory of evolution by **natural selection** in 1859, after observing the correlation between beak sizes and feeding behavior of ground finches in the Galapagos Islands. This theory has helped to shape a conceptual framework for modern biology.

natural selection process by which organisms best suited to their environments achieve greater reproductive success, thus creating more "fit" future generations

Between 1930 and 1950, Konrad Lorenz, an Austrian naturalist, and Nikolas Tinbergen, a Dutch-born zoologist, developed the field of ethology, the modern science of animal behavior. Their field studies of animals,

Gray wolves (*Canis lupis*) exhibiting submissive behavior. Studies of animal behavior seek the causes of behavior, how it has evolved over time, and how it contributes to a species' survival.

NICE, MARGARET MORSE (1883–1974)

American biologist and psychologist who published over 250 papers and books. Nice was one of the first scientists to study the behavior of individual animals living in the wild, much as later biologists would study chimpanzees, gorillas, hyenas, and other species. In the late 1920s and early 1930s, Nice captured and marked individual song sparrows in her backyard, then studied them for their entire lives.

such as ducks, geese, gulls, butterflies, fish, wasps, and bees, led to studies of animal behavior becoming more organized and systematic in seeking the causes of instinctive behavior, how it has evolved over time, and how it contributes to a species' survival.

Lorenz and Tinbergen used little more than binoculars and a notebook for documenting careful and detailed descriptions of animal behaviors. Today, modern technology also plays a role in studies of animal behavior. For example, radio telemetry is used to track the movements and behavior of various animals from reptiles and amphibians to large mammals, satellite telemetry is used to document bird and sea turtle migration routes, and depth recorders are placed on diving seals and whales.

Field investigations address many different types of behavior, including social behavior, mating systems, sheltering and feeding habits, predator-prey relationships, migration, and navigation. Although field studies have taught scientists many things about animal behavior, questions still remain. The study of these questions helps reveal the roles individuals play within a

species, the niches a species fills in relation to other species, including humans, and even how humans behave and how their actions affect other species. For example, the apparent grieving rituals of elephants and the environment of mutual care in which they rear their young continue to fascinate many people, and the "self-sacrificing" behavior of bees and ants have contributed to the science of sociobiology.

Field studies of animal behavior have the practical value of increasing researchers' understanding of how to conserve threatened and endangered species, as well as how to control pest species. English zoologist Jane Goodall is known for her work with chimpanzees in Tanzania, which began in 1960. Through her extensive fieldwork and detailed reports, she has greatly increased human understanding of primate behavior and has documented behaviors, such as tool use and warfare, which were previously believed to be unique to humans. Goodall's efforts have helped to prolong the survival of chimpanzees in the wild and have brought the issues of wildlife conservation to the attention of the world. SEE ALSO CONSERVATION; DARWIN, CHARLES; ENDANGERED SPECIES; MATING SYSTEMS; MIGRATION; SOCIAL BEHAVIOR; SOCIOBIOLOGY; WILDLIFE BIOLOGIST

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Field Studies in Plant Ecology

Some of the most important ecological research taking place today is in field studies in plant ecology. These are studies undertaken to answer such important questions as: How much carbon dioxide do plants take up from the atmosphere? Does the number of plant species in a community such as a prairie or forest affect productivity? How much carbon dioxide is taken up by these communities? Why do some plant communities such as tropical forests have so many species, whereas others like salt water marshes have so few? What effects are introduced species having on native plant communities? Although laboratory experiments are useful in trying to understand how individual plants respond to different conditions, only studies conducted in the field can answer questions such as these.

Field plant studies vary in the degree of experimental manipulation that is imposed on the environment under investigation. Some field studies are strictly observational with no experimental manipulation at all. Long-term monitoring studies of patterns of tree growth and mortality are examples of observational studies. At the other end of the spectrum are studies in which entire plant communities are created by the investigator. In these studies, the scientist tills and prepares the soil, sows the seeds of the target species, and then often imposes various experimental treatments on portions of the vegetation. These treatments can include altering the vegetation's water and nutrient regimes to excluding certain herbivores (animals that eat plants). In the middle of the spectrum are studies conducted in natural environments

Agronomists place a plastic greenhouse over crops that will be exposed to simulated rain with varying pH levels. The greenhouse provides a closed environment that will allow scientists to assess the plants' reaction to the rain.

in which the investigator manipulates only a single or a few variables, such as fire frequency.

The advantage of field experiments over strict observational studies is that the investigator has more control over the variables of interest, and hence it is often easier to test specific hypotheses. The potential pitfall of field experiments is that the investigator may so alter the natural environment that the findings may not be relevant beyond the experiment itself. Often, scientists will employ both field experiments and field observational studies in order to answer important plant ecological questions.

Field studies in plant ecology serve two major purposes. First, they help researchers understand how the natural world functions, thereby satisfying human curiosity. Second, they provide information that can be of great practical value. For example, some plant studies show how plant species are affected if their habitat is reduced in size. Others show how certain plant species are dependent on particular animals for their pollination or seed dispersal. These findings aid conservation biologists who are trying to preserve plant species diversity in natural areas and in urban and suburban environ-

ments. Many ongoing field plant studies are trying to increase scientists' understanding of global climate change. It is hoped that findings from these studies will help scientists better predict the nature and extent of future climate change. In turn, these field studies may show how changes and elimination of plant communities (for example, through deforestation and urbanization) might be affecting global and regional climate patterns. SEE ALSO ESTUARIES; FOREST, TROPICAL; GLOBAL CLIMATE CHANGE; NATURAL SELECTION; THEORETICAL ECOLOGY.

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Fire Ecology

Fire is one of the leading natural forces that has shaped nearly all land-based **ecosystems** for several thousand years. Fire is especially important in regulating the species composition of vegetation. Fire is particularly important in forests of cold northern regions, such as Canada and Siberia, and in **savannas**, grasslands, and shrubby vegetation types in temperate and tropical regions, such as Australia and California.

Fire has become more important in tropical forests due to human disturbance. Fires are caused naturally by lightning and by people both accidentally and intentionally for management purposes. Native peoples around the world have used fire to maintain favored vegetation types and manage wildlife.

Surviving Fire

Some plant species have adaptations that allow them to survive or reproduce after fire. Survival adaptations include sprouting from underground roots (aspen, grasses), sprouting from stumps (birches, oaks), and growing thick bark that insulates trees from fire (many species of pine and oak). Adaptations that lead to reproduction after fire include serotinous cones on species such as jack pine and lodgepole pine. **Serotinous** cones are held high in the forest canopy in closed condition and do not shed their seeds unless scorched by fire. Buried seeds of some species survive in the forest floor until fire kills the tree canopy, allowing sufficient light to stimulate seed germination (pin cherry and some geraniums).

Some plant species have none of these adaptations to fire. They survive fire in refuges, such as rocky areas without continuous fuel to carry fires, or wetlands that rarely burn. They may also grow in parts of the world where rainfall is frequent and fires are rare.

Natural vegetation types of the world experience several "fire regimes," or characteristic occurrence of fire in terms of the frequency and intensity of fire. A fire regime with very frequent, low-intensity fire (two- to ten-year recurrence) occurs in moderately dry climates supporting grasslands and savannas around the world. Frequent, low-intensity fires (ten- to forty-year recurrence) constitute the fire regime in many temperate and **boreal** forests

ecosystem an ecological community and its environment

savanna open grassland with sparse trees

serotinous developing late in the season

boreal of, relating to, or located in northern regions

89

A plant ecologist measures lodgepole pine seedling growth in Yellowstone National Park in Wyoming. Seven years after the fire of 1988, there were ten times as many seedlings in the area than before the fire.

dominated by tree species with thick bark, especially oaks and pines. The fires kill invading tree species with thin bark while allowing oak and pine to survive.

A fire regime of moderately frequent, high-intensity fire (thirty- to one-hundred-year recurrence) occurs in oak and manzanita-dominated chaparral in California and in dry boreal forests dominated by trees with serotinous cones, such as jack pine in North America. These high-intensity fires kill the forest from the ground up and initiate a new, young forest. Infrequent, high-intensity fires (one-hundred- to five-hundred-year recurrence) occur in many conifer forests of the Rocky Mountains and wetter parts of the boreal forest.

"Helpful" Fire

A number of ecosystems have a regime in which fires are rare, including hemlock and sugar maple forests of eastern North America, arctic tundra, and very dry deserts. Surprisingly, fire may still be important in these systems. For example, lightning strikes in maple forests of Michigan sometimes burn a fraction of an acre of forest, called a spot fire. These spot fires are usually invaded by oak trees, which then live for up to three hundred years. These spot fires have a long-lasting impact where they occur and they enhance biodiversity by maintaining fire-dependent oak as a component of the forest landscape where big fires never occur.

Many vegetation types around the world require fire for their maintenance over time, and they are replaced by different vegetation in the absence of fire. People have suppressed fire during the nineteenth and twentieth centuries in many parts of the world. Fire suppression in savannas and prairie remnants has allowed invasion by forest in many cases. Restoration of prairies requires the use of "prescribed fire," purposely set by people, to reestablish the fire regime required by the prairie plants.

Pine forests throughout the United States (ponderosa pine in the west, white pine in the east) were formerly kept in a parklike condition with open understories by the occurrence of surface fires. After several decades of fire

suppression, these forests have accumulated a high density of trees, including the invasion of other species such as spruce and fir. The buildup of high fuel loads and smaller trees that can function as a ladder to carry fire into the crowns of large pines means that fires become more intense than in the past, possibly too intense to be controlled by fire fighters, and intense enough to kill the old pines.

Fire and Wildlife

Fires kill relatively few numbers of wildlife species directly. The major impact of fires on wildlife is that it alters their habitat. Any substantial alteration in habitat is sure to affect some species positively and others negatively. For example, if an old-growth boreal forest of pine, spruce, and fir is replaced by a young aspen forest after a fire, then a whole suite of conifer-dependent birds, such as spruce grouse, gray jay, and boreal chickadee, will fare poorly after the fire. Conversely, birds that prefer young aspen forest such as ruffed grouse will increase in population.

Forest fires generally only consume 10 to 20 percent of the wood in tree trunks, leaving many standing dead trunks referred to as snags. Snags are good habitat for woodpeckers that seek insects living within the dead wood and cavity-nesting birds that use the cavities excavated by the woodpeckers. Deer and elk also prefer young post-fire forests, whereas the pine marten prefers mature forests.

If a major forest fire were to burn an entire forest, for example, an entire national park or wildlife refuge, then all of the habitat after the fire would be young forest, and those species that lived in mature forests could be excluded from the park. Conversely, if there were never any fires, those species of wildlife that require young, regenerating forests would be excluded.

An ideal solution to this problem is to have relatively small fires occur on a regular basis so that a mix of young, middle-aged, and mature habitat is always present to accommodate all species of wildlife that could live in the area. This concept is known as landscape diversity. The distribution and size of fires on the landscape over time is, together with human disturbance such as logging, the most important factor in determining landscape diversity and the consequent ability of the landscape to provide for a variety of wildlife. SEE ALSO ADAPTATION; FOREST, TEMPERATE; GRASSLAND

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Flight

Flying organisms include insects, birds, and bats, all of which evolved the ability to fly (and the wings that flight requires) independently. Flying squirrels, flying fish, and other animals that only glide are not considered

According to the National Office of Fire and Aviation, more than 57,000 acres of land in the United States burned as a result of prescribed fires in 2000. Oregon and Idaho had the most, with an estimated 12,400 and 10,300, respectively.
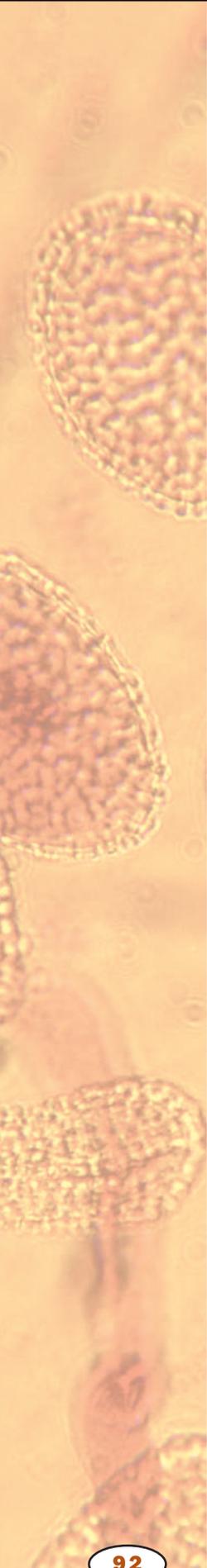
capable of true flight. In general, flight requires an animal to generate enough lift to overcome the force of gravity. Unless it is hovering, the animal also needs to generate directional thrust, to move once it is in the air. The different groups of animals manage these tasks in different ways.

Insects

Among the many other titles insects hold (including being the most numerous and diverse group of animals) they can claim the title of the first flying organisms, having taken to the air tens of millions of years before the pterosaurs (extinct flying dinosaurs), and hundreds of millions of years before birds and bats. Most insects can fly, or are descended from flying ancestors, and are grouped in the subclass Pterygota ("having wings"). The more primitive, nonflying insects are grouped in the class Apterygota ("not having wings"). Unlike wings of the other flying animals, insect wings are not modifications of legs but rather separate **appendages**, outgrowths of the thorax. It is not known how insect wings evolved—the fossil record is not that complete—but there are many hypotheses, including the ideas that wings first evolved for gliding, as solar collectors, or as gills on aquatic juvenile insects.

appendage attached organ or structure

Insects manipulate their wings using two kinds of muscles: direct, which are attached to the wing, and indirect, which alter the shape of the thorax. In flight with the indirect muscles, the wing acts as a lever, with a part of the thorax as its **fulcrum**, and tilts up or down as the thorax changes shape.

fulcrum pivot point of a lever

Many insects are so small that the relative thickness of the air is too great for them to fly as birds, bats, and airplanes do. Instead, because of the viscosity of the air, they move in a way more akin to swimming than gliding or soaring.

Vertebrates

Flight has evolved independently in vertebrates at least three times: in pterosaurs, birds, and bats. Although scientists know that pterosaurs, like bats, flew on wings consisting of skin stretched from the hand to the body, it is not known how they kept such large bodies airborne. Bird wings, on the other hand are made up of flight feathers. Both birds and bats provide most of the thrust for flight with their wing tips, tilting them on both the down stroke and the upstroke so that they cut into the air at an angle and pull the body forward. Most of the lift, however, is provided by the base of the wing. In both birds and bats, as in airplanes, the wing is thicker at the front, convex on the top, and concave or flat on the bottom. As this shape slices through the air, a low-pressure zone is formed by the faster-moving air on top of the wing, and the higher pressure air beneath the wing pushes up on the wing, creating lift. To lighten their bodies and minimize the amount of lift they have to create, both birds and bats are usually relatively small, and birds have hollow bones. SEE ALSO BIRD; INSECT; EVOLUTION; SCALING

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Flowers

Flowers are the typically showy reproductive organs of angiosperms (flowering plants). Their diverse blooms generate countless horticultural products; functionally flowers are essential for sexual reproduction. Flowers may occur individually on the plant or together with other flowers forming inflorescences. Their flowers and inflorescences are: (1) highly adapted to the plant's ecology and pollination strategy; (2) highly variable among the flowering plants; (3) critically important to plant identification; and (4) subject to their own rich and specialized terminology.

Morphologically and evolutionarily, the flower is regarded as a terminal shoot with variably leaflike **lateral appendages**. The stem of the flower, known as a pedicel, is connected to the other floral parts via the receptacle. From the outside rim of the receptacle, the first appendages are typically green, leaflike **sepals**, collectively called the calyx. The next whorl is composed of variously colored and often complex petals, collectively called the corolla.

The androecium forms the next whorl, formed of stamens, each made of a filament and anther. Anther sacs are filled with pollen at maturity. Anthers release the pollen timed to match the receptivity of the female of either the same flower or others of the same species.

The center of the flower is occupied by the gynoecium, which is formed of one or more carpels. Carpels may fuse to form a compound **pistil** or may remain separate and unfused. The carpel is divided into three regions, from the tip: the stigma, a receptive surface for pollen; the style, a specialized region for pollen tube elongation; and the ovary, a location where immature seeds called **ovules** occur, containing the female **gametophyte** or embryo sac. **Meiosis** occurs deep within the anther to produce many **haploid** male gametophytes (which become pollen) and deep within the ovule to produce the female gametophyte (or embryo sac).

The group of angiosperms known as monocotyledons typically have floral organs in multiples of three, whereas dicotyledons have floral organs in multiples of four or five. Fusion of floral organs often occurs obscuring these parts and increasing the diversity of floral form. Similar organs fuse in the example of the corolla tube (as in the morning glory), but dissimilar organs fuse in the example of apple flowers.

Organs may also be modified to perform different functions. For example, roses have five petals (as do most dicots), but some or all of the numerous stamens form petal-like staminodes, sterile petal-like stamens that give horticultural roses the appearance of having many more petals. Symmetry of individual flowers may be radial (forming mirror images around the center), or bilateral (forming mirror images along only one plane).

The flower is the focus of considerable metabolic activity for the plant, producing reproductive organs with high energy content. Flowers attract

lateral side-to-side

appendage attached organ or structure

sepal whorl of flower organs outside of the petals, usually green and serving to protect the flower before it opens

pistil female reproductive organ of a flower

ovule multicellular structure that develops into a seed after fertilization

gametophyte a haploid plant that makes gametes by mitosis

meiosis cell division that forms eggs or sperm

haploid having single, non-paired chromosomes in the nucleus

The largest flowers are species of *Rafflesia,* a carrion flower measuring up to 2 meters (6 feet) wide. This flower, native to the tropical rain forests of Sumatra, has no leaves or aboveground organs except for the flower. Living up to its name, *Rafflesia* attracts and is pollinated by carrion flies.

Snapdragons in bloom. Insects and other animal pollinators that visit flowers are often rewarded in return with pollen or nectar to assure this continued relationship.

The smallest flower is a duckweed. The smallest duckweeds are members of the genus *Wolffia*, with the whole plant measuring less than 1 millimeter (.039 inch) across. The flower of this plant is reduced to one pistil and one anther, which are borne on different plants. Other floral parts are vestigial or fail to form.

insects and other animal pollinators to visit the flower. In return, pollinators are often provided with a food reward of pollen or nectar to assure this continued relationship. After the flower is fertilized, floral organs, including petals, stigma, and style, die back while seeds form inside the carpels. The tissues surrounding the ovary are dramatically modified to become the fruit. SEE ALSO ANGIOSPERMS; FRUITS; POLLINATION AND FERTILIZATION; SEEDS

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Forensic DNA Analysis

Forensic DNA analysis is the use of deoxyribonucleic acid (DNA) specimens in legal proceedings. Just as people can leave fingerprints when they touch

a surface, so too can they leave biological material that contains DNA. When a person's fingerprint matches the latent print found at the scene of a crime, the match provides evidence linking the person to the crime. Similarly, DNA recovered from stains of blood, saliva, or semen or from material such as bone, hair, or skin can be matched to a person's DNA. DNA can even be recovered from fingerprints.

A man could be associated with a rape in a private home by several types of evidence: he may have smoked a cigarette and left the butt outside the house; he may have cut his hand while breaking a window to get inside; or he may have left semen on the victim's body. For each type of evidence, DNA could be used to strengthen the case against a suspect identified by the police by some other means. If the DNA profile from a blood sample or cheek cell scrape is found to match that at the scene of the crime, the suspect is implicated in the crime. If the police have no suspect, they can take the crime scene profiles and use them to search a database of profiles of previously convicted offenders, in the same way that fingerprint records can be searched.

Not only can DNA be used to associate people with crimes, but it can also be used to exonerate them. Several people have been released from prison because DNA testing, not available when they were convicted, has since shown that it could not have been their blood, for example, on an item of evidence.

These forensic uses of DNA rest on the fact that DNA is found in every **nucleated** cell in the body and is the same in all those cells. The other great advantage for DNA as a means of identification is that it is transmitted from parent to child. Paternity disputes can be settled by comparisons of the DNA profiles of mother, child, and alleged father. Just one or two components of the child's DNA profile may be sufficient to exclude a man from being the father, whereas if the man and child match paternal **alleles** at many loci (sites on a **chromosome**), it may be highly probable that the man is the child's father.

nucleated having a nucleus

allele a particular form of a gene

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

base pair two nucleotides (either DNA or RNA) linked by weak bonds

evidentiary DNA profile analyzed DNA from a sample used as evidence

The sharing of some aspects of DNA profiles among family members is also used to identify remains after mass disasters, such as aircraft crashes or battles of war. Particularly when bone or hair is used for identification, **mitochondrial** DNA may be preferred over nuclear DNA because it is more abundant in the cell and because its smaller size means that it is less susceptible to degradation over time.

Exclusion by DNA is taken to be absolute. If the DNA profile from a bloodstain is different from that of a suspect in a crime, that person could not be the source of the stain. Failure to exclude a "match" is not absolute, however, because two people may have the same profile. On average, two people are expected to differ at the DNA level about once per 1,000 **base pairs**. This means that they have about three million differences, and this would certainly be detected if complete DNA sequences were used in forensic science. Current technology, however, limits DNA profiles to just a few genetic markers, often thirteen in the United States, and coincidental matches have been found for up to six markers.

When a person is not excluded as being the source of an **evidentiary DNA profile**, the strength of the evidence is given in terms of probabilities. Although the evidentiary profile may *match* the DNA of the suspect, this is not proof that the stain *came from* the suspect. All that can be said is that there is a certain probability that it did. Because related people share more markers, the probabilities may need to allow for the suspect being a close relative to the person who was the source of the evidence, and the calculations should also allow for the chance of people in the same subpopulation having the same DNA profiles because of a shared ancestry or evolutionary history.

There are two probabilities the forensic scientist can determine. The first probability is for obtaining a match between the suspect's profile and the evidentiary profile if the suspect *is* the source of the evidentiary profile. Obtaining a match in this case is usually taken as certain. This probability has a value of one. The second probability is for obtaining a match between the suspect's profile and the evidentiary profile if the suspect *is not* the source of the evidentiary profile. This probability varies with the tests done and the characteristics of the population in the area of the crime scene. In many cases, it has the value of one in one million, or much less.

Thus, what the forensic scientist reports is: "If the suspect is innocent, there is a one in one million chance of obtaining this match." Far too often that statement is misinterpreted as, "If this DNA matches, there is a one in one million chance the suspect is innocent." The reversal of proposition and conclusion is known as the Prosecutor's Fallacy. It is a very common misinterpretation of DNA forensic evidence by prosecutors, juries, and the press.

To understand why it is wrong to reverse these clauses, consider this analogous example. If one is a citizen of Spain, there is a 95 percent probability that one speaks Spanish. However, if one speaks Spanish, it does not follow that there is a 95 percent probability that one is a citizen of Spain—there are many other likely sources of Spanish speakers. Similarly, if the DNA matches, it does not follow that the suspect is the source. In a city of ten million people, there are, on average, nine other people whose DNA

would match the evidentiary sample to the same degree of certainty that the suspect's did (one in one million). With only the DNA evidence, each of them might be regarded as being equally suspect. Many other circumstances, including age and sex, could be evidence against such equal probabilities, of course, and the exact number of people with the same profile in the city is unkown. Only by considering other incriminating evidence can the prosecutor proceed with the case against the suspect. SEE ALSO DNA; DNA SEQUENCING; ELECTROPHORESIS; MITOCHONDRION; POLYMERASE CHAIN REACTION; SEPARATION AND PURIFICATION OF BIOMOLECULES

B. S. Weir

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Forest, Boreal

Boreal forests are the northernmost forests in the world. These are vast forests that include 29 percent of all the world's forest area in a belt around the Northern Hemisphere, including Scandinavia, Russia, and Canada. In the United States, boreal forests occur in central Alaska and northeastern Minnesota. Boreal forests are dominated by species of spruce, fir, pine, larch, birch, and aspen. Their forest floors are usually covered with mosses and many species of wildflowers.

The distinguishing climatic features are long winters with five to seven months of snow cover and a short cool summer. July mean temperatures fall between 13 and 18 degrees Celsius (55 to 64 degrees Fahrenheit). If summers are cooler than this temperature range, trees are unable to complete their summer growth cycle, and tundra is the dominant vegetation. If summers are warmer, temperate forest trees such as maples and oaks become dominant.

Boreal forests can be divided into southern and northern zones. Southern boreal forests have a high density of trees 15 to 30 meters (50 to 100 feet) in height and are productive enough to produce timber and fiber for paper pulp. Those southern boreal forests in the interior of North America and Asia, away from the oceans, periodically experience very large, high-intensity crown fires that range from 40,485 to 404,858 **hectares** (100,000 to 1 million acres). These forests are composed of species that reproduce well after fires, such as jack pine, aspen, and black spruce. Some southern boreal forests change little in species composition over time, even after fire.

hectare 10,000 square meters (2.47 acres)

For example, central North American jack pine forests on shallow rocky soils burn in high-intensity crown fires and regenerate directly back to jack pine. In other regions, with deeper more fine-textured soils, boreal forests of spruce and fir are replaced by aspen and birch after fire, and the conifers take several decades to regain dominance. Northern boreal forests occur on permanently frozen ground so that they are stunted (6 to 15 meters [20 to 50 feet] in height), with low tree density. These forests, also called taiga, have thick mats of water-soaked moss and burn infrequently.
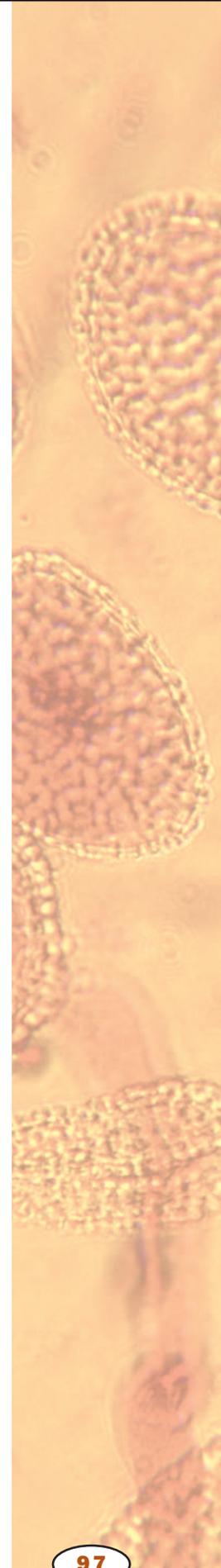
Boreal forests are dominated by species of spruce, fir, pine, larch, birch, and aspen.
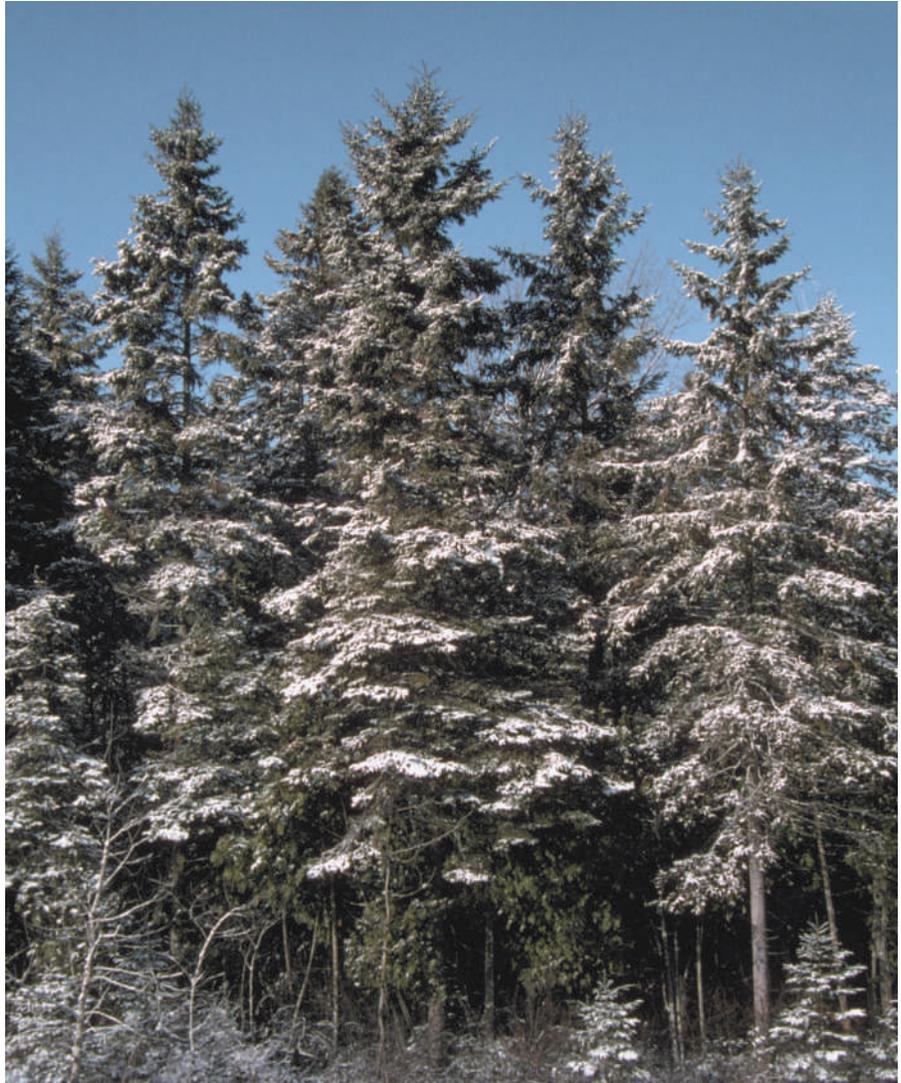
niche the habitat supplying the right environment for a particular species

Tree and plant species in boreal forests have broader environmental **niches** than in temperate or tropical forests. For example, black spruce can grow in poorly drained bogs and on well-drained rocky hills. It can reproduce well after major forest fires and in older forests that have not burned for some time. Thus, it is both a lowland and upland species and a pioneer and old-growth species.

Characteristic wildlife in the boreal forests includes bear, moose, woodland caribou, wolves, lynx, and wolverine. Deer are restricted to the southern margin of the boreal forest. Many migratory birds use the boreal forest during summer, including warblers, pelicans, seagulls, and hawks. Species of owls and ravens are year-round residents.

The North American boreal forest is still mostly primary forest (first growth) but is now being logged for timber and paper pulp. The Russian boreal forest has seen much less logging, but that began to change in the 1990s. Logging often changes dominance of boreal forests from conifers to aspen and birch. Global warming also has the potential to change boreal forests more than most other forest types; the predicted temperature change

for the boreal forest is greater in magnitude than for temperate and tropical forests. SEE ALSO BIOME; FOREST, TEMPERATE; FOREST, TROPICAL; TUNDRA; WOOD AND WOOD PRODUCTS.

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Forest, Temperate

Temperate forests occur in a latitudinal belt between tropical and boreal forests. Most of the world's temperate forests are in the Northern Hemisphere, although Southern Hemisphere occurrences are found in Chile, Argentina, Australia, and New Zealand.

North American temperate forests fall into six main groups: (1) temperate evergreen rain forests along the West Coast from California to Alaska, dominated by sitka spruce, western red cedar, and western hemlock; (2) **montane** evergreen forests of the western mountains, dominated by Douglas-fir, several species of true fir, spruce, and pine; (3) southeastern evergreen pine forests with longleaf and other pines; (4) central deciduous oak-hickory forest; (5) northeastern **deciduous** beech-maple-hemlock forests; and (6) northern pine forests with red, white, and jack pines.

montane mountainous region

deciduous trees that shed their leaves in the fall

Disturbance regimes include frequent fire in forests on sandy soils (oak and pine), to rare fire (hemlock, maple, and beech-dominated forests). Wind is a common form of disturbance in temperate forests. Mid-latitude, low-pressure systems hit the Pacific Coast, hurricanes traverse the southern and eastern coast of the United States, and severe thunderstorms and tornadoes often form in the interior of the country. On rare occasions hurricanes and severe thunderstorms can level hundreds of square miles of forest. Many species of trees can sprout from the stump after such blowdowns, and seedlings of shade-tolerant species present on the forest floor are also free to grow when the large trees above them blow down.

Small gaps caused by the felling of single or small groups of trees by ordinary storms are very common. These gaps are important for maintaining a diversity of tree species in the forest. For example, yellow birch, green ash, and basswood enter the forest primarily through gaps. Deciduous temperate forests are known for their diverse understory of spring-blooming wildflowers, including trillium, violets, bluebells, bloodroot, and many others.

Deer, elk, squirrels, and black bear are characteristic wildlife species. All of these animals eat acorns produced by oak trees. Deer also browse tree seedlings during the winter. When a given area is settled by humans the deer population usually rises and is high enough in some areas to change

A temperate forest in autumn. The central deciduous oak-hickory forest is just one of the six main North American temperate forest groups.

the composition of the future forest. In mixed hemlock-maple forests of eastern North America, for example, deer prefer hemlock seedlings and effectively prevent them from successful regeneration. Such forests will eventually be dominated solely by maple.

A vast majority of the world's temperate forests have been logged, and nearly half have been converted to croplands, highways, and cities. For example, less than 1 percent of all temperate forest in eastern North America remains in primary (never logged) condition. Logging by clear-cutting is common in coniferous forests and selection cutting—whereby small groups of trees are cut—is common in deciduous forests. Woods from the deciduous forest, such as cherry, walnut, oak, and maple, are used for furniture, woodwork, and flooring. Douglas-fir, longleaf pine, and other conifers are used primarily for lumber.

Much of the secondary temperate forest is fragmented in small farmers' woodlots, city parks, and nature reserves. These small fragments (4 to 40 **hectares** [10 to 100 acres]) face problems from invasive exotic species, high deer populations, and fire exclusion. The combination of these forces can

hectare 10,000 square meters (2.47 acres)

cause massive changes to forest species composition. SEE ALSO BIOME; FIRE ECOLOGY; FOREST, BOREAL

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Forest, Tropical

With their towering trees and tiny orchids, great apes and minute insects, tropical forests are magnificent expressions of nature. Tropical forests may contain half the species on Earth, but many of those species will disappear because of continuous deforestation. More than half the original forests have already been lost, and therefore conserving tropical forests is an urgent concern for ecologists.

Tropical forests include many forest types. True tropical rain forest is warm and wet, occurring mainly near the equator, where the monthly temperature never dips below 18 degrees Celsius (64 degrees Fahrenheit), rainfall exceeds 1700 millimeters (66 inches) per year, and no month gets less than 100 millimeters (almost 4 inches). Away from the equator one usually finds drier tropical forests, and on mountains one finds cooler and wetter, **montane** tropical forests. At sites with extreme conditions such as flooding or very poor soils, specialized tropical forests, such as mangrove, occur.

montane mountainous region

Tree and Plant Species

True rain forest usually has 100 to 250 different tree species in 1 **hectare** (2.47 acres), including palms and stranglers (which germinate in a tree crown then grow up and down, eventually surrounding the host). These trees are mostly evergreen and come in many forms: with round, fluted, deeply furrowed, or spiny trunks; with swollen base or buttresses (flanges extending from lower trunk to the ground) or perched on stilt roots; with large leaves or tiny leaflets.

hectare 10,000 square meters (2.47 acres)

Added to this tree diversity are other plant types: shrubs, giant vines, herbs large and small, epiphytes (plants growing on other plants and not rooted in the ground), hemi-epiphytes (which begin life as epiphytes then extend roots to the ground), lichens, and mosses. With all these kinds of plants, and with trees falling and making gaps where regrowth proliferates, the three-dimensional structure of the forest is complex. Despite the fairly uniform climate, flowering, fruiting, and leaf production are somewhat seasonal.

In the other tropical forest types that are drier or cooler than true rain forest, or on extreme sites, there is more seasonal plant behavior, shorter trees, more **deciduous** trees, and fewer species, but plant diversity is still higher than outside the tropics.

deciduous trees that shed their leaves in the fall
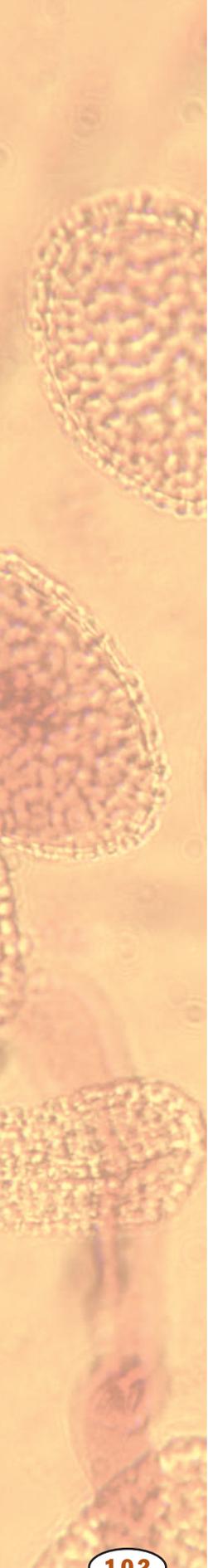
Animals

Tropical forest animals are also diverse. In Borneo there are squirrels the size of mice and squirrels 75 centimeters (29.5 inches) long. Fourteen monkey species and 230 bird species frequent 100 hectares (247 acres) of mature forest at Cocha Cashu, Peru. Eighty-six frog and toad species and fifty-three snake species inhabited Santa Cecilia, Ecuador, before that forest was destroyed. Insects are the most diverse of all; a scientist found forty-six ant species in one large Brazilian tree, as many as inhabit all of Canada. A major goal of tropical forest scientists has been to describe and explain this tropical diversity.

The diversity of plants is not completely understood but is due to a combination of many factors: a long growing season; variety in growth form; specialization on particular light levels, soil types, or topography (such as slopes versus ridges); **mutualisms** with animals; variable conditions created by disturbances such as hurricanes; chance results of reproduction; and the tendency for common species to attract many animals to eat them, creating space for many less common ones.

mutualism symbiosis between two organisms in which both benefit

Moss-covered lianas in the Daintree National Park in Queensland, Australia.

An Agile gibbon (*Hylobates agilis*) with a baby in a Borneo rain forest.

Animal diversity stems mainly from specialization. Many animals specialize on the different resources provided by the great variety of plants and complex forest structure. For example, different plant species are food for different insect species, and flowers and fruit of many types support various kinds of nectar, pollen, fruit, and seed eaters, including insects, birds, bats, and monkeys. Birds catch insects in specialized ways that reflect forest structure and the activities of other species. For instance, different flycatcher species launch themselves from characteristically different perch heights to catch aerial prey; antwrens search the undersides of leaves; woodcreepers glean tree trunks; leaftossers scour the ground; hummingbirds steal prey from spider webs; and antbirds pluck insects fleeing swarming army ants.

Many animals survive in tropical forest through specialized mutualisms, in which animals and plants interact for mutual benefit. This happens, for example, when insects gather nectar from individual plants of one species and transfer pollen among them. These plants often have special features to attract particular insect species. Mutualism also occurs when animals eat fruits and scatter the seeds within, promoting plant reproduction. Some

plants and animals truly live together. Cecropia trees house Azteca ants within hollow stems and feed them nectar; in return the Azteca exclude leaf-eating insects and vines from the tree.

The Effects of Deforestation

Humans have inhabited and used tropical forests for millennia, but widespread deforestation only began in the late twentieth century. Forest loss varies among countries and, depending on location, results from small-scale farming, ranching, logging followed by farming, fuelwood gathering, and other causes. At many places the cleared land is used briefly before soil nutrients are exhausted, and natural reforestation is hindered by the unsuitable conditions created for trees, especially by repeated burning, which also eats into remaining forest stands.

When the forest is cleared, the marvelous variety of plants and animals it contained is lost. Some can survive in small forest patches, but many cannot because light and moisture conditions are changed, critical mutualists are absent, or too few individuals of a given species are present to breed successfully. In addition to this loss of biological diversity, other consequences of tropical deforestation, depending on location, are the loss of native forest peoples, reduced rainfall, increased erosion, silting of coastal **ecosystems**, and possible net release of carbon dioxide and other gases that lead to global warming.

Concerned with these negative effects, local, national, and international groups are trying to stem tropical forest loss. Conservation strategies range from completely protecting remaining forest to promoting sustainable economic uses that leave the forest mostly intact to reforesting degraded lands. Sustainable means using a resource in such a way that future uses are not impaired, which requires sound knowledge of tropical forest ecology. Sustainable timber harvest is one such possibility, which can succeed only if management plans are properly implemented. The success of all conservation efforts depends on ensuring that local people benefit economically, which requires strong cooperation among peoples and nations. SEE ALSO BIODIVERSITY; BIOME; CARBON CYCLE; ETHNOBOTANY; WOOD AND WOOD PRODUCTS

Nicholas Brokaw

ecosystem an ecological community and its environment

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Forester

In common parlance any person who has something to do with raising and managing forest timber resources is in some sense a forester. Foresters go back in history to individuals responsible for managing the harvest of trees on the property of castles and estates and for the management and disposition of the valuable timber asset. Their intuition, practical experience, and natural history knowledge contributed greatly to decision making.

In the twenty-first century, the field has changed, and for the most part a professional forester has a college education and academic credentials, ranging from an associate degree in forest technology to a graduate degree from a school of forestry with specialization in a particular subject area. In addition to the traditional implements of forestry such as shovels, axes, meter sticks, and cruising prisms (which allow the rapid estimation of the number of board feet of timber in a wood lot), foresters now depend on global positioning systems, computer models, and sophisticated research tools in their work. These are used to evaluate such properties of the forest as the quality of wood, the site conditions of the habitat, and fire susceptibility during dry seasons.

Many tasks carried out by foresters involve applications of **silviculture**, chemistry, plant physiology, and biotechnology. Some professional areas, such as forest and paper engineering and scientific resource management, require quantitative skills, while others, such as forest biochemistry, natural products chemistry, and forest ecology, depend on an extensive basic science background. The work environment can be a private practice as a consulting forester, or with industries, government, or academic institutions. While much of the work time is spent outdoors in forests, office and laboratory work is often involved as well. As is the case with virtually all professions, strong writing, verbal, and management skills all place an individual in a favorable position for advancement. SEE ALSO FOREST, BOREAL; FOREST, TEMPERATE; FOREST, TROPICAL

silviculture cultivation of forest trees

Dean Cocking

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Fruits

Fruits are produced only by flowering plants (angiosperms). Following pollination of the flower, the fertilized ovules develop into seeds while the surrounding ovary wall forms the fruit tissue, or pericarp.

Types of Fruits

The botanical definition of a fruit is an organ that contains seeds, protecting these as they develop and often aiding in their dispersal. This may be at odds with everyday usage of the word "fruit." Botanically, pineapples, oranges, and apples are fruits, but so too are "vegetables" like tomatoes and cucumbers. The pods that contain peas and beans are fruits, as are the dry, inedible structures that bear the seeds of many wild plants.

A strawberry plant with blossoms and fruit. The true fruit of the strawberry is not the fleshy tissue but the tiny seedlike achenes on the surface of the berry.
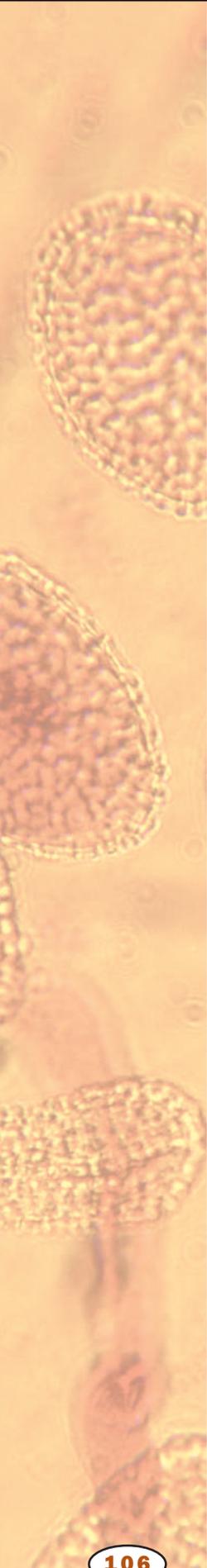
MAJOR FRUIT TYPES

Type	Definition	Examples
SIMPLE	From a single pistil	
DRY INDEHISCENT	At maturity dry; does not split open	
Achene	Close-fitting pericarp surrounding a single seed	Sunflower
Grain	Close-fitting pericap fused to a single seed	Corn, wheat
Nut	Thick, woody pericarp surrounding a single seed	Walnut, hazelnut
DRY DEHISCENT	At maturity dry and splits open	
Legume	Pod that splits along two opposite sides	Beans, peas
Capsule	Fruit opening by several splits or pores	Cotton, poppy
Schizocarp	Fruit splitting into 1-seeded segments	Dill
FLESHY	Mostly fleshy at maturity; do not usually split open	
Drupe	1- to 2-seeded; the innermost pericarp layer, stony and enclosing the seed(s)	Plum, peach
Berry	1- to many-seeded; no stony innermost layer of pericarp	Tomato, grape, (all citrus fruit are berries of a special type termed a hesperidium)
AGGREGATE	Formed by fusion of several separate pistils of one flower	Raspberry, cherimoya
MULTIPLE	Formed by fusion of several separate pistils of several grouped flowers	Pineapple, fig

There are many ways to classify fruits, but the simplest distinction is between fleshy and dry fruits. Fleshy fruits are made of living cells and are often juicy and sweet (oil-rich olives and avocados are exceptions). Dry fruits at maturity are made up of dead cells and are divided into those that split open (dehiscent fruit) and those that do not (indehiscent fruit). Within these broad categories many specialized fruit types are recognized. Nuts (for example, hazelnuts and pecans) are one such category, defined as dry, indehiscent fruits with a hard, stony wall. Everyday usage of the word "nut" is, however, quite different, and includes cashew nuts and peanuts (which are actually seeds not fruits).

True fruits are formed by the ovary, which is the lower region of the **pistil** and the female sex organ of the flower. Sometimes the bulk of the fruit is not derived from the ovary but from some other part(s) of the flower. Such fruits are termed false fruits or accessory fruits. Strawberry is a good example of this. The fleshy tissue people consider the fruit is derived from the receptacle (the swollen tip of the flower stalk), and the true fruits are the tiny, seedlike achenes on the surface.

Apart from strawberry, all the fruit types discussed so far are simple fruits derived from single pistils. In contrast to simple fruits are aggregate and multiple fruits, which are formed from many pistils and, in turn, many

pistil female reproductive organ of a flower

Berry-
A simple, fleshy fruit in which the fruit wall is soft throughout.

Seed

Tomato *(Lycopersicon lycopersicum)*

Drupe-
A simple, fleshy fruit in which the inner wall of the fruit is hard and stony (the pit).

Single seed inside pit

Peach *(Prunus persice)*

Follicle-
A simple, dry fruit that splits open along one suture to release its seeds.

Seed

Soft hairs covering seeds

Milkweed *(Asclepias synaca)*

Legume-
A simple, dry fruit that splits open along two sutures to release its seeds.

Seed

Green bean *(Phaseolus vulgaris)*

Capsule-
A simple, dry fruit that splits open along three or more sutures or pores to release its seeds.

Split open suture

Seed

Iris *(Iris sp.)*

Grain-
A simple, dry fruit in which the fruit wall is fused to the seed coat.

Fused fruit wall and seed coat

Single seed

Wheat *(Triticum sp.)*

Achene-
A simple, dry fruit in which the fruit wall is separate from the seed coat.

Single seed

Fruit wall

Seed coat

Sunflower *(Helianthus annuus)*

Nut-
A simple, dry fruit that has a stony wall, is usually large, and does not split open at maturity.

Woody fruit wall

Cup of fused bracts

Single seed

Oak *(Quercus sp.)*

Aggregate fruit-
A fruit that develops from a single flower with several to many pistils (i.e., carpels are not fused into a single pistil).

Seed

Blackberry *(Rubens sp.)*

Multiple fruit-
A fruit that develops from the ovaries of a group of flowers.

Seed

Mulberry *(Morus sp.)*
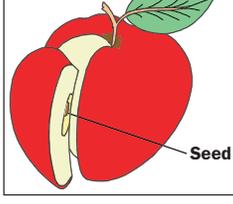
Accessory fruit-
A fruit composed primarily of tissue (such as the receptacle) other than ovary tissue.

Seed

Apple *(Malus sylvestris)*

ovaries. Aggregate fruits like raspberries and blackberries are formed from the several ovaries of a single flower. Multiple fruits like pineapples and mulberries develop from the fusion of the ovaries of several flowers. Interestingly, some fruits (such as banana) develop without seed formation, a phenomenon termed parthenocarpy.

Examples of the many classifications of fruits. The botanical definition of a fruit may be at odds with everyday usage of the word.
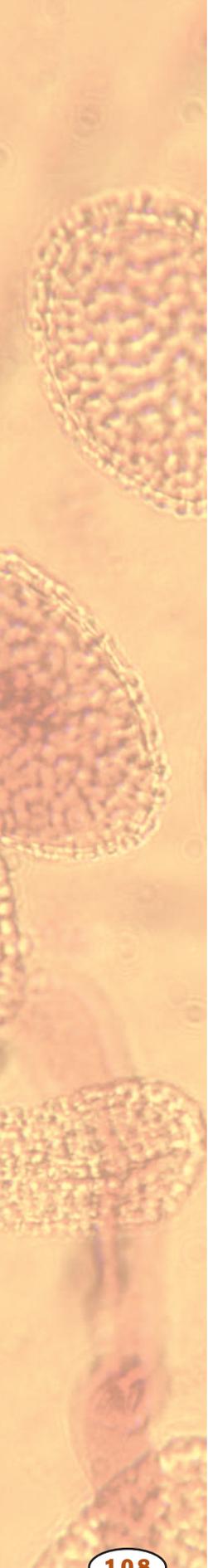
Dispersal

Fleshy, edible fruits serve as food for animals. Animals in turn spread the enclosed seeds of the fruits they eat and so disperse what will be the next

generation of that plant. The coconut provides a good example of a fruit adapted for dispersal by water. Its corky, buoyant outer layer allows this fruit to be carried great distances by ocean currents before the seed within germinates on the seashore. Many dry, dehiscent fruits split explosively, flicking their seeds into the air where they are carried by the wind. Some fruits may have spines for attachment to animal fur, whereas others are winged or feathery for wind dispersal.

Economic Importance

Many fleshy fruit are major food crops of great economic importance. Prime areas of cultivation may be far removed from the original "home" of that particular plant; for example, *Citrus* species like orange are native to Asia, as are apples. Fruits, like other types of produce, comprise living tissue and require special handling and storage to ensure optimal quality for the consumer. Ripening of fruit involves a range of processes that ultimately make the fruit more attractive for consumption, such as color change, softening, sweetening, and aroma production.

hormone molecule released by one cell to influence another

Physiologically, fleshy fruit fall into two categories: climacteric and nonclimacteric. Climacteric fruit can be picked mature but unripe and then stored for extended periods at low temperature before being ripened and sold. Such fruit include mangoes, bananas, papayas, avocados, and tomatoes. Special methods for handling such fruits allow tropical fruits grown thousands of miles away to be on sale weeks later in supermarkets in temperate regions with no apparent loss of quality. Ripening of climacteric fruit is triggered by the gaseous plant **hormone** ethylene, and this is exploited by shippers to artificially induce fruit ripening. In several fruit crops, including tomato, it has been possible to use genetic engineering to knock out ethylene production thus preventing ripening and extending the shelf life of the fruit.

Nonclimacteric fruits such as grapes, citrus, and strawberries do not respond dramatically to ethylene as is the case of climacteric fruits. These fruits ripen only while still attached to the parent plant and so cannot be picked early and stored for later ripening. SEE ALSO ANGIOSPERMS; FLOWERS; HORMONES, PLANT; POLLINATION AND FERTILIZATION; SEEDS

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Fungal Diseases

About fifty fungal species cause human disease, usually by one of three major mechanisms. First, some fungi cause an immune response, resulting in hypersensitivity (allergic) reactions to the fungi. (The fungi themselves thus act as **antigens**.) For example, several Aspergillus species can cause asthma and other allergic reactions. The second mechanism is found in fungal species producing poisons or mycotoxins. *Aspergillus flavus* grows on improperly stored grain and can produce aflatoxins that cause tumors in birds and various other animals.

antigen foreign substance that provokes an immune response

The third disease mechanism is infection. Mycoses (singular, mycosis) are fungal infections found in or on the body. Most mycoses are "nuisance" diseases, although some can be quite serious or even life-threatening. Many of the mycoses are caused by **opportunistic** organisms, organisms taking advantage of the patient whose defense mechanisms are down (such as persons suffering from AIDS [acquired immunodeficiency syndrome]). Examples of opportunistic mycoses include histoplasmosis (usually respiratory), cryptococcosis (affecting any organ, often the brain), coccidioidomycosis (often respiratory), and candidiasis (the common yeast infection affecting any part of the body). (Candidiasis in the mouth and throat of newborns is called thrush.)

Superficial mycoses affecting the skin, scalp, hair, or nails are spread by contact with infected persons or contaminated objects. These common mycoses are generally self-limiting. Tinea is a categorical term used to describe fungal infections by their location, such as tinea capitis (head, also known as ringworm), tinea barbae (beard), tinea corporis (body), tinea cruris (genital and anal areas, also known as jock itch), tinea pedis (foot, also known as athlete's foot).

Subcutaneous mycoses develop in wounds and often resemble ulcers or chancres. Sporotrichosis (caused by *Sporothrix schenckii*) is a common subcutaneous mycosis.

The **systemic** mycoses, which develop when a fungus invades the internal organs (or systems), are extremely difficult to treat, particularly in immunocompromised patients. Yeast, classified as a type of fungus, can cause infection of the urinary tract. SEE ALSO FUNGI; SEXUALLY TRANSMITTED DISEASES

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Fungi

Fungi are **eukaryotic** organisms distinct from plants and animals and members of several other smaller kingdoms. Common fungi include mushrooms, conks, corals, jellies, puffballs, stinkhorns, morels, cups, truffles, lichens, yeasts, rusts, smuts, bread molds, mildews, and molds on bathroom tiles.

In 1959, R. H. Whittaker introduced a five-kingdom taxonomy that granted fungi equal status with plants and animals. The five-kingdom system has been supplanted by a multiple-kingdom classification, and species traditionally treated as fungi are now distributed across several kingdoms. Those believed to form a **monophyletic lineage** are assigned to kingdom Eumycota (often called kingdom Fungi). Mycology, the science devoted to fungi, still covers all traditional fungi.

opportunistic infectious in an immunosuppressed person but not a healthy person

subcutaneous below the skin

systemic throughout the body

eukaryotic cell with a nucleus

monophyletic a group that includes an ancestral species and all its descendants

lineage ancestral line

Characteristics of Fungi

The Eumycota consist of eukaryotic, nonchlorophyllous heterotrophs that absorb nutrients from dead or living **organic** matter, have cell walls composed of **chitin**, and store excess energy as **glycogen**. The kingdom contains four phyla: Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota. All true fungi have a definite cell wall throughout all developmental stages. Fungal cell walls are composed of chitin, the compound also found in arthropod **exoskeletons** (for example, lobster shells). Most fungi produce a vegetative mycelium (filamentous thallus) composed of hyphae that branch and extend via tip elongation, although some groups (like yeasts) consist only of individual cells. Hyphae (singular, hypha) are tube-like filaments with either single **multinucleate** cells (coenocytes) that lack septa (cross-walls) separating nuclei, or many septate cells containing one, two, or more nuclei.

Fungal Nutrition: Saprobes, Parasites, and Mutualists

A fungal thallus may be as small as a single microscopic cell (baker's yeast, *Saccharomyces cerevesiae*) or exceedingly large (*Armillaria gallica*, the several-acre-sized "humungous fungus" reported in 1992 as the world's largest organism). Sporocarp (fruit body, or "mushroom" size) also ranges from microscopic to meters in diameter (*Bridgeporus nobilissimus*, an endangered bracket fungus found on noble fir trees).

Not unexpectedly, such a diverse kingdom manifests several different life cycles. Virtually all fungi produce spores. Both asexual and sexual spores may germinate to form vegetative thalli from primary and secondary mycelia. Thalli may be **haploid** dominant, **diploid** dominant, or exhibit haplo-diploid alternation of generations. Here it is important not to confuse the chromosomal state of individual nuclei (haploid versus diploid) with the number of nuclei per cell (monokartyotic versus dikaryotic). Fungi are unusual in that they often exhibit dikaryotamy, wherein hyphal cells contain two (usually haploid) nuclei that migrate, multiply, and divide together.

Although **superficially** similar to plants, fungi are probably more closely related to animals. Like animals, fungi lack chlorophyll and do not photosynthesize, must obtain nutrients from organic sources, and store energy as glycogen instead of starch. Unlike animals, however, fungi do not engulf, but rather absorb, their nutrients after breaking them down via **enzymatic** action, earning them the nickname "absorbotrophs."

Fungi absorb their nutrients in three different ways: (1) saprobes decompose dead organic matter; (2) **parasites** feed on living hosts; and (3) mutualists live in symbiotic unions with other living organisms. Saprophytic fungi, such as edible meadow mushrooms (*Agaricus campestris*), shiitake (*Lentinula edodes*), and oyster mushrooms (*Pleurotus ostreatus*), decompose dead plant and animal tissue by releasing **enzymes** from hyphal tips, thereby recycling organic materials back into the surrounding environment. Parasitic fungi also use enzymes to break down living tissue, usually sapping the energy of the host and frequently causing its demise.

Lichens and **mycorrhizae** are two important mutualistic associations. Lichens represent partnerships between a fungus (mycobiont) and one or more algae (phycobiont). Although there are a few basidiolichens, almost all

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organic composed of carbon, or derived from living organisms

chitin nitrogen-containing carbohydrate found in arthropod exoskeletons and fungus cell walls

glycogen complex carbohydrate used as storage in animals and some other organisms

exoskeleton external skeleton

multinucleate having many nuclei within a single cell membrane

haploid having single, non-paired chromosomes in the nucleus

diploid having pairs of chromosomes in the nucleus

superficial on the surface; not deep

enzymatic related to function of an enzyme

parasite organism living in close association with another from which it derives most of its nutrition

enzyme protein that controls a reaction in a cell

mycorrhizae symbioses between soil fungus and plant root to maximize absorption

Dark yellow Witches' Butter (*Tremella* species) jelly fungus.

lichen mycobionts are Ascomycota (approximately 20,000 ascolichens described thus far). Mycorrhizae are symbiotic or non to slightly **pathogenic** fungus-plant unions formed with approximately 85 percent of the vascular plants. Mycorrhizae are identified as ectomycorrhizal, arbuscular mycorrhizal (AM), ericoid, orchid, arbutoid, and monotropoid based on anatomical form and association. Ectomycorrhizal fungi (predominantly basidiomycetes such as boletes, amanitas, and coral fungi) form thick mycelial mantles around rootlets of many trees (oaks, firs, pines, poplars) to which they transport water and **minerals** from the soil, receiving sugars and other organic nutrients in return. AM fungi (in the Zygomycota order Glomales) form an endo-infection by penetrating rootlets to form coils and **vesicles** or finely branched arbuscules. The last four mycorrhizal types are specific to individual plant groups.

pathogenic disease-causing

minerals iron, calcium, sodium, and other elements needed by living organisms

vesicle membrane-bound sac

Ecological and Economic Importance

Fungi have a profound biological and economic impact. As decomposers, plant pathogens, and symbiotic partners, their ability to grow anywhere, on anything, makes them both beneficial and harmful recyclers of carbon and nitrogen. Beneficially, they are used as food (mushrooms, truffles) and in baking and brewing (yeasts). They are being developed to detoxify pollutants (soil fungi), control insects (pathogenic Zygomycota), and regulate plant growth (pathogenic Ascomycota). Detrimentally, rusts, smuts, and molds cost billions of dollars through crop disease and spoilage while forest pathogens such as the honey mushroom (*Armillaria ostoyae*) and root-butt rot (*Heterobasidion annosum*) similarly threaten the timber industry. Some are toxic when eaten, such as the infamous destroying angel (*Amanita phalloides*). Natural LSD, a hallucinogen produced by ergot (*Claviceps purpurea*), is associated with medieval hysterical frenzies produced by consumption of infected grain, and the **aflatoxin** produced by *Aspergillus flavus* in improperly stored grain is one of the most potent carcinogens yet discovered. As human and animal pathogens, fungi cause infections that range from the vexing (athlete's foot, yeast infections) to life threatening (histoplasmosis). Fortunately,

aflatoxin toxic compound produced by a mold fungus

other fungi (such as *Penicillium*) have been used to develop modern antibiotics and beneficial **immunosuppressants**.

Classification

With the introduction of deoxyribonucleic acid (DNA) sequence analyses, previous fungal evolutionary theory is undergoing rapid transformation, not surprising when one considers the extremely fragmentary fungal fossil record. Mycologists generally agree that true fungi (with animals and plants) diverged from the protozoan fungi (for example, slime molds and Oomycota) before fungi and animals diverged from plants. The chytrids separated from the remaining phyla approximately 550 million years ago, followed by splintering of the Zygomycota from the other two phyla, which share septate **hyphae** and **dikaryotic** stages in their life cycles. The Ascomycota split from the Basidiomycota approximately 400 million years ago, followed by an increase in fungal diversity throughout the Paleozoic. Most yeasts and "asco-molds" are thought to have evolved in approximately the last 200 million years.

hyphae threadlike part
of the vegetative portion
of a fungus

dikaryotic cell with a
pair of nuclei

While most plants and vertebrates appear to have been described, most fungi have yet to be discovered or named. The 1995 edition of the *Dictionary of Fungi* counts 566,360 described species (about 100,000 in the Eumycota) but notes that there may be approximately 1.5 million species of fungi in the world. Elias Fries (1794–1878), often regarded as the "father of mycology," classified fungi based primarily on spore print color and sporocarp appearance. Friesian-based nomenclature, reflecting similarity of form (phenetic) rather than genetic relationships, is still used in many field guides. Now, however, taxonomists are integrating molecular and morphological characters to develop natural classifications that more adequately reflect evolutionary relationships. Realizing that fungal taxonomy and nomenclature will remain somewhat fluid until new species and data are analyzed and integrated, most mycologists generally accept the classification below.

motile able to move

phylum taxonomic level
below kingdom, e.g.,
arthropod or chordate

mitochondria subcellular organelle that creates ATP used for
energy-requiring
processes in a cell

anaerobic without
oxygen, or not requiring
oxygen

Chytridiomycota. The fact that chytrids alone among the Eumycota produce **motile** zoospores explains why their **phylum** is sometimes assigned with the flagellate oomycetes to kingdom Chromista. Chytrids possess posteriorly uniflagellate spores, **mitochondria** with flattened cristae, and cell walls composed of glucan and chitin. Among the simplest and smallest fungi, they live as saprobes in water and damp organic-rich habitats, or as parasites on invertebrates, plants, and other fungi. The so-called "frog chytrids" (*such as Batrachochytrium dendrobatidis*) are implicated in the current worldwide decline of amphibian species. Other chytrids are host-specific "rumen fungi" (*such as Piromyces communis*) that thrive in **anaerobic** conditions in the guts of herbivores, such as cattle and sheep. There are five orders and about 800 species of chytrids recognized thus far.

appendage attached
organ or structure

Unicellular members of the order Chytridiales lack a mycelial stage and consist of a central body with a few rudimentary **appendages** (haustoria) that attach to and invade the host tissue. Other chytrids, such as the Blastocladiales, develop true mycelia with sporangia and male/female gametangia that produce uniflagellate zoospores. Chytrid thalli may be either haploid or diploid, and some, like the aquatic chytrid *Allomyces*, exhibit an isomorphic alternation of generations with similar appearing sexual and asexual zoospores.

Zygomycota. The chytrids and this phylum are assigned the two "bottom" branches of the fungal evolutionary tree. There are more than 1,000 species in two classes (Trichomycetes, Zygomycetes) and ten orders, representing a diverse assemblage of saprobes, soil fungi, **obligate** insect and fungal parasites, and mycorrhizal formers. Common representatives of the saprobic order Mucorales include the dung-inhabiting "cap-thrower" (*Pilobolus*), the black bread mold (*Rhizopus stolonifera*), and *Phycomyces blakesleeanus*, sometimes referred to as the "body in the basement" because of the rapid growth of long, hairlike sporangiophores over a substrate under the right conditions.

Zygomycota are characterized by large, thick-walled, coenocytic zygospores and hyphae with relatively thin walls composed of chitin and chitosan. Both asexual sporangiospores and sexual zygospores germinate into haploid mycelia, with the hyphae functioning as gametangia during the sexual stage. In *Rhizopus*, for instance, close proximity of two hyphal strands of different mating types chemically triggers each to grow branches toward the other to form septate suspensor cells and gametangia. Eventual fusion produces a diploid zygosporangium that undergoes **meiosis** to become a thick-walled zygospore with large numbers of haploid nuclei.

Ascomycota. In addition to most lichens and so-called "imperfect fungi," about 33,000 species of unicellular yeasts, green and black molds, powdery mildews, morels, cup fungi, and ascotruffles ("true" truffles) belong to this phylum. The phylum is characterized by ascospores produced within a saclike sporangium called an ascus. Mycelia (more complex than Zygomycota mycelia) are composed of septate hyphae with chitin-glucan hyphal walls. Most species produce specialized fruiting bodies called ascocarps whose details of structure help define different species, classes, or orders. Nonascocarpic representatives (such as unicellular yeasts and mildews that reproduce primarily by budding) do not form mycelia. Both sexual and asexual reproduction are found within this phylum.

Basidiomycota. This phylum, which also features septate hyphae and chitin-glucan cell walls, is characterized by basidiospores borne upon a clublike structure called a basidium. Approximately 22,500 species are assigned to three classes: Basidiomycetes, Teliomycetes, and Ustomycetes. Basidiomycetes include mushrooms, polypores, crusts, corals, clubs, basidiolichens, and jellies, which propel their spores, and "gastromycetes" (or "stomach fungi") that passively release their spores (puffballs, basidiotruffles ["false truffles"], stinkhorns, and birds' nests). Teliomycetes (rusts) and Ustomycetes (smuts) are obligate parasites of insects or plants. Rusts and smuts have exceedingly complex cycles involving up to five separate spore stages and multiple hosts. This ability to produce spores on different hosts in multiple ways presents a significant economic challenge to agriculture.

Oomycota. Oomycetes (kingdom Chromista) are distinguished from true fungi by having glucan-cellulose cell walls that only occasionally incorporate small amounts of chitin. These algae-like fungi occur in aquatic or moist terrestrial habitats as single cells or mycelial mats composed of multinucleate, nonseptate hyphae. Their life cycle generally mirrors that of plants, with a transitory haploid stage. Both resting oospores and motile zoospores are diploid, the latter propelled by two unequal flagella (tinsel type plus whiplash). This phylum contains about 700 species in nine orders, including

obligate required or necessary, especially referring to a metabolic process or mode of nutrition

meiosis cell division that forms eggs or sperm

The gills of a mushroom. Although superficially similar to plants, fungi are members of a distinct kingdom.

the generally saprophytic water molds (Saprolegniales) and the pathogenic Peronosporales and Pythiales. Most water molds are saprophytic, but there are a number of parasites that invade plants (white rusts, downy mildews, tobacco blue mold) or fish. Among the economically significant wilts, blights, and pathogens are *Phytophthora infestans* (responsible for the Irish potato famine in the 1850s), *Plasmopara viticola* (the causative agent of downy mildew of grapes), and the fish parasite *Saprolegnia parasitica*, a twenty-first-century threat to salmon migrating through dams in western North America. SEE ALSO ALTERNATION OF GENERATIONS; KINGDOM; MYCORRHIZAE; PLANT PATHOGENS AND PESTS; SYMBIOSIS

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Gas Exchange

Gas exchange is the process by which oxygen and carbon dioxide (the respiratory gases) move in opposite directions across an organism's respiratory membranes, between the air or water of the external environment and the body fluids of the internal environment. Oxygen is needed by cells to extract energy from organic molecules, such as sugars, fatty acids, and amino acids. Carbon dioxide is produced in the process and must be disposed.

Principles of Gas Exchange

The random movement of molecules is called diffusion. Although individual molecules move randomly, a substance can have directed movement, or net diffusion. The net diffusion of a substance occurs because of a difference in its concentration, or **gradient**, along its course. Within an animal's body as oxygen is used up and carbon dioxide produced, the concentration gradient of the two gases provides the direction for their diffusion. For example, as air or water nears the respiratory membrane, the oxygen concentration on the outside of the membrane is higher than on the internal side so oxygen diffuses inward. The concentration gradient for carbon dioxide is in the opposite direction, and so net diffusion of carbon dioxide keeps it diffusing out of the body.

The solubility of the respiratory gases in water is low, and the solubility of oxygen is only about one-twentieth that of carbon dioxide. Special transport molecules within body fluids increase the oxygen content by holding oxygen molecules within circulating fluids. These molecules are called respiratory pigments and include **hemoglobin**, which is red, and hemocyanin, which is blue. These molecules combine with oxygen at the respiratory membrane, where oxygen concentrations are relatively high and easily release the oxygen in deeper tissues, which are low in oxygen.

Filaments of a salmon's gills. In fish, water is pumped across gills to enable gas exchange.

GILL

Deoxygenated blood

Oxygenated blood

Gill filament

Oxygen-bearing
water
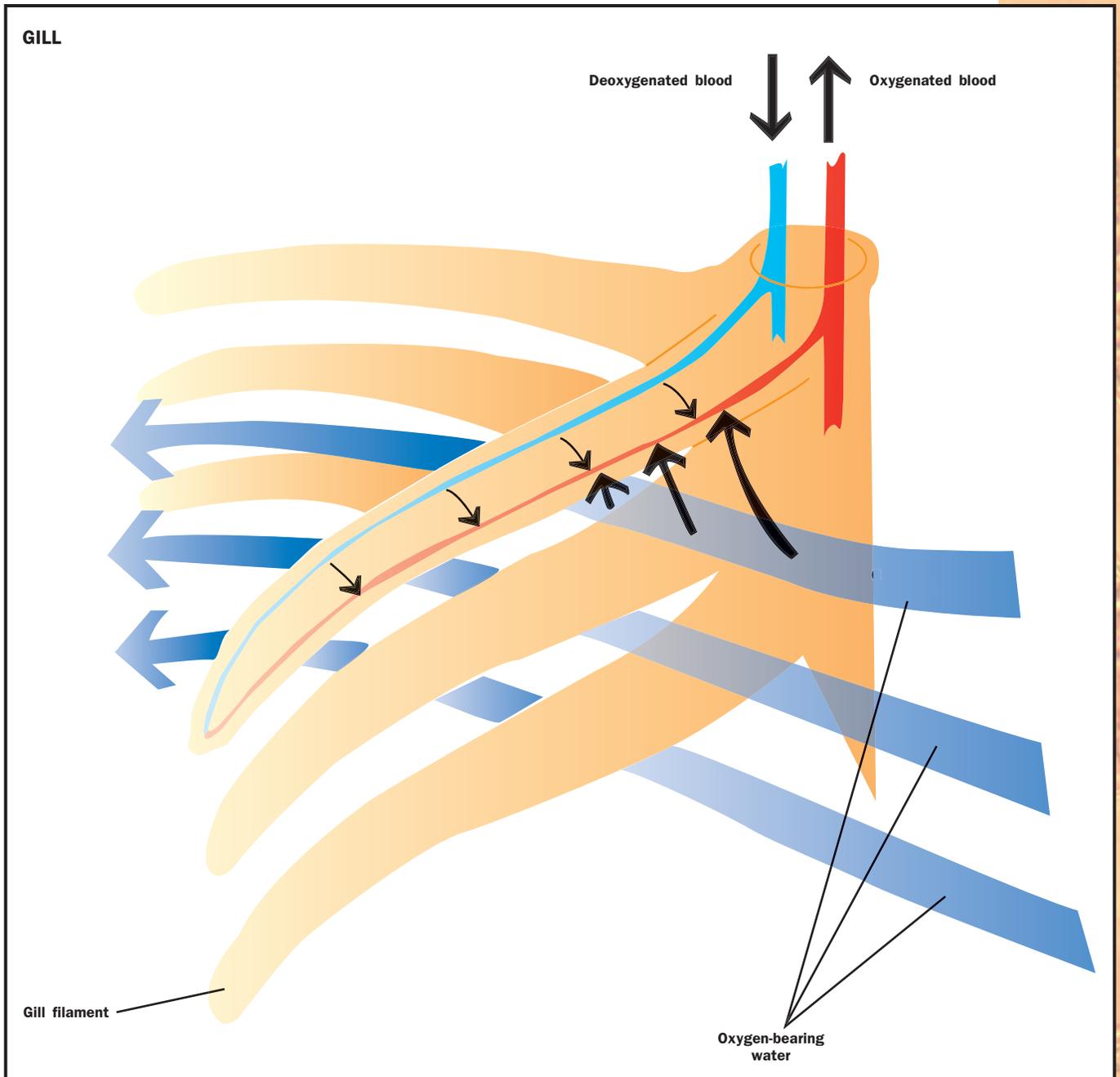
Variety in the Animal Kingdom

Animals with small bodies exchange respiratory gases sufficiently through the body surface without specialized respiratory membranes. Even some vertebrates, such as small, slender salamanders, exchange respiratory gases solely across the skin, which is richly supplied with blood vessels. Larger animals require an extended surface for gas exchange. This specialized respiratory membrane is often folded to increase its surface area without occupying excessive space. For most fish, many aquatic invertebrates, and some terrestrial invertebrates the specialized respiratory organs are the gills. In crustaceans, gills are often found where the legs attach to the body; moving

Gills are respiratory organs that absorb oxygen from water as it flows over the gill surface.

gradient difference in concentration between two places

hemoglobin oxygen-carrying protein complex in red blood cells

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BOOK LUNG

fold

blood
flow
between
folds

air flowing in through
opening in body surface

atrium
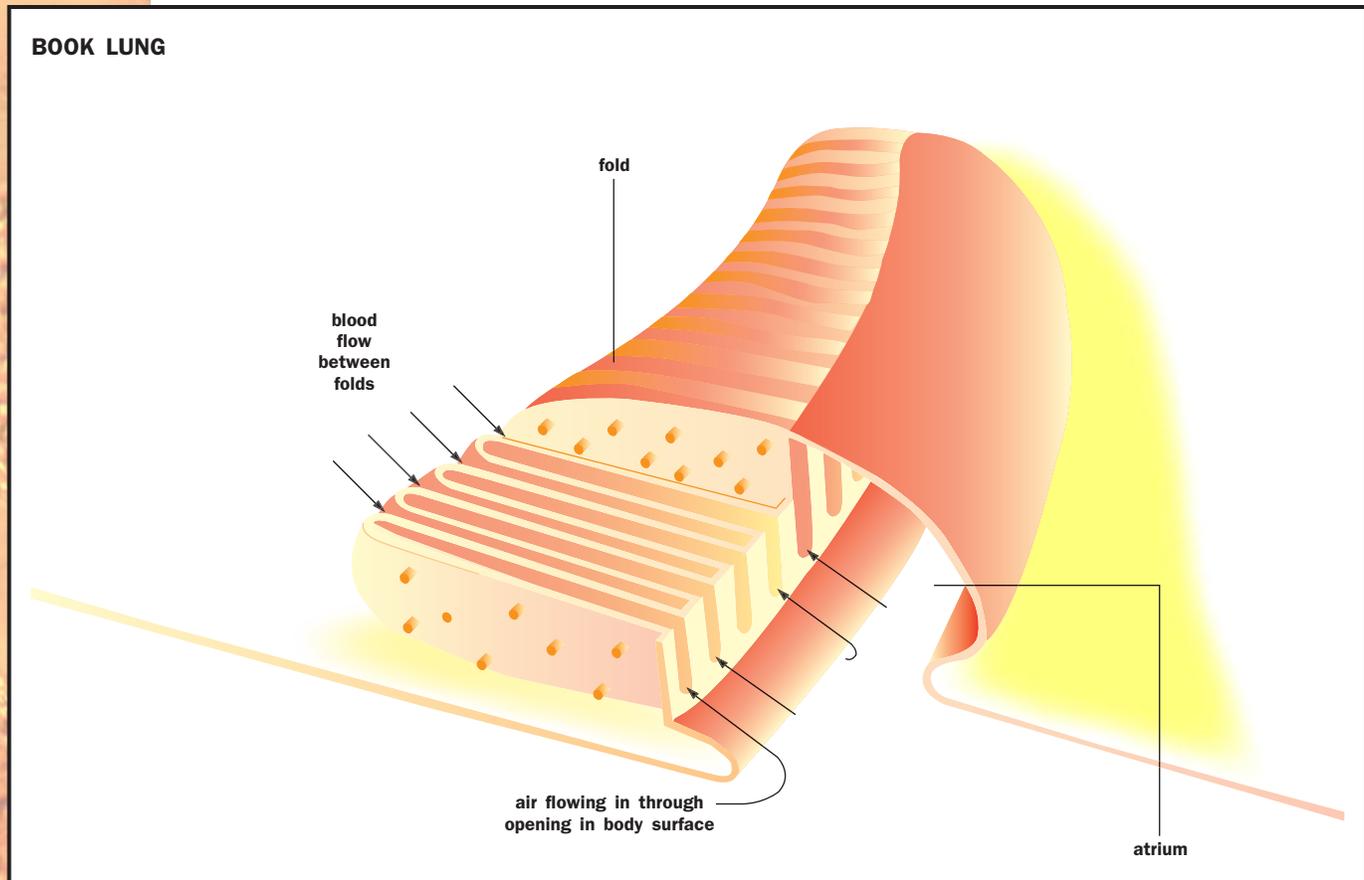
Book lungs are specialized, leaf-shaped, inward folds of the cuticle, surrounded by an air chamber that can be ventilated with muscular contractions.

the legs sweeps water across the gill surfaces. In fish and some mollusks, gills are ventilated by muscular contractions that pump water across the respiratory surface.

Terrestrial animals must protect their respiratory membranes from drying out. Many spiders have book lungs, which are specialized, leaf-shaped, inward folds of the cuticle, surrounded by an air chamber that can be ventilated with muscular contractions. In larger terrestrial insects, the respiratory organs are inward, branching, tubular extensions of the body wall called tracheae. The system is so extensive that most cells are in close proximity to a tracheal branch and the tissues do not depend on blood circulation for gas transport.

Terrestrial vertebrates generally have lungs. The surface area for gas exchange is correlated with metabolic rate. Endotherms, such as birds and mammals, have a high metabolic rate and a correspondingly high respiratory surface area. Birds have one-way flow through their lungs, enabled by a complex system of air-storing sacs. Since fresh air is always flowing through the lung, the oxygen concentration can be maintained at a constant, high level.

Mammals, reptiles, and amphibians have saclike lungs with tidal (two-way) air flow. This results in residual air remaining in the lungs, reducing the concentration of available oxygen in comparison to bird lungs. Reptile lungs have fewer air sacs and less respiratory surface area than mammals, and

amphibian lungs have less surface area than reptilian lungs. SEE ALSO BLOOD; AMPHIBIAN; ARTHROPOD; BIRD; CIRCULATORY SYSTEMS; INSECT; KREBS CYCLE; MAMMAL; OXIDATIVE PHOSPHORYLATION; REPTILE; RESPIRATION

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Gene

Considering the central role that genes play in the understanding of biology, it is surprising that no single, simple definition of a gene exists. This is partly because genes are under multiple evolutionary constraints, and partly because the concept of a gene has both structural and functional aspects that do not always align perfectly. A modern description of a gene must consider not only its structure, as a length of DNA, but also its function, as a unit of heredity in transmission from one generation to the next and in development as a carrier of coded information of the sequence of a **protein** or RNA molecule. In addition, the description should recognize the multiple roles a single gene can play in different tissues during various stages of development and over the course of evolution.

In the table on page 118, some different sorts of geneticists are listed along with the aspects of genes on which they focus and what kinds of phenomena they investigate. In order to understand someone who is discussing genes, it is critical for the listener or reader to know sufficient context such that s/he can ferret out which of the possible interpretations of "gene" in this list is most likely implied.

Units of Heredity

The modern conception of genes begins with the work of Gregor Mendel (1822–1884), who showed that inheritance involved discrete factors passed from parent to offspring. (While Mendel is given credit as the originator of modern genetics, the word "gene" was not coined until well after his death.) In this view, genes are those elements responsible for the "phenotype," the set of observable traits that make up the organism. In the original Mendelian conception, genes came in pairs, as did possible **phenotypes**. Classic examples include round versus wrinkled seeds in peas, or presence or absence of hairs on the middle section of the fingers in humans.

The competing school of thought for the first thirty years of the twentieth century was Darwinism, which considered characters with a continuous distribution such as speed, strength, skin color, height, weight, number of **progeny**, etc., for which no simple paired set of elements could account. By 1930, these seemingly incompatible views had been combined in the "neo-Darwinian synthesis," which incorporated features of both sides of the debate. This involved a transformation of the "one gene, one trait"

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

phenotype observable characteristics of an organism

progeny offspring

WEISMANN, AUGUST (1834–1914)

German biologist who kept alive English naturalist Charles Darwin's theory of natural selection as the mechanism for evolution, when most biologists were looking for other mechanisms. Weismann also predicted the existence of deoxyribonucleic acid (DNA), arguing that parents pass traits, such as eye color, to their children by means of molecules of some kind.

Ways of Investigating Genes

Kind of Biologist	Aspects of Genes of Major Concern	Phenomena Investigated
Molecular Biologist	A piece of DNA	Physical isolation; knock-out experiments
Classical Geneticist	A mapped position on a chromosome; a new mutant; a functional unit	% recombination; mappable and unique; satisfy complementation or cis-trans test
Cytogeneticist	A band or knob on a stained chromosome (insertions, deletions, translations)	Presence or absence of genetic function and occurrence of physical chromosome feature
Quantitative Geneticist	Contributing alleles in an additive or multiplicative fashion	Polygenic ratios; inbreeding effects; path analysis
Population Geneticist	Selection, mutation, migration, genetic drift	Multigenerational change in allele or genotype frequency, polymorphism, heterozygosity
Molecular Evolutionist or Phylogenetic Systematicist	Evolutionary tree of changes in DNA sequence	A traceable molecular character inherited by all progeny
Bioinformatician	One of six reading frames of DNA with a particular pattern	"Gene finding" by computer algorithms and heuristics
Developmental Geneticist	Homeotic mutant	Embryonic changes
Genetic Epidemiologist	Marker	Can be studied for spatial distribution and diffusion
Sociobiologist	Selfish genes; "junk DNA"	Replication without function
X-ray Crystallographer	Geometry	Relationship of three-dimensional structure to function
Mathematical Biologist	Topology	Knots, Catenanes
Biotechnology Entrepreneur	Commodity	Commercial value
Genetic Therapist	Surgically insertable piece or "fixable" DNA	Alleviation of cause of symptoms

relationship to a recognition that single inheritable genes could influence many different observable traits (called pleiotropy), and a single definable trait could be influenced by many different genes called polygenes.

Pleiotropy is a one-to-many genetic phenomenon. If a human has two copies of the gene for **hemoglobin** S, then with high probability the individual is likely to develop a broad constellation of symptoms that constitute sickle cell disease. Complications of swelled heart, ulcerated skin, spleen failure, and shortness of breath are all associated with this single gene.

On the other hand, polygenic inheritance, **epistasis**, gene interaction, operons, and regulatory circuits all involve a many-to-one relationship between genotype and phenotype. Wheat color provides a good example of polygenic inheritance, the contribution of more than one gene to a single trait. When a very dark red, completely **homozygous** individual is crossed with a white, completely homozygous individual, all of their progeny are

hemoglobin oxygen-carrying protein complex in red blood cells

epistasis suppression of a characteristic of one gene by the action of another gene

homozygous containing two identical copies of a particular gene

phenotypically red. When these red progeny are self-crossed, their offspring include individuals that are very dark red, dark red, red, light red, and white, in a ratio of 1:4:6:4:1. The inference drawn by geneticists is that two independently assorting genes are interacting to determine color, and that each gene has two **alleles**, one that contributes red color and the other that does not. Hence, the genotypes range from four contributing alleles (making very dark red) to zero (making white). Involvement of more genes can give even more complex and more continuous distributions.

It is important to realize that in none of these cases is any information provided about the physical nature of the gene. In classical genetics, a gene is a unit of heredity, and understanding inheritance patterns does not require knowledge of gene structure.

However, without an understanding of structure, it is tempting to think of genes as being "for" the trait they influence, in the sense that a hammer is "for" pounding nails or a CD player is "for" listening to music. However, the whole notion of "for" is an unacceptable concept to most research biologists. "For" connotes a determinism that is inconsistent with our understanding of the complexities of cellular processes. There is no gene for intelligence, although many genes influence intelligence through their actions within individual cells. Intelligence, like any other complex trait, arises as the result of many genes interacting.

Genes Are Carried on Chromosomes

Long before the discovery that genes were made of DNA, geneticists realized that hereditary factors—genes—were carried on **chromosomes**. Unlike genes themselves, chromosomes can be easily seen under the microscope, and their movements can be followed during the processes of **mitosis** and **meiosis**. Beginning around 1910, Thomas Morgan and colleagues showed that the patterns of Mendelian inheritance could be correlated with the patterns of movement and recombination of the chromosomes. Morgan's group showed that one of the central events of meiosis is crossing over, in which genes trade places between maternal and paternal chromosomes. In this way, Morgan and colleagues developed the chromosomal theory of inheritance and gave a physical reality to the abstract concept of the gene.

From this point, much work was devoted to discovering the physical nature of the gene. Throughout the next several decades, a series of experiments showed that genes were made of DNA (deoxyribonucleic acid), and finally that the double-helical structure of DNA accounted for the faithful replication and inheritance of genes.

Genes Encode Enzymes and Other Proteins

Parallel to the growing understanding of the structure of the gene came discoveries about how genes affect the phenotype. From patients who suffered from Mendelian diseases and from experiments on bread mold, early researchers inferred that mutant genes were frequently associated with disfunctional **enzymes** that could not **catalyze** particular metabolic steps. Thus, they concluded that enzymes perform the actual functions in a cell that lead to phenotype. These observations led to the first definition of a

allele a particular form of a gene

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

mitosis separation of replicated chromosomes

meiosis cell division that forms eggs or sperm

enzyme protein that controls a reaction in a cell

catalyze aid in the reaction of

CHASE, MARTHA (1927–)

American biologist who, with Alfred Hershey, used a friend's blender to show that genes are made of deoxyribonucleic acid (DNA). In their ingenious experiment, Chase and Hershey labeled virus proteins with one radioactive label and virus DNA with another label. When the viruses then infected bacteria, Hershey and Chase found DNA, not protein, inside the bacteria.

Figure 1. This simplified gene is composed of four regions. The promoter binds to an RNA polymerase in an on-off fashion and controls whether mRNA can be made. The beginning stretch of RNA is not ultimately translated into protein at the ribosome, and neither is the terminal region.

polypeptide chain of amino acids

transcription factor protein that increases the rate of transcription of a gene

nucleotide the building block of RNA or DNA

amino acid a building block of protein

transcribe creation of an RNA copy of a DNA gene

ribosome protein-RNA complex in cells that synthesizes protein

genetic code relationship between triples of RNA nucleotides and the amino acids they code for during protein synthesis

genome total genetic material in a cell or organism

TONEGAWA, SUSUMU (1939–)

Japanese molecular biologist and immunologist who won the 1987 Nobel Prize in physiology for discovering how the immune system makes billions of unique antibodies to fight disease and other unwanted intruders of the human body. Tonegawa showed that white blood cells mix and match a few genes to make billions of combinations that are then translated into billions of unique antibodies.

gene that combined structure and function, stated as "one gene, one enzyme." In this formulation, a gene was thought to be enough DNA to bring about the production of one enzyme. This view had to be modified slightly with the realization that many enzymes are composed of several subunits, called **polypeptides**, whose corresponding DNA sequences (genes) may be on entirely different chromosomes. In addition, not all proteins are enzymes; there are structural proteins, **transcription factors**, and other types. This led to the reformulation "one gene, one polypeptide."

Information Sequences that Code for Production of RNA

The discovery of the structure of DNA led quickly to an unraveling of the means by which it controls protein production. RNA was discovered to be an intermediate between DNA and protein, and this led Francis Crick to formulate the "central dogma of molecular genetics":

$$DNA \rightarrow RNA \rightarrow Protein$$

The sequence of DNA subunits, called **nucleotides**, was found to correspond to the sequence of **amino acids** in the resulting protein. This led to the explicit formulation of a gene as a coded instruction.

Three major aspects of DNA as a code—a sequence of symbols that carry information—are widely employed. First, molecular biologists describe genes as messages that can be decoded or translated. The letters in the DNA alphabet (A, C, G, T) are **transcribed** into an RNA alphabet (A, C, G, U), which in turn is translated at the **ribosome** into a protein alphabet (twenty amino acids). A word in DNA or RNA is a sequence of three nucleotides that corresponds to a particular amino acid. Thus, translating the messenger RNA word AUG via the standard **genetic code** yield the amino acid methionine.

In this conception, the gene is a DNA molecule with instructions written within it. The analogy to words, books, and libraries has been drawn repeatedly, because it offers a way to understand the hierarchy of information contained in the **genome**.

Further work showed that not all DNA sequences are ultimately translated into protein. Some are used only for production of RNA molecules, including transfer RNA (tRNA) and ribosomal RNA (rRNA). This led to yet another formulation of the gene definition, as the code for an RNA molecule. This encompasses tRNA, rRNA, and the mRNA that ultimately is used to make proteins.

Genes Have Complex Structures

A surprising fact about gene structure was revealed in 1977 with the discovery of intron. Introns are segments of DNA within the gene that are not ultimately translated into protein. The introns alternate with exons, seg-

EUKARYOTIC DNA

P1	ex'	P2	ex''	P3	ex'''	P4	ex''''	P5	ex'''''	Intron 1	Exon 2	Intron 2	Exon 3	Intron 4	Exon 4

↓ **transcription**

primary RNA transcript

↓ **alternative RNA splicing and capping**

messenger RNA

poly A cap	P4	ex'''	Exon 2	Exon 3	Exon 4

↓ **translation**

protein

ments that are translated. The entire gene is first transcribed to make RNA, but then the intronic sections are removed, and the RNA exons are spliced together to form mature mRNA. The transcribed DNA of a gene is also flanked by nontranslated and nontranscribed regions that are essential to its function. These include the **promoter** region, a section of "upstream" DNA that binds RNA polymerase, the enzyme that forms the RNA copy. In Figure 1, an overly simplified version of a genetic message is presented. Other DNA segments called enhancers also regulate gene transcription, and these may be located upstream, downstream, within the gene, or far from it.

Genes Have Complex Functions

Further complexity arose with the discovery of alternative splicing and multiple promoters. In many eukaryotic genes, the exons can be combined in different ways to make closely related but slightly different proteins, called isoforms. There can be multiple promoters, some within the gene, that begin transcription at different sites within the gene. Such an example is illustrated in Figure 2. The dystrophin gene codes for a muscle protein that, when absent, causes Duchenne muscular dystrophy. Other isoforms of dystrophin are expressed in white blood cells, **neurons**, and the Schwann cells that wrap neurons with insulation.

Thus, it is difficult to speak of "the" dystrophin gene because the alternative splicing of noncontiguous pieces of RNA produces a variety of

Figure 2. The dystrophin gene codes for slightly different proteins—isoforms—in a variety of differentiated cell types. A simplified version is illustrated above. The dystrophin gene is thought to have eight promoters, each with its own initial exon and as many as seventy-eight downstream exons.

promoter DNA sequence to which RNA polymerase binds to begin transcription

neuron nerve cell

121

Figure 3. Gene tree illustrating the transfer of genes from one biological ancestor to descendents.
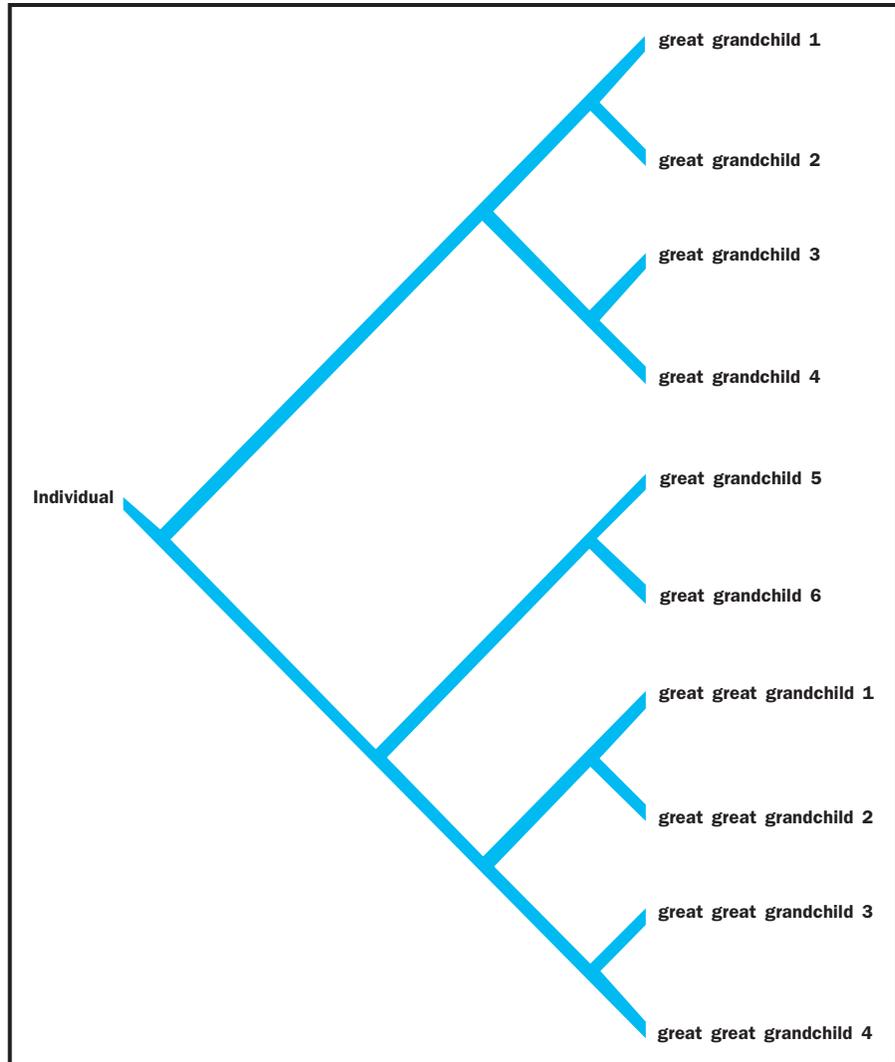
different proteins. Isoforms help generate the differences between tissues, and are thus partly responsible for the complexity of the fully differentiated organism. Similarly, the vast variety of antibodies we produce are coded for a much smaller number of exons, shuffled and expressed in a combinatorial fashion.

With these complications, defining a gene becomes yet more complicated. While it would be possible to describe the set of dystrophin isoforms as arising from an equal-numbered set of genes, most biologists find that unnecessarily complex. Instead, the gene is defined as a DNA sequence that is transcribed as a single unit, and one that encodes one set of closely related polypeptides or RNA molecules. Thus there is one dystrophin gene, which at varies times in various tissues codes for each of the known dystrophin isoforms. This has been summarized as "one gene, many polypeptides."

Genes Act in Evolution, Heredity, and Development

Finally, some fruitful connections can be made by looking at genes in three different contexts and from three different points of view. First, develop-
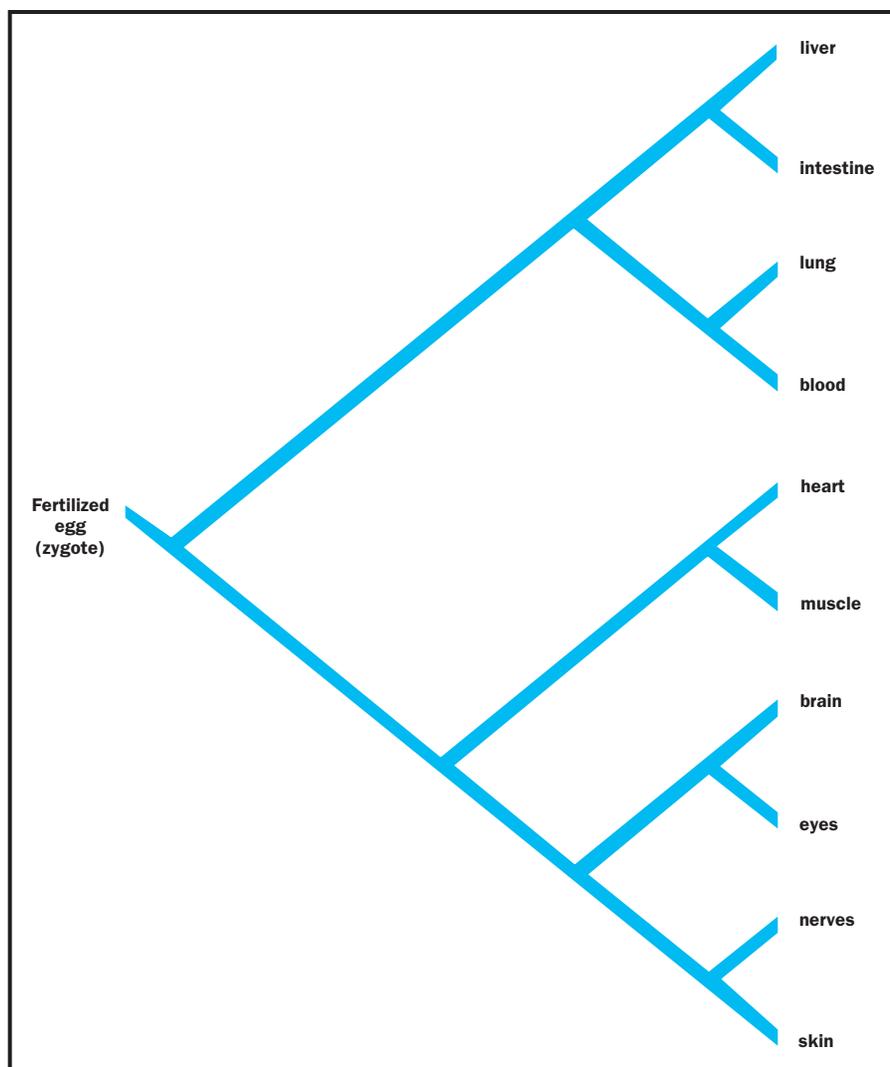
Figure 4. Gene tree illustrating the different cell types that arise by division of one original cell (a zygote; fertilized egg) and differentiation of subsequent daughter cells.
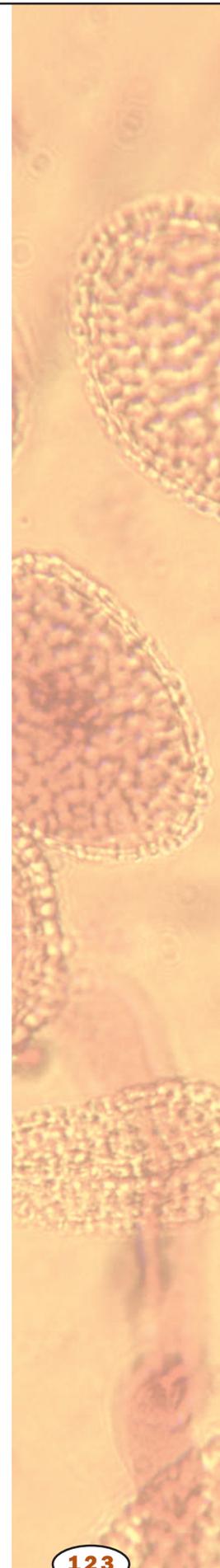
mental biologists focus on the action of genes at different times and places over the life history of an individual from conception to death. Over time, a particular gene will be expressed or silenced depending on stage of development and the tissue it is in. Second, geneticists focus on transmission of information, assortment and recombination of markers, and reproduction within families and populations within one species. Over time, a particular gene will be copied and transmitted to offspring and may accumulate mutations in the process. Third, evolutionary biologists focus on history, mutation, variability, and gene duplication. Over time in different species, as mutation and natural selection have their effects, there is divergence of each duplicate's structure and function.

These perspectives can be understood by displaying multiple views as graphs called trees. In Figures 3 and 4, the general form of the tree, representing the transfer of genes from one biological ancestor to descendents, can be identical, yet the diagrams illustrate a passage of genes with a variety of spatial, temporal, and biological changes in different contexts.

A gene is a unit of both structure and function, whose exact meaning and boundaries are defined by the scientist in relation to the experiment he

or she is doing. Despite an inability to define a gene precisely, the concept of gene has been a fruitful one for a century. In fact, these ambiguities have helped scientists to develop a concept of "gene" that has attained a robustness. This dynamic richness of meaning has contributed to the endurance of "the gene" in biologists' vocabulary. All of these meanings will have value as we face genetic problems in the future and try to establish wise policy in using our knowledge of genes. SEE ALSO GENE THERAPY; GENETIC ANALYSIS; GENETIC CODE; GENETIC CONTROL OF DEVELOPMENT; GENETIC DISEASES; HISTORY OF BIOLOGY: INHERITANCE; MENDEL, GREGOR; PROTEIN SYNTHESIS

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Gene Therapy

Gene therapy is an experimental disease treatment in which a gene is delivered to cells in the body. The **protein** made by the new gene compensates for the absence of normal proteins or interacts with some abnormal protein already in the cell to interrupt its function. Gene therapy is not yet a routine treatment for any disease, but it may become so as researchers solve the many technical problems it presents.

Humans are prey to numerous diseases due to single-gene defects, such as adenosine deaminase deficiency (defective **enzyme**), cystic fibrosis (defective **ion** channel), and Duchenne muscular dystrophy (defective muscle protein). Replacement of the defective gene is conceptually simple, but practically very difficult. Effective gene therapy requires delivering the gene to each cell in which it acts, integrating the gene with the thousands of others on the **chromosomes** and regulating the expression of the gene.

Gene delivery is a major hurdle. Viruses are the most commonly used vehicle, or **vector**, since they have been designed by evolution to deliver their own genes to our cells. Adenovirus (a type of cold virus) has been the most commonly used vector, since it can carry a very large gene and will infect most cell types. However, the immune system is designed to prevent this type of infection, and immune rejection has so far thwarted most gene therapy efforts. While most patients have not been harmed by this prob-

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

enzyme protein that controls a reaction in a cell

ion an electrically charged particle

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

vector carrier

lem, one gene therapy patient has died from immune response to the adenovirus. Modifications of the virus, using fewer immunogenic viruses (such as adeno-associated virus, herpes virus, or retrovirus), immune-suppressive drugs, and nonviral delivery systems are all possible solutions. Curiously, the brain does not mount a strong immune response, and as such, represents a promising site for gene delivery in neurological diseases.

Getting the gene to enough target cells is also a significant challenge. Adenosine deaminase deficiency affects white blood cells and causes severe combined immune deficiency ("bubble boy" disease). This disease can be treated by removing white blood cells, inserting the adenosine deaminase gene into them, and returning the cells to the bone marrow. Cystic fibrosis presents a much bigger challenge, since it affects the airways and pancreas. Inhalation of the vector may treat the lungs, but the pancreas is more difficult to reach without injecting vector into the bloodstream. Duchenne muscular dystrophy is an even bigger challenge, since it affects all muscles, and muscles make up 45 percent of the body. The only realistic treatment option in this case is **systemic** delivery, which poses the added challenge of preventing delivery to nonmuscle tissue.

Once inside the target tissue, genes usually become active whether or not they are integrated into the host chromosome. However, long-term expression requires that the gene join the host chromosome. Directing the gene to do so, and to integrate in a way that doesn't disrupt other genes, is still a significant challenge. Regulating its expression, so that enough of the protein (but not too much) is made, is also a problem. Currently, most virally delivered genes do not integrate successfully, and stop making protein after several weeks to months.

While correction of gene defects was the original inspiration for gene therapy research, treatment of other diseases is now being explored. Cancers are an appealing target, and several strategies are possible. Currently the most promising is delivering a so-called "suicide gene," whose protein product renders a tumor more sensitive to cell-killing drugs, allowing lower doses of chemotherapy to be effective. This works well for solid tumors, which can be injected with the gene. Delivery to more diffuse locations is still problematic. Further research on cellular properties of cancer cells may broaden the reach of this and similar cancer-targeting strategies. SEE ALSO CHROMOSOME, EUKARYOTIC; CRICK, FRANCIS; GENE; GENETIC DISEASES; MENDEL, GREGOR; RECOMBINANT DNA

Richard Robinson

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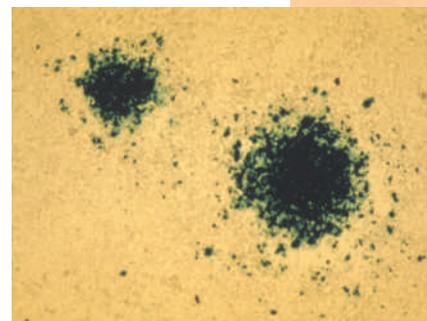
Cancer cells infected with a bioengineered adenovirus.

systemic throughout the body

Genetic Analysis

Genetic analysis refers to experimental procedures designed to identify the genes influencing physical characteristics in organisms and to study their

Punnett Square for Mendelian Cross of Pure-bred Purple with Pure-bred White

White

p   p   ← pollen or ova carrying "p" allele

	p	p
P	Pp	Pp
P	Pp	Pp

Purple

all offspring are heterozygous and show purple color

↑ pollen or ova carrying "P" allele
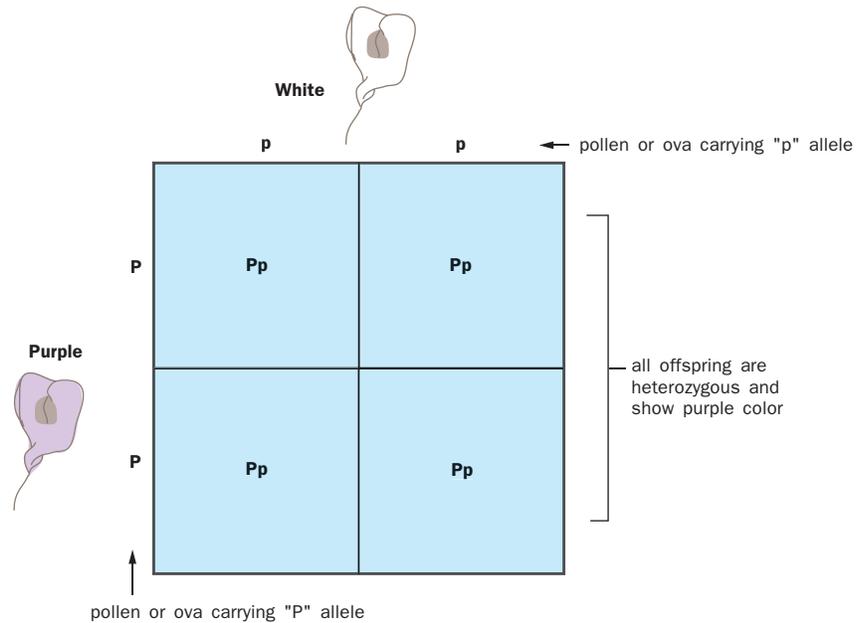
Punnett Square for Cross of Two Heterozygous Purples from the First Cross

	P	p
P	PP	Pp
p	Pp	pp
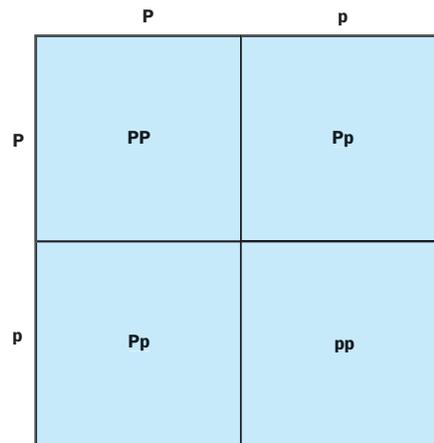
Ratio of Purple to White is 3:1

patterns of inheritance. Historically, genetic analysis originated as a standard program of breeding experiments, first performed and interpreted in a systematic quantitative manner by the Austrian monk Gregor Mendel, the founder of the science of genetics. In 1865, Mendel's experiments provided the first clear evidence of the discrete units of inheritance that are now called genes, although Mendel himself had no knowledge of genes or the **chromosomes** on which they are carried.

Mendelian Genetics

Mendel performed his experiments with the common garden pea, a species that shows well-defined variation in several characteristics, such as flower

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

color, seed color, and seed shape. Mendel followed the inheritance of such characteristics, including flower color, which in peas has two easily distinguished alternative forms, white or purple. In preparation for performing his crosses, Mendel was careful to establish genetically uniform stocks by repeatedly inbreeding or self-fertilizing his stocks for many generations to ensure that all of the plants had flowers of the same color. He also began his analysis by following the inheritance of only one trait at a time.

In a typical experiment, he crossed white-flowered with purple-flowered peas and found that all of the **progeny** from the cross had purple flowers. When these second-generation purple-flowered plants were then self-fertilized, the third generation included both purple- and white-flowered plants in the ratio of one to three.

progeny offspring

The mathematical regularity and the reproducibility of the pattern of transmission of the trait, and the reappearance of white flower color in the third generation convinced Mendel that the trait of flower color, as well as the other traits he analyzed, were carried by physical particles that were passed along unchanged from one generation to the next. Mendel called these particles unit factors, later renamed genes.

Mendel proposed that each adult plant had two genes (factors) for flower color and that each parent randomly passed on only one of its two genes to its offspring during reproduction. For the following discussion, let us use the capital letter *P* to symbolize the gene for purple flower color and the lowercase letter *p* to symbolize the gene for white flower color. Such different forms of a particular gene are called **alleles**.

allele a particular form of a gene

Since Mendel's first-generation plants were true-breeding, the purple-flowered plants had two "purple" alleles (PP), and the white-flowered plants had two "white" alleles (pp). (Each is "homozygous" for the alleles they carry.) If each parent passed one of its alleles to its offspring, all of the second-generation plants would therefore have had one "purple" and one "white" allele (Pp). (These offspring are "heterozygous.") Since all of the second-generation plants had purple flowers, Mendel hypothesized that the "purple" allele masked, or was dominant to, the "white" allele, which he therefore called the "recessive" allele. The **phenotype**, or outward appearance, of these purple-flowered plants is the same as that produced by PP, even though the genotype, or genetic makeup, is different.

phenotype observable characteristics of an organism

When the second-generation, purple-flowered peas (Pp) were allowed to reproduce by self-fertilization, they passed on one of their two alleles for flower color at random in each of the male and female reproductive cells. This means that half of the male reproductive cells (pollen) and of the female reproductive cells (ova) carried a "white" allele and half carried a "purple" allele. The process of this separation and random distribution of one member of each pair of alleles into each reproductive cell is known as Mendel's Law of Segregation.

Since **fertilization** of eggs by sperm occurs randomly, one-quarter of the third-generation progeny inherit two "purple" alleles (PP), one-half inherit one "purple" and one "white" allele (Pp), and one-quarter inherit two "white" alleles (pp). Because of the dominance of the purple allele to the white allele, Mendel observed a three-to-one ratio of purple-flowered to white-flowered progeny.

fertilization union of sperm and egg
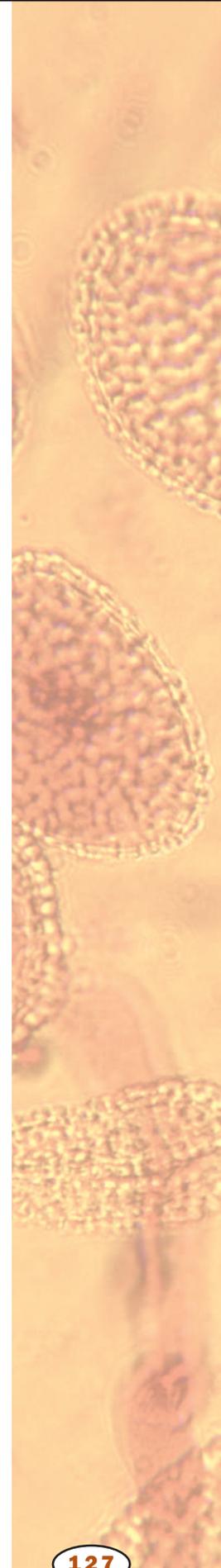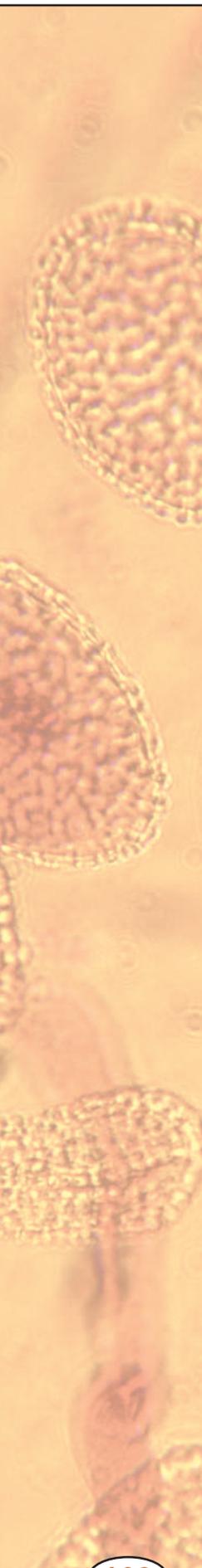
Mendel made another important observation in which he analyzed the simultaneous inheritance of two pairs of alternate alleles, such as purple or white flower color and yellow or green seed color, in the same set of crosses. He found that each pair of alleles was inherited independently. This observation is known as Mendel's Law of Independent Assortment.

About fifty years after Mendel performed his experiments with peas, improvements in the microscope led to the discovery of chromosomes and the description of their behavior during **meiosis**, the type of cell division that occurs during the formation of eggs and sperm. It was observed that the behavior of chromosomes during meiosis was parallel to the behavior of genes as proposed by Mendel. Further work confirmed that allele pairs, such as purple versus white flowers, are carried on **homologous chromosomes**. Homologous chromosomes are separated during meiosis, accounting for the Law of Segregation.

Modifying Mendel

Although Mendel's studies established most of the important general principles of inheritance, some important extensions of his laws have since been discovered. The discovery of chromosomes led to an important exception to Mendel's laws. Mendel assumed that any two pairs of traits would sort independently. However, two traits carried on the same chromosome cannot separate as freely as two traits carried on different chromosomes, thus limiting the Law of Independent Assortment. Traits carried on the same chromosome are said to be linked. If the chromosomal locations (loci) for the two traits are very close together, a particular pair of alleles (for example, purple flowers and thick stems) is likely to remain together. If the loci are far apart, the two alleles may become separated during the crossing over phase of meiosis. In that case, Mendel's assortment law will be more likely to hold. The frequency with which a particular pair of alleles on a chromosome is separated during meiosis can be used to determine their distance apart, and is a first step in mapping chromosomes.

The simple Mendelian concepts of dominance and recessiveness have also undergone important refinements and extensions. In many cases, recessiveness is known to be due to a mutation that makes the genes or resulting **protein** nonfunctional. Presence of one functional allele is often enough to produce adequate levels of protein, and so the functional allele has a dominant effect on the phenotype of the organism. Only when both alleles are defective does the recessive phenotype appear. In some cases, a gene will become mutated to take on a new, harmful function. Such "toxic gain-of-function" mutations are often dominant.

In the case of all of the pairs of allelic genes studied by Mendel, one of the two alleles was completely dominant to the other. However, it is more often the case that an organism with two different alleles of a gene will exhibit characteristics that are intermediate between those determined by either allele separately. For example, the progeny of a cross between red-flowered and white-flowered snapdragons have pink flowers. This type of interaction between alleles is called incomplete dominance. In a related phenomenon, co-dominance, both alleles present affect the phenotype.

The discovery around 1950 that genes are made of deoxyribonucleic acid (DNA), and the elucidation of the structure of DNA in 1953 by James

meiosis cell division that forms eggs or sperm

homologous chromosomes chromosomes carrying similar genetic information

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

Watson and Francis Crick, led to a virtual explosion of scientific and technical advances in the analysis and manipulation of the genetic material. Thanks to these developments, Mendelian analysis has been largely replaced by techniques in which the analysis is carried out at the cellular and molecular level. Individual genes can simply be identified, isolated, and copied, and their precise molecular structure and function can usually be determined. An example of this type of analysis is represented in the Human Genome Project, in which the structure of all of the genes in human chromosomes is being elucidated. The origins of all of this sophisticated technology, however, can be traced back to the nineteenth-century pioneering methodical studies on inheritance in peas by Gregor Mendel. SEE ALSO GENE; HUMAN GENOME PROJECT; MENDEL, GREGOR; PATTERNS OF INHERITANCE

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Genetic Code

The genetic code allows an organism to translate the genetic information found in its **chromosomes** into usable **proteins**. Stretches of deoxyribonucleic acid (DNA) are built from four different **nucleotide** bases, while proteins are made from twenty unique subunits called **amino acids**. This numerical disparity presents an interesting problem: How does the cell translate the genetic information in the four-letter alphabet of DNA into the twenty-letter alphabet of protein? The conversion code is called the genetic code.

Requirements of a Code

The information transfer from DNA to protein, called **gene expression**, occurs in two steps. In the first step, called **transcription**, a DNA sequence is copied to make a **template** for protein synthesis called messenger ribonucleic acid (messenger RNA, or mRNA). During protein synthesis, **ribosomes** and transfer RNA (tRNA) use the genetic code to convert genetic information contained in mRNA into functional protein. (Formally speaking, the genetic code refers to the RNA-amino acid conversion code and not to DNA, though usage has expanded to refer more broadly to DNA.)

Mathematics reveals the minimum requirements for a genetic code. The ribosome must convert mRNA sequences that are written in four bases—A, G, U, and C— into proteins, which are made up of twenty different amino acids. A one base to one amino acid correspondence would code for only four amino acids (4^1). Similarly, all combinations of a two-base code (for example, AA, AU, AG, AC, etc.) will provide for only sixteen amino acids (4^2). However, blocks of three RNA bases allow sixty-four (4^3) combinations of the four nucleotides, which is more than enough combinations to correspond to the twenty distinct amino acids. So, the genetic code must use blocks of at least three RNA bases to specify each amino acid. (This reasoning assumes that each amino acid is encoded by the same size block of RNA.)

In addition, a ribosome must know where to start synthesizing a protein on an mRNA molecule and where to stop, and start and stop signals

chromosomes "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

nucleotide the building block of RNA or DNA

amino acid a building block of protein

gene expression use of a gene to create the corresponding protein

transcription messenger RNA formation from a DNA sequence

template master copy

ribosome protein-RNA complex in cells that synthesizes protein
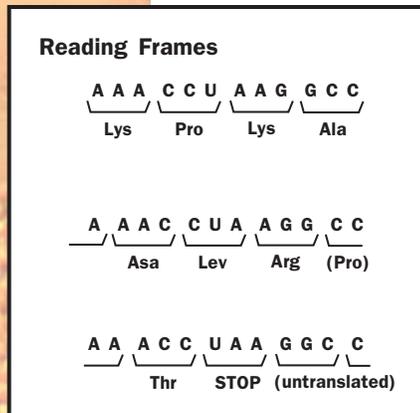
require their own RNA sequences. A series of experiments carried out in the 1960s confirmed these mathematical speculations, and went on to determine which triplet sequence (called a **codon**) specifies which amino acid.

Indeed, the genetic code uses codons of three bases each, such as ACC or CUG. Therefore, the protein synthesis machinery reads every triplet of bases along the mRNA and builds a chain of amino acids—a protein—accordingly. Reading triplets, however, would allow a ribosome to start at any one of three positions within a given triplet (see Fig. 1). The position that the ribosome chooses is based on the location of the start signal and is called the "reading frame."

Experiments have shown all but three of the sixty-four possible codons that A, G, U, and C specify code for one amino acid each. This means that most amino acids are encoded by more than one codon. In other words, the genetic code is said to be redundant or degenerate. This redundancy allows the protein-synthesizing machinery of the cell to get by with less, as will be seen below. The three that don't, the "nonsense" codons, indicate the end of the protein-coding region of an mRNA, and are termed stop codons.

Starting, Stopping, and Making Protein

In any mRNA molecule, one codon always marks the beginning of a protein. That "start" codon is usually AUG in both eukaryotes and **prokaryotes**, although eukaryotes use GUG on rare occasions. AUG codes for the amino acid methionine. To start synthesizing at an AUG, however, ribosomes require more information besides a start codon; this information is found in the sequence surrounding the initial AUG. AUG codons in the middle of a protein-coding sequence are translated like any other codon.

Three codons signal the end of the mRNA template. These so-called stop codons, UAA, UAG, and UGA, do not code for any amino acid. Instead, the ribosome gets stuck, waiting for the tRNA that never comes, and eventually falls off, releasing the newly synthesized protein.

The **complementary** sequence of a codon found on a tRNA molecule is called its anticodon. The tRNA molecule matches up its anticodon with the correct codon on the mRNA. A tRNA molecule holds an amino acid in one of its molecular arms and works with the ribosome to add its amino acid to the protein being synthesized. Each tRNA is then reloaded with its specific amino acid by an **enzyme** in the **cytosol**.

Codons that code for the same amino acid are called redundant codons. The first two bases of redundant codons are usually the same and the third is either U or C, or alternatively A or G. For example, two redundant codons for the amino acid arginine are CGU and CGC, both of which pair with the same tRNA, despite having different third bases. This characteristic of the codon-anticodon interaction is called "wobble," and it allows organisms to have fewer than sixty-four distinct tRNA genes. In some tRNAs, wobble is made possible by a modified base within the anticodon. This modified base is called inosine (designated by I) and is made from adenine.

Evidence for Evolution

For almost all organisms tested, including humans, flies, yeast, and bacteria, the same codons are used to code for the same amino acids. Therefore,

---

Reading Frames

A A A C C U A A G G C C
Lys   Pro   Lys   Ala

A A A C C U A A G G C C
Asa   Lev   Arg   (Pro)

A A A C C U A A G G C C
Thr   STOP (untranslated)

Figure 1. The genetic code reads codons of three bases each and builds a chain of amino acids accordingly.

codon sequence of three mRNA nucleotides coding for one amino acid

prokaryote single-celled organism without a nucleus

complementary matching opposite

enzyme protein that controls a reaction in a cell

cytosol fluid portion of a cell, not including the organelles

1st position (5' end)	2nd position				3rd position (3' end)
	U	**C**	**A**	**G**	
U	Phe	Ser	Tyr	Cys	U
	Phe	Ser	Tyr	Cys	C
	Leu	Ser	STOP	STOP	A
	Leu	Ser	STOP	Trp	G
C	Leu	Pro	His	Arg	U
	Leu	Pro	His	Arg	C
	Leu	Pro	Gln	Arg	A
	Leu	Pro	Gln	Arg	G
A	Ile	Thr	Asn	Ser	U
	Ile	Thr	Asn	Ser	C
	Ile	Thr	Lys	Arg	A
	Met	Thr	Lys	Arg	G
G	Val	Ala	Asp	Gly	U
	Val	Ala	Asp	Gly	C
	Val	Ala	Glu	Gly	A
	Val	Ala	Glu	Gly	G

Figure 2. The universal genetic code.

the genetic code is said to be universal. The universality of the genetic code strongly implies a common evolutionary origin to all organisms, even those in which the small differences have evolved. These include a few bacteria and protozoa that have a few variations, usually involving stop codons.

Mammalian **mitochondria**, which contain DNA, use the codon UGA not as a stop signal but instead to specify the amino acid tryptophan, and they have four stop codons instead of three. Also, the modified base inosine is not used in mitochondrial anticodons. Mitochondrial genetic codes from different organisms can also be distinct from each other as well as from the universal code, reflecting both their ancient bacterial origins and their long isolation within their host species. SEE ALSO ARCHAEA; CELL EVOLUTION; DNA; EUBACTERIA; GENE; MITOCHONDRION; NUCLEOTIDES; PROTEIN SYNTHESIS; PROTISTA; RIBOSOME; TRANSCRIPTION

Mary Beckman

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

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Genetic Control of Development

The transformation of a single-celled **zygote** (product of the union between egg and sperm) to a multicellular embryo and then to an adult organism is a complex and amazing process. A fully developed organism has many different cell types that serve many different functions. For example, red blood cells carry oxygen, muscle cells contract, fat cells store nutrients, and nerve cells transmit information. In fact, a human has about 350 different types

zygote fertilized egg

A chicken embryo. During pattern formation, communication between cells of a developing embryo is crucial, so that each cell will "know" its position within the emerging body plan.
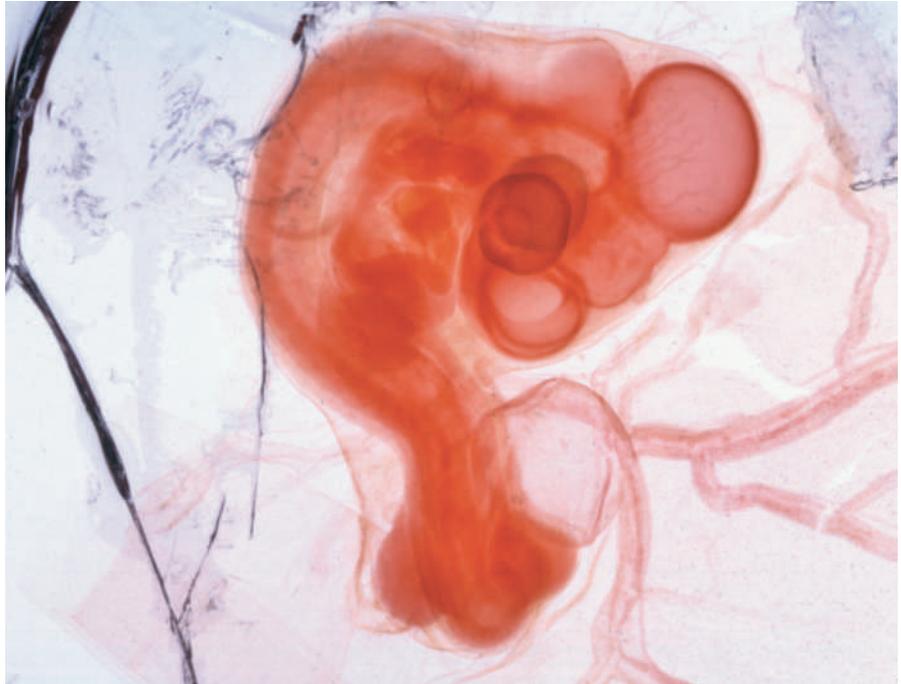
protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

nucleus membrane-bound portion of cell containing the chromosomes

lineage ancestral line

genome total genetic material in a cell or organism

MANGOLD, HILDA (1898–1924)

German biologist who discovered that a small part of an embryo determines the organization of the entire embryo. When Mangold moved this bit of tissue, called the "primary organizer," in a frog embryo, it developed a second backbone and other organs. Mangold died young in an accident, but her professor, Hans Spemann, received the Nobel prize for their work on the primary organizer.

of cells that are distinguishable in both form and function. However, all of the cells of a very early embryo appear to be identical. How, then, do cells become specialized as they divide?

Differentiation

The process of cell specialization during development is called differentiation. The differentiation process proceeds by the progressive specialization of the **protein** contents of a cell. Each type of cell in a mature organism has a unique collection of proteins. The blueprints for making these proteins are found in the **nucleus** of each cell in the form of deoxyribonucleic acid (DNA). Therefore, the starting place for understanding the process of differentiation lies in the nucleus of the original zygote, which contains all of the genetic instructions (DNA) to make all of the cell type repertoire of the mature organism. The original cell is totipotent, which means that it can give rise to any cell type. As the embryo develops, some cells differentiate, while others, called stem cells, remain pluripotent, which means that they can give rise to a certain subset of cell types called a **lineage**.

One hypothesis to explain how differentiated cells have a specialized pool of proteins is that differentiating cells retain only the genes (DNA) that encode the proteins they need, and they lose all the other genes. Such a mechanism would produce mature cell types with a different **genome**. Experiments, however, disproved this hypothesis. In 1968, John Gurdon removed the nucleus of an unfertilized frog egg and replaced it with the nucleus from a fully differentiated tadpole epithelial cell. The egg developed into a normal tadpole. Gurdon's classic experiment demonstrated that the nucleus of the differentiated cell still retains the full genome: no genes are lost as a cell's descendents specialize.

Other experiments supported an alternative hypothesis: that cell specialization reflects the differential regulation of the full set of genes in each cell type. This means that all cells in a mature organism (muscle cells, brain cells) all have the same set of genes, but only a subset of those genes are turned "on" in any specific cell type. Therefore, the process of differentiation involves the activation (turning on) of some genes and the inactivation (turning off) of other genes, in order to get the specific collection of proteins that characterizes that cell type.

The point during development at which a cell becomes committed to a particular fate is called determination. Differentiation (specialization) is the end product of determination. Determination happens when certain genes are activated or inactivated, and differentiation completes when the cell synthesizes all of the tissue-specific proteins that the activated genes encode. For example, when particular cells in a mammalian embryo activate the gene for the protein MyoD and thus begin making MyoD protein, they are determined to be muscle cells. As it turns out, the MyoD protein is a **transcription factor** that controls the expression of several other genes. Therefore, MyoD activates and inactivates many of the genes that encode muscle-specific proteins.

transcription factor protein that increases the rate of transcription of a gene

What is it, then, that activates MyoD in some cells and not in others during development? Two important types of signals "tell" the developing organism which genes to express and when to express them. Firstly, the uneven distribution of substances (such as messenger RNA, protein, **organelles**) in the **cytoplasm** of the unfertilized egg is important to the initial stages of determination. Once the egg is fertilized and the nucleus begins to divide (via **mitosis**), the resulting nuclei are exposed to different cytoplasmic surroundings. These different internal environments contain different sets of molecules (collectively called cytoplasmic determinants) that regulate the expression of certain genes. Secondly, as the embryo enlarges and increases in cell number, molecules in the extracellular environment can act as signals to developing cells. More often than not, these signal molecules are released from other cells in the embryo and affect target cells by regulating the expression of certain genes in those cells. This process is called induction, and is the process by which cells of the embryo communicate and spur on the processes of determination and differentiation. Induction was discovered in the 1920s by the embryologist Hans Spemann and Hilde Mangold.

organelle membrane-bound cell compartment

cytoplasm material in a cell, excluding the nucleus

mitosis separation of replicated chromosomes

Morphogenesis

As cells become specialized they organize into a hierarchy of tissues, organs, and organ systems in which they work as a set, providing a certain function. Morphogenesis is the process by which differentiated cells are organized into these functional groups. In many species, morphogenesis begins before differentiation is completed. For example, in the sea urchin embryo, cells begin to migrate and the embryo changes shape long before the cells are fully differentiated. The process of morphogenesis reflects the differential expression of genes in different cells. The complex interactions of actively differentiating cells actually drives the process of morphogenesis. It is useful to look at the **gene expression** patterns that characterize one component of morphogenesis.

gene expression use of a gene to create the corresponding protein

Pattern Formation

During morphogenesis, a process called pattern formation drives the spatial organization of tissues and organs into a defined body plan, or final shape. For example, both dogs and humans have legs made up of bone, muscle, and skin. During development, differentiation produces muscle cells, bone cells, and skin cells from an unspecialized set of embryo cells. Morphogenesis then organizes the bone cells into bone tissue to form bones and the muscle cells into muscle tissue to form muscles. However, it is the process of pattern formation that organizes those bones and muscles into the specific spatial organization that makes a dog look like a dog and a human look like a human.

The Role of Positional Cues in Pattern Formation.   During pattern formation, it is crucial for cells of the developing embryo to communicate with one another so that each cell will "know" its relative position within the emerging body plan. The intercellular molecular signals that ultimately drive the process of pattern formation provide positional information. These signals may be chemicals released by certain embryonic cells that diffuse through the embryo and bind to other cells. These diffusible signals are called morphogens. Oftentimes it is the concentration of the morphogen the target cell senses that provides information about the target cell's proximity to the releasing cell.

The development of a chicken wing is a good example of this phenomenon. During development, the chick wing develops from a structure called the limb bud. Lewis Wolpert discovered a small collection of cells that lie along the rear margin of the limb bud and that specify the position of cells along the front-rear axis of the bud. Ultimately, these cells control the pattern of digit development in the wing (chicken digits are like human fingers). Wolpert named these cells the polarizing region. They release a morphogen that diffuses through the limb bud. The cells that are exposed to the highest concentration of morphogen (the ones closest to the polarizing region) develop into a particular digit, the cells that are exposed to an intermediate concentration of morphogen develop into a differently shaped digit, etc. Ultimately the positional cue directs differentiation of the target cell by changing its pattern of gene expression.

The Role of *Hox* Genes in Pattern Formation.   The basic three-dimensional layout of an organism is established early in embryonic development. Even an early embryo body has dorsal and ventral axes (top and bottom) as well as anterior and posterior axes (front and back). The differential expression of certain genes in different cells of the embryo controls the emergence of this organization. Interestingly, while different types of organisms have dramatically different morphological features, a similar family of genes controls differential gene expression during pattern formation. The *Hox* family of genes (also called homeotic genes) is found in many different organisms (including plants and animals), and is important in controlling the anatomical identity of different parts of a body along its anterior/posterior axis. Many species have genes that include a nearly identical DNA sequence, called the homeobox region. These genes comprise the *Hox* family of genes, and they encode proteins that function as transcription factors. In fruit flies, for example, homeotic genes specify the types of **appendages** that develop on each body segment. The homeotic genes antennal and leg development

appendage attached organ or structure

WAELSCH, SALOME (1907–)

German-born U.S. biologist whose work helped lay the foundation for modern genetics. Waelsch overcame anti-Semitism and sexism both in Nazi Germany and later in the United States in her efforts to continue studying the genetics of development in mammals. In 1993, she was awarded the National Medal of Science.

by regulating the expression of a variety of other genes. The importance of the *Hox* genes is vividly evident when one of these genes is mutated: the wrong body part forms. For example, mutation in the *Antennapedia* gene causes fruit flies to develop legs in place of antennae on the head segment. SEE ALSO CELL CYCLE; CONTROL OF GENE EXPRESSION; DEVELOPMENT; GENE; TRANSCRIPTION

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Genetic Counselor

A genetic counselor is a medical professional who serves as a liaison between an individual or family and a physician or medical team. The counselor interprets genetic test results and provides information to help patients make medical or lifestyle choices, based on knowledge gained from genetic tests.

Genetic counselors are trained in genetics, statistics, and psychology, and usually have master's degrees from genetic counseling programs. Nurses, social workers, physicians, and Ph.D. geneticists also do genetic counseling. The job requires a combination of technical expertise and compassion—a genetic counselor must love working with people and be able to offer comfort under stressful circumstances.

During a typical session, the counselor asks many questions from which he or she constructs a pedigree, which is a family tree that depicts certain traits or illnesses. From this information, he or she can recognize or deduce the mode of inheritance (dominant or recessive, sex-linked or autosomal), predict which family members are likely to be affected, and suggest specific medical tests.

The first genetic counselors graduated from Sarah Lawrence College in Bronxville, New York, in 1971, against a backdrop of concern over such medical matters as test tube babies, heart transplants, and recombinant DNA (deoxyribonucleic acid) technology. At that time, genetic testing for sickle cell disease and Tay-Sachs disease was a prelude to the more widespread testing of the twenty-first century.

Until the early twenty-first century, patients seeking genetic counseling either had family histories of rare, single-gene disorders or were at high risk of carrying a fetus with a chromosomal or **congenital** problem, due to "advanced maternal age" or exposure to harmful substances (teratogens), respectively. With the sequencing of the human **genome**, the spectrum of

congenital present at birth; inherited

genome total genetic material in a cell or organism

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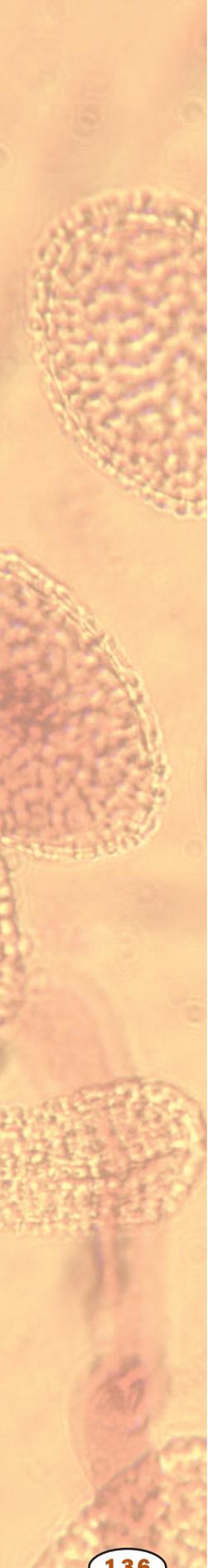
conditions that a genetic counselor confronts is broadening considerably to include much more common disorders, such as cancers and cardiovascular disease, that reflect the input of several genes and the environment. Rather than offering definitive diagnoses based on detecting single abnormal genes, genetic information is more likely to take the form of elevated risk estimates. SEE ALSO GENE; GENETIC ANALYSIS; HUMAN GENOME PROJECT; PATTERNS OF INHERITANCE

Ricki Lewis

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Genetic Diseases

A genetic disease is due to a faulty gene or group of genes. While not all gene defects cause disease, many do. New genetic diseases are discovered every month; as of 2001, there are estimated to be approximately 1,100 genetic diseases.

How Gene Defects Cause Disease

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

nucleotide the building block of RNA or DNA

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

nucleus membrane-bound portion of cell containing the chromosomes

A gene is a recipe for making a **protein**. Proteins control cell functions, and defects in the instructions for making a protein can prevent the cell from functioning properly. Genes are made of deoxyribonucleic acid (DNA), a chemical composed of units called **nucleotides**, and are carried on **chromosomes** within the cell **nucleus**. Most genes are present in pairs (corresponding to the two sets of chromosomes inherited from one's parents). As well as coding for proteins, genes are the hereditary material. Therefore, genetic diseases can be inherited.

Genetic defects cause diseases in a variety of ways. The simplest way is through a "loss-of-function" mutation. In this type of defect, a change in the DNA nucleotides prevents the gene from making protein, or prevents the protein from functioning once it is made. Genetic diseases due to loss-of-function mutations are very common, and include cystic fibrosis (which affects the lungs and pancreas), Duchenne muscular dystrophy, and the hemophilias, a group of blood-clotting disorders.

A second mechanism for causing disease is called a "toxic-gain-of-function" mutation. In this type of defect, the gene takes on a new function that is harmful to the organism—the protein produced may interfere with cell functions, or may no longer be controllable by its normal regulatory partners, for instance. Many degenerative diseases of the brain are due to this type of mutation, including Huntington disease.

More complex mechanisms are possible. Most traits are multifactorial, meaning they are determined by many different genes. In the human population, there are several variants (alleles) of most genes, each form of which

Punnett Square for Duchenne Muscular Dystrophy

unaffected father

X → sperm

$X_D X$ $X_D Y$

carrier mother

X_D

XX   XY

X

eggs

Male offspring have a 50:50 chance of inheriting the X_D chromosome and thereby developing Duchenne muscular dystrophy.

= carrier female

= affected male

= parents
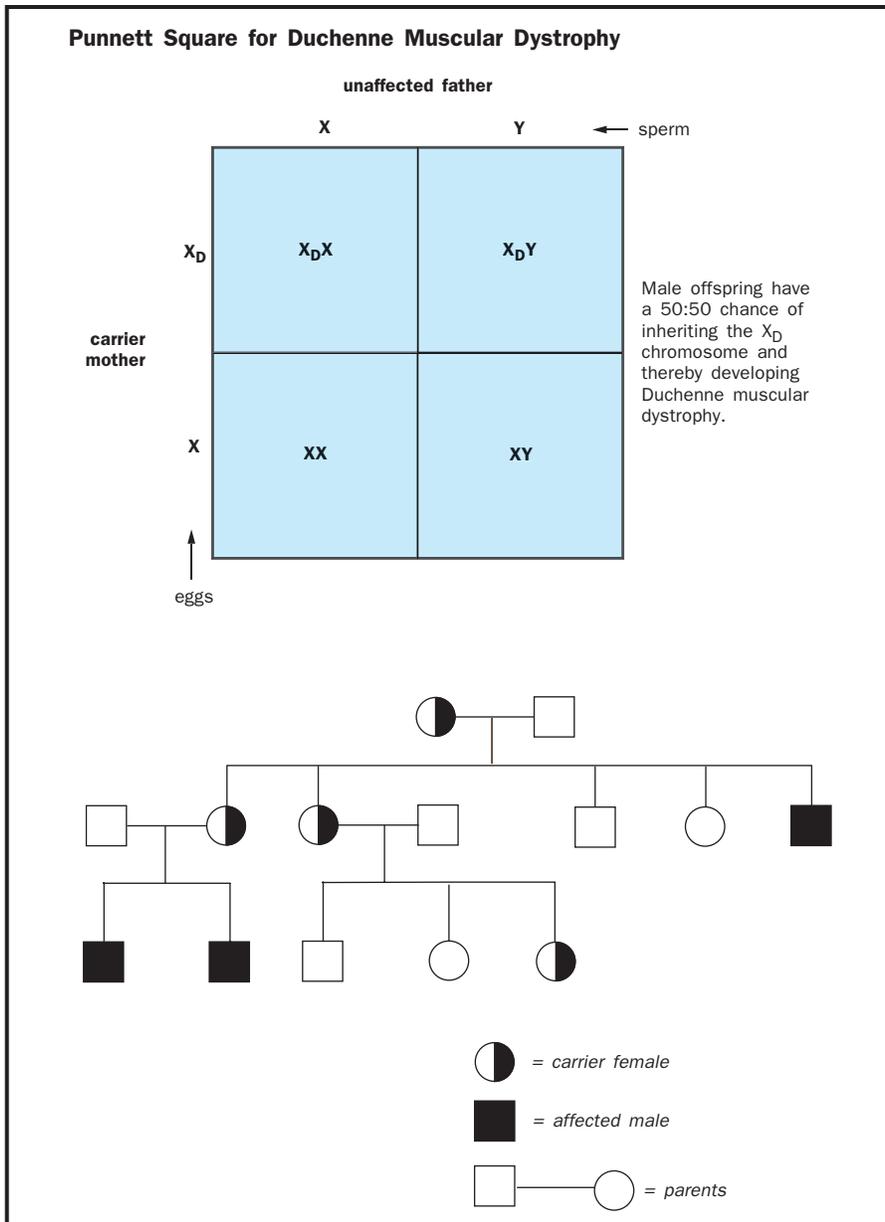
Duchenne muscular dystrophy is a genetic disease due to the loss-of-function mutation. The bottom diagram shows a typical pedigree for inheritance of an x-linked trait such as Duchenne muscular dystrophy.

is functional and does not cause disease by itself. However, some **alleles** may predispose a person to a certain disease, especially in combination with other alleles or environmental factors that influence the same trait. Such susceptibility alleles have been found in breast cancer and colon cancer, for instance. Carriers of these alleles have an increased likelihood of developing that disease, a risk that can be increased or decreased by such factors as diet, exposure to environmental toxins, or presence of particular alleles for other genes. As more is learned about the human **genome**, a large number of susceptibility genes are likely to be discovered for a wide variety of conditions.

Disease can also be caused by chromosome abnormalities rather than gene defects. Down syndrome is due to having three copies of chromosome 21, instead of the normal two copies. It is likely the extra protein from the extra gene copies lead directly to the disease symptoms, but this is not yet clear.

allele a particular form of a gene

genome total genetic material in a cell or organism

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Condition	Chromosome Location and Inheritance Pattern	Protein Affected	Symptoms and Comments
Gaucher Disease	1, recessive	glucocerebrosidase, a lipid metabolism enzyme	Common among European Jews. Lipid accumulation in liver, spleen, and bone marrow. Treat with enzyme replacement
Achondroplasia	4, dominant	fibroblast growth factor receptor 3	Causes dwarfism. Most cases are new mutations, not inherited
Huntington's Disease	4, dominant	huntingtin, function unknown	Expansion of a three-nucleotide portion of the gene causes late-onset neurodegeneration and death
Juvenile Onset Diabetes	6,11,7, others	IDDM1, IDDM2, GCK, other genes	Multiple susceptibility alleles are known for this form of diabetes, a disorder of blood sugar regulation. Treated with dietary control and insulin injection
Hemochromatosis	6, recessive	HFE protein, involved in iron absorption from the gut	Defect leads to excess iron accumulation, liver damage. Menstruation reduces iron in women. Bloodletting used as a treatment
Cystic Fibrosis	7, recessive	cystic fibrosis transmembrane regulator, an ion channel	Sticky secretions in the lungs impair breathing, and in the pancreas impair digestion. Enzyme supplements help digestive problems
Friedreich's Ataxia	9, recessive	frataxin, mitochondrial protein of unknown function	Loss of function of this protein in mitochondria causes progressive loss of coordination and heart disease
Best Disease	11, dominant	VMD2 gene, protein function unknown	Gradual loss of visual acuity
Sickle Cell Disease	11, recessive	hemoglobin beta subunit, oxygen transport protein in blood cells	Change in hemoglobin shape alters cell shape, decreases oxygen-carrying ability, leads to joint pain, anemia, and infections. Carriers are resistant to malaria. About 8% of US black population are carriers
Phenylketonuria	12, recessive	phenylalanine hydroxylase, an amino acid metabolism enzyme	Inability to break down the amino acid phenylalanine causes mental retardation. Dietary avoidance can minimize effects. Postnatal screening is widely done
Marfan Syndrome	15, dominant	fibrillin, a structural protein of connective tissue	Scoliosis, nearsightedness, heart defects, and other symptoms
Tay-Sachs Disease	15, recessive	beta-hexosaminidase A, a lipid metabolism enzyme	Accumulation of the lipid GM2 ganglioside in neurons leads to death in childhood
Breast Cancer	17, 13	BRCA1, BRCA2 genes	Susceptibility alleles for breast cancer are thought to involve reduced ability to repair damaged DNA
Myotonic Dystrophy	19, dominant	dystrophia myotonica protein kinase, a regulatory protein in muscle	Muscle weakness, wasting, impaired intelligence, cataracts
Familial Hypercholesterolemia	19, imcomplete dominance	low-density lipoprotein (LDL) receptor	Accumulation of cholesterol-carrying LDL in the bloodstream leads to heart disease and heart attack
Severe Combined Immune Deficiency ("Bubble Boy" Disease)	20, recessive	adenosine deaminase, nucleotide metabolism enzyme	Immature white blood cells die from accumulation of metabolic products, leading to complete loss of the immune response. Gene therapy has been a limited success
Adrenoleukodystrophy	X	lignoceroyl-CoA ligase, in peroxisomes	Defect causes build-up of long-chain fatty acids. Degeneration of the adrenal gland, loss of myelin insulation in nerves. Featured in the film *Lorenzo's Oil*
Duchenne Muscular Dystrophy	X	dystrophin, muscle structural protein	Lack of dystrophin leads to muscle breakdown, weakness, and impaired breathing
Hemophilia A	X	Factor VIII, part of the blood clotting cascade	Uncontrolled bleeding, can be treated with injections or replacement protein
Rett Syndrome	X	methyl CpG-binding protein 2, regulates DNA transcription	Most boys die before birth. Girls develop mental retardation, mutism, and movement disorder
Leber's Hereditary Optic Neuropathy	mitochondria, maternal inheritance	respiratory complex proteins	Degeneration of the central portion of the optic nerve, loss of central vision
Mitochondrial Encephalopathy, Lactic Acidosis, and Stroke (MELAS)	mitochondria, maternal inheritance	transfer RNA	Recurring, stroke-like episodes in which sudden headaches are followed by vomiting and seizures; muscle weakness

Inheritance Patterns in Genetic Disease

Genetic diseases are heritable, meaning they may be passed from parent to child. A disease gene is called *recessive* if both copies of the gene must be defective to cause the disease. Loss-of-function mutations are often recessive. If the second copy of the gene is healthy, it may be able to serve adequately even if the first copy suffers a loss-of-function mutation. In this case, the carrier of the disease gene will not have the disease.

All humans are thought to carry a number of such defective genes. Close relatives are likely to carry similar genes and gene defects, and are therefore more likely to bear children with recessive genetic diseases if they mate. Because of this, a prohibition against marriage of close relatives is found in virtually every culture in the world.

A disease gene is called *dominant* if inheriting one copy of it causes the disease. Toxic gain-of-function mutations often create dominant genes, as in the case of Huntington disease.

If having one defective gene causes a different condition than having two, the gene is called *incompletely dominant*. In familial hypercholesterolemia, having two disease genes leads to very high blood cholesterol levels and death in childhood or early adulthood. Having one disease gene and one normal gene leads to less-elevated cholesterol and a longer but still reduced life span.

Most genes are carried on autosomes, the twenty-two pairs of chromosomes that do not determine sex. Males and females are equally likely to inherit disease genes on autosomes and develop the related diseases, called *autosomal disorders*. Unlike autosomes, the pair of chromosomes that determine sex (called X and Y) have almost no genes in common. While the Y carries very few genes, the very large X chromosome contains many genes for proteins unrelated to sex determination. Males have one X and one Y, and are more likely than females to develop diseases due to recessive X-linked genes, since they do not have a backup copy of the normal gene. Such disorders are termed *X-linked disorders*. Females have two X chromosomes, and so usually do not develop recessive X-linked disorders. Duchenne muscular dystrophy, for instance, is an X-linked condition due to a defective muscle protein. It affects boys almost exclusively. Females are carriers for the condition, meaning they have the gene but seldom develop the disease.

The cell energy **organelles** called **mitochondria** also contain a small number of genes. Mitochondria are inherited only from the mother, and so mitochondrial gene defects show *maternal inheritance*. Leber's hereditary optic neuropathy is a maternally inherited mitochondrial disorder causing partial blindness.

In some diseases, not every person who inherits the gene will develop the disease. Such genes are said to show *incomplete penetrance*. For instance, fragile X syndrome does not affect about one-fifth of boys who inherit it. This syndrome is due to a large increase in the number of CCG nucleotides at the tip of the X chromosome and leads to characteristic facial features, mental retardation, and behavioral problems.

organelle membrane-bound cell compartment

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

Unique Features of Genetic Diseases

If a parent is known to carry a disease gene, it is possible to predict the likelihood that an offspring will contract the disease, based on simple laws of

probability. In Duchenne muscular dystrophy, for instance, if the mother carries the defective gene, there is a 50 percent chance that each male child will develop the disease, since she will give the child one of her two X chromosomes. It is also possible with many disorders to test the fetus to determine if the gene was in fact inherited. Such information can be used for purposes of family planning.

Different populations may have different frequencies of disease alleles because of long periods of relative genetic isolation. For instance, Jews of European ancestry are much more likely to carry the gene for Tay-Sachs disease, a fatal autosomal recessive disorder of **lipid metabolism**. Healthy adults in such populations may choose to be tested to see if they carry one Tay-Sachs allele. A person with one disease allele might use this information to avoid choosing a mate who also has one disease allele.

Treatment of genetic diseases is possible in some but not all cases. Missing proteins can be supplied relatively easily to the blood, as for hemophilia, but not to most other organs. The effects of phenylketonuria, which is due to a defect in an **enzyme** that breaks down phenylalanine, can be partially avoided by reducing the amount of the **amino acid** phenylalanine in the diet. (This is the reason some diet soft drinks carry a notice that phenylalanine is used in the artificial sweetener.) Most genetic diseases can't be treated, though, except by supplying the missing gene to the tissues in which it acts. This treatment, called gene therapy, is still experimental, but may become an important type of therapy for genetic diseases in the coming decades. SEE ALSO GENE THERAPY; GENETIC ANALYSIS; GENETIC COUNSELOR; MUTATION; PATTERNS OF INHERITANCE; PEDIGREES AND MODES OF INHERITANCE; SEX CHROMOSOMES

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Genome

The genetic material of an organism consists of deoxyribonucleic acid (DNA). A gene is a segment of DNA that encodes a **protein** (or a structural ribonucleic acid [RNA] for example, ribosomal RNA), along with the regulatory elements that control expression of that gene. The entire complement of DNA within the **chromosomes** of an organism is called the genome. The more complex organisms, that is, eukaryotes, contain much more DNA in their genomes than is found in genes. This nongene DNA has often been called "junk DNA," as scientists have yet to find a specific function for it. The junk DNA can amount to 90 to 99 percent of the total DNA in the cell **nucleus**.

Within the nucleus the DNA is part of the chromosomes. The number of chromosomes varies with species but is generally about twenty to forty pairs. However, there are exceptions: The round worm *Ascaris megalocephala*

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lipid fat or waxlike molecule, insoluble in water

metabolism chemical reactions within a cell

enzyme protein that controls a reaction in a cell

amino acid a building block of protein

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

nucleus membrane-bound portion of cell containing the chromosomes

has but one pair of chromosomes, while the fern *Ophioglossum reticulatum* has six hundred thirty. Humans have twenty-three pairs. In **prokaryotes**, such as bacteria, the DNA is found in a single chromosome, and this constitutes the bacterial genome.

The concept of a genome can be extended. **Mitochondria**, the cellular **organelles** found in all eukaryotes, as well as plastids such as the chloroplast found in plants, originally evolved from bacteria-like ancestors that took up residence within the primitive **eukaryotic cell**. These are called endosymbionts. Mitochondria and chloroplasts retain some of the genes of these ancestral endosymbionts, and one can then speak of the mitochondrial or chloroplast genome. In addition, many bacteria harbor **plasmids**, small circular pieces of DNA containing a few genes that form a plasmid genome.

Genomes do not have to consist of double-stranded DNA. Indeed, it is among the viruses that one finds a wide variety of genome forms. These genomes may be composed of double-stranded or single-stranded DNA. The DNA molecules may be linear or form a circle. Other viruses use RNA as their genetic material. These RNA genomes may be single-stranded or double-stranded. Viroids are another interesting group. Viroids are disease-causing entities in plants, such as the tomato stunt viroid or the avocado sunblotch viroid. Viroids resemble viruses, but unlike viruses they lack a coat protein(s) and consist of a genome of only approximately 240 to 400 bases of RNA.

The study of genomes has been made possible by the development of automated DNA sequencers and high-powered computers that can overlap pieces of genome sequence to derive the entire DNA base sequence. This led to the development in the late 1990s of a new field of study called genomics. Genomics uses genome sequence data to identify genes, to predict the structure of gene products, to study the evolution of individual genes, or to examine the genetic relationships among species. With this technology, genome sequencing is progressing rapidly. The National Institutes of Health maintains a genome database (www.ncbi.nlm.nih.gov). As of May 2001, more than six hundred complete genomes have been deposited in the database. Most of these are viruses, along with four eukaryotes and almost fifty prokaryotes. Several hundred more partial sequences are also available. A first draft of the entire three-billion-plus bases of the human genome was completed in early 2000 and announced on June 26 of that year. The work is expected to be completed in 2003. SEE ALSO CELL EVOLUTION; CHLOROPLAST; CHROMOSOME, EUKARYOTIC; DNA; DNA VIRUSES; GENE; HUMAN GENOME PROJECT; MITOCHONDRION

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Genomics

Genomics is the study of the **genome**, or deoxyribonucleic acid (DNA), of an organism and associated technologies. Genomics evolved from a series

prokaryote single-celled organism without a nucleus

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

organelle membrane-bound cell compartment

eukaryotic cell a cell with a nucleus

plasmid small ring of DNA found in many bacteria

genome total genetic material in a cell or organism

A scientist using a computer to design complex proteins. Proteins are more difficult to manipulate than DNA, and each must be approached individually.

chromosomes "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

proteins complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

polymerase enzyme complex that synthesizes DNA or RNA from individual nucleotides

electrophoresis technique that uses electricity to separate molecules based on size and electric charge

of experimental and conceptual advances that allowed researchers to decipher the DNA sequences of whole genomes from virtually any organism, including humans. Single experiments can scrutinize many genes and compare genomes of different species.

Before the development of genomics, DNA studies in humans were mostly relegated to observing highly condensed **chromosomes** under a microscope. Many human studies were done in medical centers where families with visible chromosomal mutations came for evaluation. While it was possible in a few cases to determine on which chromosome a gene was located or whether two genes were located on the same chromosome, without molecular techniques these were difficult tasks at best.

Tools of Genomics

Genomics developed from advances in recombinant DNA technology, while in turn, developed from earlier progress in biochemistry and genetics. Recombinant DNA technology is the set of tools that make it possible for researchers to study and manipulate DNA, ribonucleic acid (RNA), and **protein** from any source, both outside of the cells (*in vitro*) and inside of the cells (*in vivo*) of the well-studied model organisms.

Relatively few techniques are used to study DNA. The basic methods that underlie genomic technologies include DNA sequencing, **polymerase** chain reaction (PCR), **electrophoresis**, cloning, and hybridization. The fact that all DNA molecules can be manipulated using a few basic techniques is a major advantage of working with DNA. In contrast, proteins are much more difficult to manipulate, and each must be approached individually.

DNA sequencing determines the order of bases in a segment of DNA, a gene, a chromosome, or an entire genome. PCR can increase the number of copies (even a millionfold) of a single gene or fragment of DNA *in vitro* within hours. Electrophoresis separates DNA by size in the presence of an electrical field. This is a simple technique used to follow changes in DNA size through different recombinant manipulations.

Cloning

The process of isolating a piece of DNA for recombinant DNA studies is called cloning. Cloning increases the number of copies of a single gene or fragment of DNA *in vivo*. Large amounts of DNA are needed for sequencing and manipulation experiments. The purified, unknown DNA is combined with another well-characterized piece of DNA called a cloning **vector**. The vector DNA has the DNA sequences needed to form an artificial mini-chromosome. A cell that contains the cloned DNA is called a clone. The clone is used to produce more copies of the DNA of interest and to produce protein encoded by the DNA. In some experiments, a modified DNA segment is returned to the original organism for further studies.

vector carrier

Cloning can be used to isolate and scrutinize a small part of the genome, such as a gene. For example, consider the cloning of an **oncogene**, which is a gene that, when overexpressed, causes cancer. DNA fragments from human cancer cells were introduced into the cells of a normal mouse. Some of the cells received a piece of human DNA that caused them to develop into cancerous cells. Recombinant DNA techniques were used to identify which piece of human DNA was responsible for converting the normal cells to cancerous cells. DNA methods enabled researchers to isolate the specific human gene that causes the cancer.

oncogene gene that causes cancer

Hybridization

Hybridization, which is also known as renaturation or annealing, is the coming together of two **complementary**, single strands of DNA to form double-stranded DNA. Denaturation is the reverse process, which separates double-stranded DNA into two single strands (see Fig. 1). Double-stranded DNA is denatured when it is incubated at a high temperature. In hybridization experiments, single-stranded DNA of unknown sequence (test DNA) is hybridized to single-stranded DNA of known sequence (probe DNA). Hybridization takes place only when the test DNA contains a complementary DNA sequence.

complementary matching opposite

Hybridization experiments can be used to sequence the test DNA a "word" at a time. A word is equal to the length of the probe sequence, which is usually greater than eight bases. This technique makes it possible to obtain information more rapidly than from ordinary sequencing methods.

DNA hybridization experiments are also used to study the expression of thousands of genes at the same time. In expression studies, messenger RNA (mRNA) from a cell is hybridized to an array (display) of complementary single-stranded DNA probe sequences unique for each test mRNA. Test mRNA hybridizes to DNA probes in the same manner as test DNA. The amount of test mRNA hybridized to each probe is measured to determine the amount of complementary mRNA present. Since the hybridization is done to the entire array simultaneously, information about all test mRNA sequences is obtained in a single experiment. The DNA probes arrayed on a microchip are recorded and the hybridization results are analyzed automatically using computers.

DNA array experiments identify and analyze mRNAs solely on the basis of their sequence. No information is needed about the proteins encoded
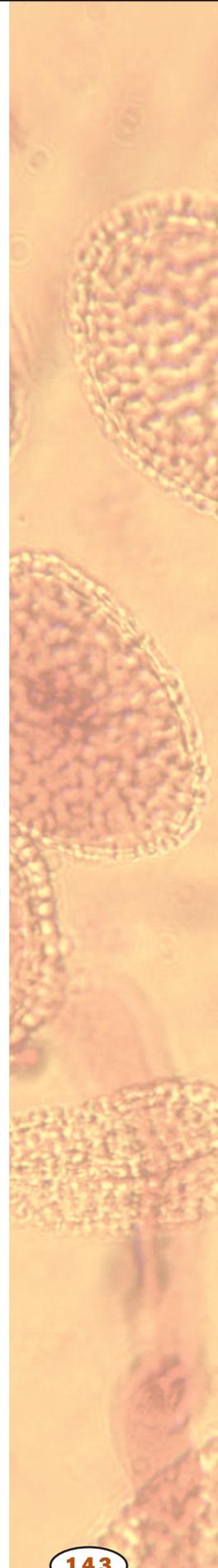
Figure 1. Denaturation uses heat or chemicals to separate the two strands of DNA in the double helix. Hybridization experiments begin by denaturing different DNAs, and then allowing them to reassemble.

Denaturation of DNA
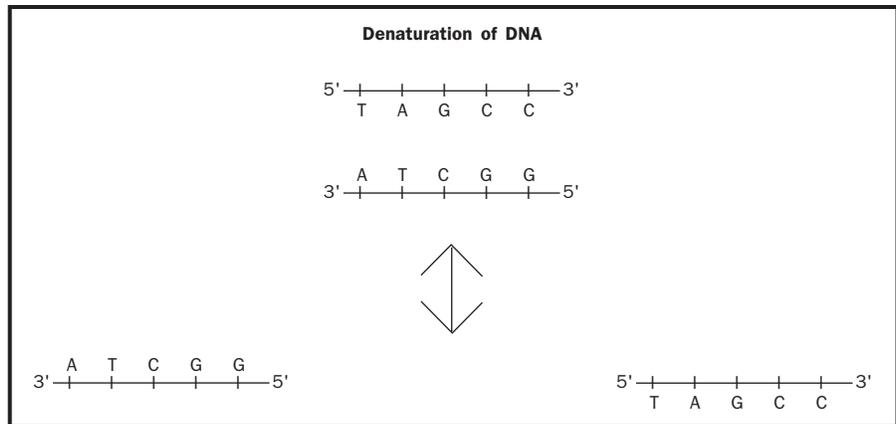
by the mRNA or their function. However, ultimately, information about the proteins and their functions is the real goal of these experiments. The array experiment is used to identify important mRNAs, which indicate which genes a particular cell is expressing. This may be related to a cell specialization (for example, brain versus heart), or to a disease state. This "whole genome" approach can lead to the discovery of new genes and identify unexpected functions of known genes.

Finding Disease Genes

Positional cloning experiments isolate genes responsible for a specific genetic disease, such as cystic fibrosis, by first identifying their location (position) in the genome (which chromosome they are on). Genetic mapping techniques locate a gene or a DNA sequence among the chromosomes by identifying which regions of the genome are inherited in the same manner as the trait of interest, such as a disease. Once the chromosomal region is found, molecular and computational methods are used to identify all genes in the region and to pick up "candidate" genes for further testing. Some of the candidate genes are identified by determining whether their encoded proteins fit the trait or disease of interest. For example, the isolation and determination of the DNA sequence of the cystic fibrosis gene made it possible to identify its product, a large protein molecule that regulates the transport of chloride across the cell membrane. Researchers were able to explain the clinical symptoms when they discovered that the protein was nonfunctional.

The power of focusing on genetic causes of disease is due to several factors. First, positional cloning is guaranteed to produce results provided enough money is available to do the experiment and large families inheriting the trait of interest are known. It is very rare in research to be sure of success. Second, the identification of a gene responsible for a disease uncovers pathways and genes that are unknown and may play a role in noninherited forms of the same or a similar disease.

Future Directions

The first stage of genomic research is coming to an end as the entire human DNA sequence is known. An understanding of that blueprint will likely take many more years of research. That understanding will require sequencing

many genomes to determine how variations in DNA sequences affect protein and cell function. Further, each gene must be understood in the context of the entire repertoire of thirty-five thousand human genes. Because of advances in genomics, scientists are no longer forced to study single genes out of context. Consequently, experiments and the information gathered in each experiment are becoming more complex. New computational tools are needed to understand the massive amount of information that is now being generated. This has developed into the field of bioinformatics.

The DNA sequences of any two individuals can differ in at least one million places. In medicine, variations in the DNA sequences will be used to develop individualized drug treatments. This new field, known as pharmacogenomics, is in its infancy, but already DNA profiles are being used to subtype different cancers, enabling physicians to prescribe the drugs most likely to be effective for a particular patient in the course of treatment.

Genomic studies are not confined to humans, but are used to learn about all organisms. The lessons that nature will provide from all these studies will have an impact on fields far beyond biology and medicine. The tools and knowledge needed to accomplish these cross-traditional boundaries of scientific disciplines. The solutions to future scientific problems will require an immense amount of collaboration and will need to take advantage of talents and knowledge of a large number of individuals. SEE ALSO BIOINFORMATICS; CLONE; DNA SEQUENCING; HUMAN GENOME PROJECT; HYBRIDIZATION; MODEL ORGANISMS: CELL BIOLOGY AND GENETICS; ONCOGENES AND CANCER CELLS; POLYMERASE CHAIN REACTION; RECOMBINANT DNA

Cassandra L. Smith and Linda G. Tolstoi

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Global Climate Change

Energy from the Sun passes through the atmosphere as light and is absorbed by soil, rock, and water at the surface of Earth. The energy is reradiated as heat and absorbed in the atmosphere by greenhouse gases, including carbon dioxide (CO_2), water vapor, methane, ozone, nitrous oxide, and the

organic composed of carbon, or derived from living organisms

human-made chemicals chlorofluorocarbons (CFCs). This atmospheric warming is called the greenhouse effect; without it Earth's average global temperature would be about –18 degrees Celsius (0 degrees Fahrenheit). Greenhouse gases are added to the atmosphere by natural events including volcanic eruptions, the decay and burning of **organic** matter, and respiration by animals. They are also removed from the atmosphere. CO_2 is absorbed by seawater and stored in plant tissue. When plants die and gradually are transformed into fossil fuels—coal, oil, natural gas—deep in the earth, their CO_2 is stored with them. The removal of greenhouse gases from the atmosphere keeps the planet from overheating.

Climate History

Besides the concentrations of greenhouse gases in the atmosphere, other factors affect global climate including Earth's orbital behavior, the positions and topography of the continents, the temperature structure of the oceans, and the amount and types of life. During much of Earth's history the climate was warm and humid with ice-free poles; global average temperatures were about 5 degrees Celsius (9 degrees Fahrenheit) higher than today. Several times glaciers covered the higher latitudes, most recently during the Pleistocene (1.6 million to 10,000 years ago), when up to 30 percent of the land was covered by ice. During the four glacial advances of the Pleistocene, average global temperature was 5 degrees Celsius lower than today and 10 degrees Celsius (18 degrees Fahrenheit) lower than the ancient global average. During the three interglacial periods, global temperature was a degree or two warmer than today. Many scientists think that Earth is in an interglacial period, and the ice sheets will return.

Since the peak of the last glacial advance 18,000 years ago, average global temperature has risen 4 degrees Celsius (7 degrees Fahrenheit), including 1 degree Celsius (1.8 degrees Fahrenheit) since the beginning of the Industrial Revolution. It is difficult to know how much of the recent warming is the result of the end of the Pleistocene and how much is the result of human activities that add greenhouse gases to the atmosphere. CO_2 is the most abundant greenhouse gas, a by-product of burning fossil fuels and modern forests. In the early twenty-first century, there is greater than 30 percent more CO_2 in the atmosphere than in 1850. There have also been significant increases in methane and CFCs. Some projections show a doubling of CO_2 over preindustrial levels by 2050 and additional increases in methane. (CFCs are being phased out by international agreement because they destroy Earth's protective ozone layer.)

Adding greenhouse gases to the atmosphere is like throwing another blanket on Earth; the consequent rise in global temperature is known as global warming. Since climate is a complex system and climate models are difficult to construct, scientists can only speculate on the effect large increases in greenhouse gases will have on global climate. Some models show average global temperature increasing as much as 5 degrees Celsius by 2100. Any temperature increase will not be uniform. Since ocean water absorbs more heat than land, the Southern Hemisphere (which has more water) will warm less than the Northern. Atmospheric circulation patterns will bring the greatest warming, as much as 8 to 10 degrees Celsius (14 to 18 degrees Fahrenheit), to the poles.

Pollution over Mexico City. Concentrations of greenhouse gases in the atmosphere have a great impact on global climate.

Possible Consequences

A rapid increase in global average temperature could have profound effects on social and natural systems. Warmer temperatures would cause ocean water to expand and polar ice caps to melt, increasing sea level by as much as 50 centimeters (1.6 feet) by 2100. This would flood coastal regions, where about one-third of the world's population lives and where an enormous amount of economic **infrastructure** is concentrated. It would destroy coral reefs, accelerate coastal erosion, and increase salinity to coastal groundwater aquifers. Warmer temperatures would allow tropical and subtropical insects to expand their ranges, bringing tropical diseases such as malaria, encephalitis, yellow fever, and dengue fever to larger human populations. There would be an increase in heat-related diseases and deaths. Agricultural regions might become too dry to support crops, and food production all over the world would be forced to move north; this would result in a loss of current cropland of 10 to 50 percent and a decline in the global yield of key food crops of from 10 to 70 percent.

infrastructure roads, phone lines, and other utilities that allow commerce

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Wild plant and animal species would need to move poleward 100 to 150 square kilometers (60 to 90 miles) or upward 150 meters (500 feet) for each 1 degree Celsius rise in global temperature. Since most species could not migrate that rapidly and since development would stop them from colonizing many new areas, much biodiversity would be lost. The decrease in the temperature difference between the poles and the equator would alter global wind patterns and storm tracks. Regions with marginal rainfall levels could experience drought, making them uninhabitable. Overall, since warmer air holds more moisture, an increase in global air and sea temperatures would increase the numbers of storms. Higher sea surface temperatures would increase the frequency and duration of hurricanes and El Niño events.

Many scientists believe that global warming is the most serious threat to our planet. By 2025 the world's energy demand is projected to be 3.5 times greater than in 1990, with annual CO_2 emissions nearly 50 percent higher. Thus far, attempts at international agreements to curb the emissions of greenhouse gases (for example, the Kyoto Protocol) have failed. This is due to several factors: (1) the scientific uncertainty of the role humans play in global warming; (2) the lifestyle changes necessary to reduce fossil fuel consumption in developed nations; (3) the possible slowdown in the economic development of developing nations; and (4) the need for true international cooperation. A high-technology alternative to decreasing greenhouse gas emissions is to sequester CO_2. Experiments are underway to inject liquid CO_2 deep into the earth, thereby effectively removing it from Earth's carbon cycle. SEE ALSO BIOGEOCHEMICAL CYCLES; CARBON CYCLE; ECOLOGICAL RESEARCH, LONG-TERM; ECOSYSTEM; EXTINCTION; TUNDRA

Dana Desonie

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Glycolysis and Fermentation

Glycolysis is an **anaerobic** metabolic pathway, found in the **cytosol** of all cells, which forms adenosine triphosphate (**ATP**) by degrading **glucose**. It also serves as a source of precursors for other pathways, and as a recipient of products of various pathways for use as metabolic fuels. Its universal and central role in **metabolism** suggests that glycolysis evolved early in the history of life.

In the overall reaction for glycolysis, one molecule of glucose is converted to two molecules of pyruvic acid. Along the way, two molecules of adenosine diphosphate (**ADP**) are **phosphorylated** to ATP, and two molecules of NAD^+ (the **oxidized** form of NAD, or nicotinamide adenine dinucleotide) are reduced to NADH. ATP serves as an energy carrier and can be used to power many cellular processes. The NADH carries high-energy electrons, which can be used to produce more ATP by **chemiosmosis**. Like-

anaerobic without oxygen, or not requiring oxygen

cytosol fluid portion of a cell, not including the organelles

ATP adenosine triphosphate, a high-energy nucleotide used by cells to power most energy-requiring reactions

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

metabolism chemical reactions within a cell

ADP adenosine diphosphate, the low-energy form of ATP

phosphorylate add a phosphate group to

oxidize to react or make react with oxygen

chemiosmosis use of proton gradients to make ATP (see Oxidative Phosphorylation entry)

The process of glycolysis. In glycolysis, the six-carbon glucose (shown without its hydrogens or oxygens) is first destabilized by the addition of ATP, and then split. Further transformations create NADH and new ATP, leaving a pair of three-carbon pyruvates.

wise, the pyruvic acid can be further oxidized by the **Krebs cycle** to yield additional ATP.

The ten steps of glycolysis can be divided into two stages. The first five steps, the preparatory, or priming, phase of glycolysis, prepare the glucose by phosphorylating it twice, using two molecules of ATP as sources of phosphate. This increases the energy content of the glucose, so the preparatory phase is also sometimes called the investment stage, reflecting the need to invest two ATP molecules before a net yield of energy can be achieved. During the second five reactions, the payoff phase, the fructose-1,6-bisphosphate formed during the preparatory phase is dephosphorylated and cleaved, forming two molecules of **pyruvate** and four of ATP. Because two ATPs are used and four are produced during glycolysis, there is a net production of two molecules of ATP for every glucose consumed.

Since glycolysis plays a central role in cellular metabolism, it has several control points. Like most pathways, it is regulated during its early steps. Hexokinase, the **enzyme** that **catalyzes** the first reaction, is inhibited by its product, glucose-6-phosphate (G-6-P). The third enzyme, phosphofructokinase (PFK), is regulated in a complex manner by several **metabolites**, and is also under indirect hormonal control. The last glycolytic enzyme, pyruvate **kinase**, is regulated by several metabolites, including ATP, which inhibits it. These control mechanisms have the effect of maintaining a constant supply of ATP for the cell, since production of ATP inhibits the process, and depletion of ATP activates it.

Aerobically respiring cells will produce even more ATP through **oxidative phosphorylation**. However, cells that cannot **respire aerobically**, either because they lack the necessary metabolic pathways or because they live in anaerobic environments, cannot do this. This presents a problem since all cells must continually regenerate the NAD^+ needed during the

Krebs cycle central metabolic pathway in mitochondria

pyruvate the ionized form of pyruvic acid, a key intermediate in cell metabolism

enzyme protein that controls a reaction in a cell

catalyze aid in the reaction of

metabolite molecule involved in a metabolic pathway

kinase enzyme that adds a phosphate group to another molecule, usually a protein

oxidative phosphorylation use of oxygen to make ATP

respire use oxygen to burn cellular fuel

aerobic with oxygen, or requiring it

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In the absence of oxygen the pyruvate is converted to NAD^+ in reactions collectively referred to as fermentations.
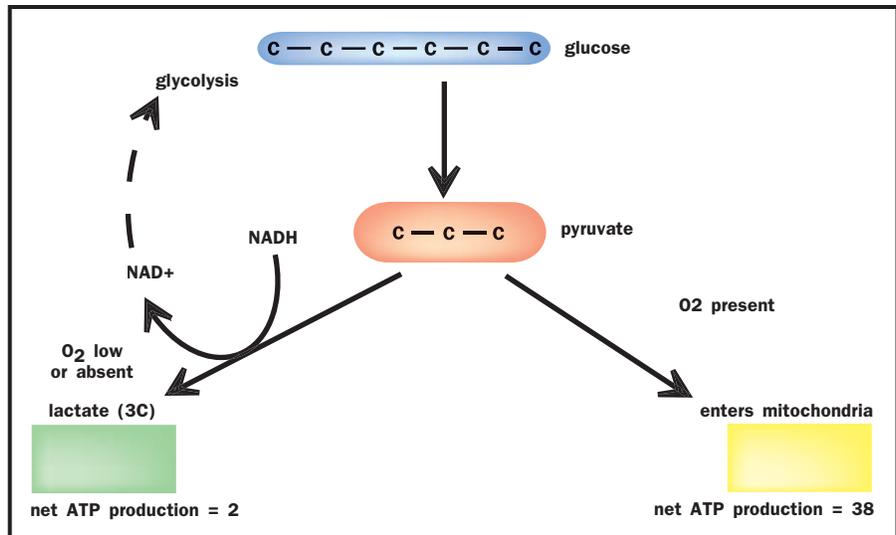
preparatory phase of glycolysis. All such cells accomplish this by converting the pyruvate to another product, oxidizing NADH to NAD^+ in the process. These reactions are collectively referred to as fermentations. Animals, some plants, and most bacteria produce lactic acid, whereas yeast and a few bacteria produce carbon dioxide and ethanol. Rarer fermentations produce a variety of **organic** molecules such as other alcohols and organic acids. Fermentations are used extensively by industry to produce these compounds cheaply, as well as to produce foods such as yogurt, bread, wine, and beer. SEE ALSO CARBOHYDRATES; KREBS CYCLE; OXIDATIVE PHOSPHORYLATION

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organic composed of carbon, or derived from living organisms

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Golgi

The Golgi (pronounced GOL-jee) complex (or Golgi apparatus or Golgi body) was discovered by Camillo Golgi (1844–1926), an Italian physician. While Dr. Golgi was staining **neurons** with silver nitrate (Golgi stain), he noticed small **intracellular** structures made up of **vesicles** and fibers known today as the Golgi complex.

neuron nerve cell

intracellular within a cell

vesicle membrane-bound sac

endoplasmic reticulum network of membranes within the cell

nucleus membrane-bound portion of cell containing the chromosomes

Structure

The Golgi complex is composed of several layers of cisternae (fluid-filled membrane sacs) arranged like stacked pancakes near the outer edges of the **endoplasmic reticulum** (ER) near the **nucleus**. The Golgi complex is organized into three biochemically distinct compartments: the *cis* Golgi, the *medial* Golgi, and *trans* Golgi; the cis Golgi is closest to the ER.

cis Golgi network | Golgi stack | trans Golgi network

Golgi apparatus

sma membrane

Protein Processing

The primary function of the Golgi complex is to modify, process, and sort newly produced **proteins** that arrive from the ER. These modifications include adding or deleting specific sugar molecules to modify the branched sugar structures found on newly formed proteins. For example, some of the mannose sugars are cut from the **oligosaccharide** branch in the cis Golgi. Upon completion of this step, the protein travels to the medial Golgi where other sugars like N-acetylglucoseamine and fucose are added to the oligosaccharide branches on the protein. Further modifications to the **carbohydrates** are completed in the trans Golgi. Carbohydrate additions may aid in the stability, transport, and/or function of the proteins.

Transport

Two models have been proposed to explain how newly produced proteins travel from the ER to the Golgi complex and travel among Golgi stacks. One model suggests that proteins are transported enclosed in vesicles. Another model proposes that one stack of the Golgi "matures" into the next stack. This is called the cisternal progression model. Regardless of which

The intracellular structures known at the Golgi complex are involved in protein processing and secretion.

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

oligosaccharide chain of several sugar molecules

carbohydrates sugars, starches, and other molecules combining carbon, hydrogen, and oxygen and serving as fuel or structural components

Camillo Golgi is most noted for his studies with the human nervous system and shared the 1906 Nobel prize with Santiago Ramon y Cajal in the field of medicine.

retrograde backward

enzyme protein that controls a reaction in a cell

organelle membrane-bound cell compartment

aggregate clump together

acidic having an excess of H$^+$ ions and a low pH

macromolecules large molecules such as proteins, carbohydrates, and nucleic acids

endocrine related to the system of hormones and glands that regulate body function

hormone molecule released by one cell to influence another

constitutive at a constant rate or continually

secretion material released from the cell

model is correct, the question remains as to how the cell maintains the size, shape, and biochemical uniqueness of the Golgi complex.

One answer is **retrograde** transport or recycling of **enzymes** and molecules from one Golgi stack back to their original stacks. Each of the vesicles that travel between the ER and Golgi stacks is coated with proteins that have "addressing tags" on them. For example, the vesicle that buds off of the ER has coat proteins that specifically direct it to the cis Golgi instead of the medial Golgi or some other **organelle**. Sometimes, enzymes and proteins that reside in the ER accidentally get caught in a vesicle going to the Golgi. When this happens, they return (retrograde transport) from the cis Golgi back to the ER in a vesicle coated with different proteins that are addressed to the ER. Therefore, the Golgi has two sets of vesicles flowing in opposite directions. The first set of vesicles are filled with newly made proteins awaiting further modifications traveling in a forward or anterograde direction. The second set of vesicles are filled with enzymes and matured proteins seeking their resident organelle traveling in the reverse or retrograde direction.

The Trans-Golgi Network (TGN)

The trans-Golgi network (TGN) is an extension of the trans Golgi where different types of vesicles are formed. The TGN can be thought of as a major protein sorting station inside the cell. Proteins maturing in the Golgi are sorted in the TGN for transport to several locations in the cell depending upon the biochemical tags that are found on the individual proteins. It is thought that proteins in the TGN are concentrated by linking up with receptor molecules in the lumen of the TGN. As proteins find their proper receptors, they may **aggregate** in one or few locations within the TGN and then bud off to form immature secretory vesicles: (1) secretory granules (vesicles that undergo further maturation and sorting of specialized cargo); (2) secretory vesicles targeted to the plasma membrane; and (3) vesicles carrying degradative enzymes to lysosomes (small, **acidic** organelles that degrade **macromolecules**). Some selectivity and sorting of proteins may exist in these secretory vesicles before they get to the plasma membrane.

First, secretory vesicles are packaged with a high concentration of a specific protein that has been transported to the TGN. For example, **endocrine** cells produce large amounts of specialized proteins called **hormones** that are packaged into secretory granules. When endocrine cells receive the correct "signal" that triggers fusion of the secretory granules with the plasma membrane, these proteins are released into the circulatory system.

Second, some proteins are produced and secreted in a **constitutive** or constant manner; these proteins do not rely on extracellular signals for release and are not sorted to secretory granules. Instead, constitutive **secretion** involves vesicles originating at the TGN and traveling directly to the plasma membrane for exocytosis.

Finally, the TGN is a sorting station for the delivery of degradative enzymes to lysosomes, vesicles containing nutrients that originated outside of the cell. Cells need to target these proteins to acidic lysosomes to assist in the digestion of internalized nutrients. Proteins destined for the lysosome

have been modified with a unique sugar called mannose 6-phosphate. These lysosomal proteins are sorted in the TGN by binding to the mannose 6-phosphate receptor that then buds off in a vesicle that fuses with a lysosome. The low pH in the lysosome causes the mannose 6-phosphate bearing protein to **dissociate** from the receptor. The empty receptor buds off from the lysosome in a small vesicle and is recycled to the TGN.

The Golgi complex plays an essential role in the sorting and targeting of proteins to various parts of the cell. Despite what is known, there are still many unanswered questions concerning the exact mechanisms involved with sorting and transporting cellular cargo throughout the cell. This is an important area of investigation since many diseases such as I cell disease, Alzheimer Disease, Batten's disease, and a host of other protein and **lipid** storage diseases are a result of cells missorting protein and lipids to the wrong locations in the cell. SEE ALSO ENDOPLASMIC RETICULUM; EXOCYTOSIS; LYSOSOMES; PROTEIN STRUCTURE; PROTEIN TARGETING

Edward Harris and James Cardelli

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Grain

Grains are seeds of grasses. More particularly, the term "grains" usually refers to the cereal grains, those that are used as food or fodder by humans. Three grains—rice, wheat, and corn—are the major source of calories in the human diet throughout the world, both through direct consumption or by providing animal feed. In addition, corn is a significant source of raw materials for some segments of the chemical industry.

Like other seeds of flowering plants, grain contains both the embryo and **endosperm**. The **diploid** embryo, often called the germ, contains the tissues that develop into the new individual after germination. The **triploid** endosperm is a rich nutritive tissue formed by the fusion of a second sperm and the two nuclei of the central cell in the embryo sac. Surrounding both endosperm and embryo is the **protein**- and oil-rich aleurone layer. This layer plus several thin outer coverings and the remains of the seed coat make up the bran.

Rice

Rice (*Oryza sativa*) is grown throughout the world, but principally in the countries of Asia, where it forms the basis of the diet. Most rice is grown under flooded conditions, with fields drained two to three weeks before harvest. Removal of the hull (remnant floral parts) leaves brown rice. Further milling removes the bran and embryo to give white rice, by far the most popular form of rice. White rice is high in **carbohydrates** but low in protein or vitamins.

Both traditional breeding and genetic engineering have been used to improve the qualities of rice. In the 1960s, shorter semidwarf varieties were

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A defect in the enzyme that tags proteins with mannose 6-phosphate causes I cell disease, marked by skeletal deformities, movement difficulty, and early death.

dissociate break apart

lipid fat or waxlike molecule, insoluble in water

endosperm nutritive tissue within a seed

diploid having pairs of chromosomes in the nucleus

triploid possessing three sets of chromosomes

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

carbohydrates sugars, starches, and other molecules combining carbon, hydrogen, and oxygen and serving as fuel or structural components

A wheat harvest in Polouse Valley, Washington. Wheat is the top food crop consumed by humans.

bred. This allowed farmers to increase yields with fertilizers without having the long thin stems of full-height rice fall over before harvest. This development was a major part of the "green revolution" in the 1960s, in which grain yields kept pace with a skyrocketing world population, preventing widespread famine. More recently, genetic engineering techniques have been used to introduce a gene for a precursor of vitamin A, lacking in white rice. This so-called "golden rice" may help prevent blindness due to vitamin deficiencies, although the quantity of vitamin A available from the rice alone is insufficient by itself for this purpose.

Wheat

Wheat (*Triticum sativum*) is the top food crop consumed directly by humans. Wheat consumption is supplementing or even replacing rice and corn consumption for many people in developing countries. Wheat is grown as a cool-weather annual, with some varieties even requiring a cold period to produce grain. Wheat is less profitable on a per-acre basis than other grains, but requires comparatively little labor and fewer inputs of fertilizer and pesticide. Wheat is milled to remove the hull to give "whole wheat," which can be ground into flour. Removal of the germ and bran before grinding gives white flour. Wheat is unique among the major grains in having a high level of the protein gluten in the endosperm. The elastic gluten protein allows dough to stretch. As yeasts added to dough release gas, the gluten expands, trapping the gas bubbles and allowing the bread to rise.

Corn

Corn or maize (*Zea mays*) is a native of the New World and is grown primarily in South, Central, and North America. It still provides the major source of calories for most people south of the United States. Ancient corn was similar to modern popcorn, with a hard seed coat that trapped heated steam until the coat burst suddenly, exposing the puffy white endosperm. Traditionally, corn has been dried and ground into meal, using the entire kernel. The meal is then used for tortillas, tamales, and other foods. The entire kernel of sweet corn is also consumed, but the harvest occurs before seed maturity and before the sugars in the endosperm have been converted to starches. Removal of the seed coat leaves primarily endosperm, which is boiled to make grits, or rolled and baked to make corn flakes. Corn is a major feed for livestock, and provides the starting materials for a number of chemical products, including a variety of alcohols, acetone, polyurethane, and acetic acid.

Other Grains

Several other grains are consumed in small quantities. The handful of species of millet are consumed mainly in Africa and Asia, with U.S. use primarily for birdseed. Rye (*Secale cereale*) is used in rye breads mainly in temperate areas in the Northern Hemisphere, and oats (*Avena sativa*) are grown for breads, breakfast cereals, and animal feed in these same regions. Barley (*Hordeum vulgare*) provides the source of carbohydrate for fermentation in beer. SEE ALSO AGRICULTURE; GRASSES

Richard Robinson

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Grasses

Grasses belong to one of the largest and most economically and ecologically important families of plants: the Poaceae, formerly called the Gramineae. There are over nine thousand species of grasses recognized by botanists. Grasses can be found on every continent and in a wide variety of habitats, both as the dominant plant type (in prairies and tundra) or as minor components of the plant community. Collectively, grasses domesticated as crops represent the world's most important source of food.

Grasses share a number of characteristics that differentiate them from other plant species. They typically have long, narrow leaves. The stems may be either flattened or round, and they are often hollow. Grasses can grow very tall (tropical bamboos can reach up to 100 meters [328 feet]) or they can grow **prostrate** along the ground. The root systems of grasses are highly branched (fibrous) and do not have a well-defined central taproot. Many grasses spread horizontally through the production of underground stems known as rhizomes, or prostrate stems aboveground known as stolons. New grass shoots can emerge from either rhizomes or stolons.

prostrate face downward

Grasses have evolved in environments where drought, grazing by large herbivores, and fires were common. Unlike many plants, the growing points (or meristems) of grasses are located near the base of the plant or below the ground, rather than at the tips of the plant. This characteristic allows grass plants to be grazed or burned without damage to the growing points. Additionally, grasses have large root systems that can store substantial food reserves that allow grasses to regrow quickly if aboveground parts are removed. These features also make grasses drought resistant and ideal for lawns that are repeatedly mowed. The large and fibrous root system of grasses has additional value for preventing soil erosion.

The flowers of grasses are small and inconspicuous. Grass flowers lack petals and other floral parts common in other plant families. Grass flowers are typically wind pollinated and therefore do not produce nectar, but they do produce pollen in large amounts. Grass flowers are so simple and small that they are sometimes referred to individually as florets. Florets are typically grouped or clustered along a central axis into units known as spikelets. The arrangement of florets and spikelets varies greatly among grasses, and individual grass species are often defined by these differences. The fruit of a grass flower is termed a caryopsis or a grain.

Grasses make up many of the most important crop species grown for human consumption. Three cereal crops—corn, wheat, and rice—are the most important source of calories in all diets throughout the world. Sugarcane is a grass that supplies most of the world's sugar. Grasses, including several species of reed and bamboo, are used in many countries as construction material and as thatch for roofs, and the fiber from many grasses is used in making paper. Finally, native and planted grasslands are used worldwide in hay production and as grazing lands for animal production.
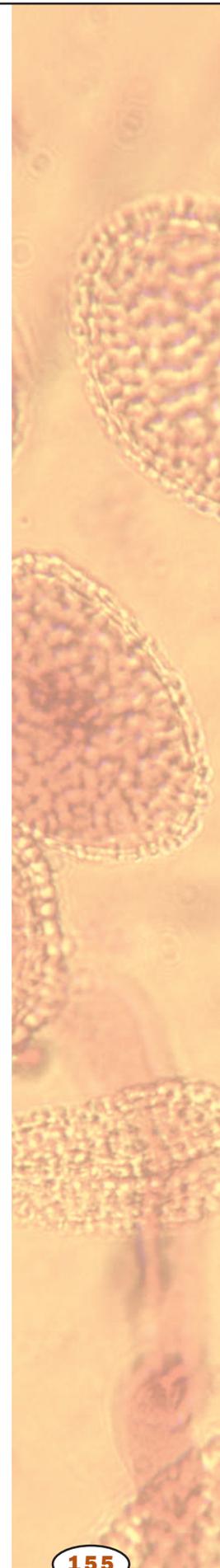
Economically Important Cereal Grasses

Global and U.S. production estimates (in millions of metric tons, 1998/1999) and the value of those crops produced in the United States (in millions of U.S. dollars, 1997). Data are from the U.S. Census Bureau and the U.S. Department of Agriculture.

	World Production	U.S. Production	Value
Corn	605.5	247.9	20,456
Wheat	588.4	69.3	8,926
Rice	394.0	5.8	1,657
Barley	136.8	7.7	799
Sorghum	59.2	13.2	1,619
Oats	26.0	2.4	—
Rye	20.3	0.3	—

As economically valuable as grasses are, the grass family, like all large plant families, also contains species that are considered pests or weeds and as such incur an economic cost. Crabgrass is a familiar example in lawns, but there are many agricultural weeds that are grasses and these consume resources meant for planted species, interfere with the harvest, and, ultimately, reduce crop yield. SEE ALSO AGRICULTURE; GRAIN; HISTORY OF AGRICULTURE; MONOCOTS

Alan K. Knapp

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Grassland

Grasslands are environments in which grasses and grasslike plants dominate the vegetation. Grasslands once covered up to 25 to 40 percent of the earth's land surface, but many of these grasslands have been plowed for crop production. Prior to the European settlement of North America, the largest grasslands in the United States stretched across the Great Plains from the Rocky Mountains and deserts of the southwestern states to the Mississippi River. Other extensive grasslands are, or were, found in Europe, South America, Asia, and Africa.

Grasslands can be categorized as temperate or tropical. Temperate grasslands have cold winters and warm to hot summers and often have deep, fertile soils. In North America, other names for temperate grasslands include prairies and steppes. Tallgrass prairies in the Midwestern United States receive the most rainfall (75 to 90 centimeters [29.5 to 35 inches]) and are the most productive grasslands with grasses growing to 3 meters (almost 10 feet) in height. Historically, these were most abundant in Iowa, Illinois, Minnesota, and Kansas.

A Montana grassland. Temperate grasslands—also known as prairies—have cold winters and warm to hot summers.

The driest grasslands (25 to 35 centimeters [9.8 to 13.7 inches] of rainfall) are termed shortgrass prairie, or steppe, with grasses seldom taller than 25 centimeters. These grasslands are found in Texas, Colorado, Wyoming, and New Mexico. Temperate grasslands are also called steppes in most of Europe and Asia, veld in Africa, and the pampas in South America.

Tropical grasslands are warm throughout the year but have pronounced wet and dry seasons with annual rainfall amounts of 50 to 130 centimeters (19.6 to 51 inches). Most tropical grasslands have a greater density of woody shrubs and trees than temperate grasslands. Other names for tropical grasslands include velds in Africa, and the compos and llanos in South America.

Grass-dominated **ecosystems** that contain a significant number of widely spaced trees are termed **savannas**. Trees may cover 5 to 30 percent of savanna landscapes, but grasses form a continuous ground cover. Africa, Australia, and South America have extensive savannas.

ecosystem an ecological community and its environment

savanna open grassland with sparse trees

Fire, drought, and herds of large grazing animals are common features in most grasslands, and most plant and animal life is well adapted to these forces. Fires are most common in grasslands with high levels of plant productivity. Fires are important for keeping trees from encroaching into grasslands—many tree species are killed by fire because their active growing parts are aboveground. Grassland plants survive and even thrive after fire because their buds are below the ground and protected from lethal temperatures. Typically, grassland animals are not harmed by fire. Those animals living below the ground are well protected, and most grassland birds and mammals are mobile enough to avoid direct contact with fire.

Years of extreme drought are more common in grassland than in forested areas, and such droughts may kill even mature trees. But grasses and other grassland plants have extensive root systems that help them survive drought periods. The most conspicuous animals in grasslands are large grazers such as bison and antelope in North America and zebras, gazelles, and wildebeest in Africa. Grasshoppers also can be important consumers of plants, but **nematodes** (roundworms) and root-feeding invertebrates below the ground

nematode worm of the Nematoda phylum, many of which are parasitic
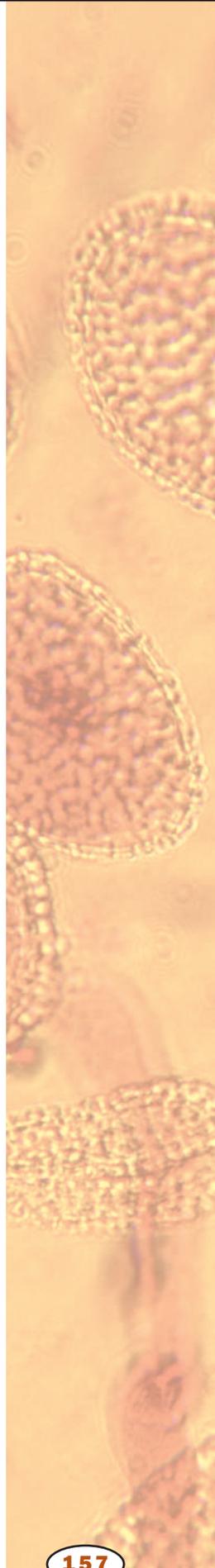
are actually the most significant consumers of plant biomass in many grasslands. SEE ALSO BIOME; TUNDRA

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Gray, Asa

American botanist
1810–1888

Asa Gray was one of the central figures in American botany in the nineteenth century. Through his writing, teaching, collection, and correspondence, he had a major influence on the study of plants in the United States. Born in New York, Gray earned a medical degree before going to work for the famed American botanist John Torrey in 1833. By 1843 Torrey and Gray had published two volumes of the *Flora of North America*. A planned third volume was never completed. During this time Gray traveled extensively in Europe, where he met with Charles Darwin. Gray later became an important proponent of Darwin's ideas in the United States. In 1842 Gray became a professor at Harvard University, founding an **herbarium** there that still bears his name. Gray worked at a time when the American West was being explored systematically, and through his correspondence with collectors he greatly influenced where and how plants were collected, and how the information gleaned was used and disseminated. His prolific writings from this period include *Manual of Botany of the Northern United States*, a highly popular textbook *Elements of Botany*, and the first half of *Synoptical Flora of North America*, which was completed by others after Gray died. SEE ALSO TORREY, JOHN

Richard Robinson

herbarium a collection of dried plant specimens systematically arranged for reference

Growth

Growth implies development, from the time of emergence or birth to the time of maturity and for many species, beyond maturity to eventual senescence or death. Growth also implies increase in size resulting from cell multiplication and cell expansion, as well as maturation of tissues. However, growth, while accentuating increased cell number and size, also necessitates programmed cell death, leading to the production of the final body form. Thus, growth is an incredibly complex phenomenon, which involves changes in body form, **metabolism**, and body processes.

metabolism chemical reactions within a cell

Patterns of Growth

In most animals, the growth pattern follows an S-shaped curve. Slow early growth occurs from first emergence, or birth, which is followed by a long

phase of rapid increase in body mass and maturation of organs, especially structural or **somatic** tissue that support the individual, up to about the time of puberty or reproductive maturity. Finally, growth slows, and in some species stops altogether after reproductive maturation. In many animals and most plants, however, growth continues throughout life, so that the oldest individuals in the population are generally the largest.

In many animals, young emerge looking like miniature adults, and gradually enlarge throughout their lifetime, going through alternating stages of rapid growth and plateaus. In contrast, in some vertebrate as well as many invertebrate species, the young emerge looking completely different from the adults and spend their early lives acquiring body mass as a larva, then go through a **metamorphosis** (complete rearrangement of body pattern) to emerge in the adult form. This is typical of some insects, such as butterflies and moths, and some amphibians, such as frogs.

In birds and mammals, young generally emerge looking vaguely like adults, but the body proportions are very different, characterized by an enlarged head and reduced supportive limb elements. During the rapid growth phase of these individuals, the head grows much less than the body, limbs elongate, and skin maturation results in the typical adult feather or fur patterns. Since young birds and mammals are usually dependent on their parents for a time after birth, the incomplete development at birth is not a disadvantage.

The pattern of human growth provides a good example of the change in body proportions throughout development from birth to adult (the ultimate size of the individual). At two months past conception, the head of the embryo makes up approximately 50 percent of its total length, and the limbs less than 25 percent. At birth, the head size makes up about 25 percent of the total length and the limbs approximately 37 percent. Throughout childhood, the head size to limb length ratio continues to decrease toward the adult pattern of head size about 12 percent of body length and limb size over 50 percent of body length.

Bone Growth

The increase in body size is supported by increased skeletal structure in vertebrates, as a soft and pliable cartilage **matrix** becomes invested with hard and resistive bone. In the early newborn, the cartilage model of the eventual skeletal structure serves as the **template** for bone deposition. Bone-forming cells called osteoblasts lay down a "collar" of calcium and phosphate crystals in a lattice matrix around the shaft of the cartilage. This provides the strength for the bone to bear weight. At the same time, the terminal ends of the cartilaginous model also develop centers of osteoblastic activity, called epiphyses (singular, epiphysis). As the bone elongates, the collar elongates and the epiphyses in the ends of the bones continue to deposit calcium and phosphate. Eventually, the cartilage between these two bony centers of ossification, called the epiphyseal plate, is completely replaced with the bony matrix, and growth (limb elongation) ceases.

The epiphyseal plate is maintained under the influence of a **hormone** from the pituitary gland (the master **endocrine** gland at the base of the brain) called growth hormone (GH). However, at puberty, the hormones

In birds and mammals, the young emerge looking vaguely like adults, but with different body proportions.

somatic nonreproductive; not an egg or sperm

metamorphosis development process that includes a larval stage with a different form from the adult

matrix a network, usually of threadlike fibers

template master copy

hormone molecule released by one cell to influence another

endocrine related to the system of hormones and glands that regulate body function
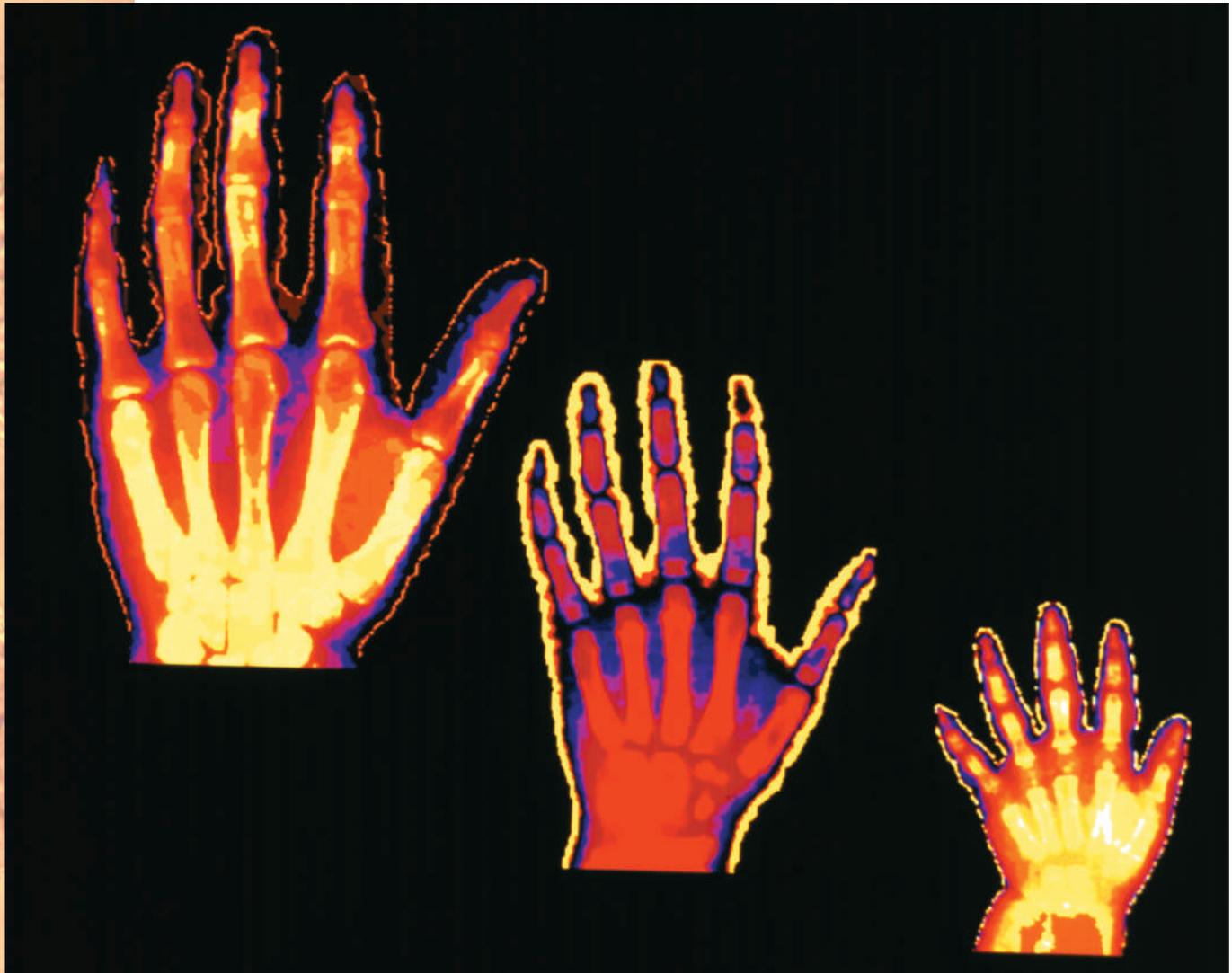
Computer color-enhanced X ray depicting the hand development of a two, six, and nineteen year old male.

associated with reproductive maturity (estrogen and testosterone) cause an initial surge in GH release and in elongation of limbs, and then cause closure of the epiphyseal plate, causing growth to cease. This "growth spurt" tends to happen earlier in human females than in human males.

Hormonal Control

Growth hormone is essential to normal growth and development. It is regulated by two hormones released from the brain (in the hypothalamus) which cause daily peaks of GH in the blood. The peaks are most closely associated with the sleep cycle, large peaks appearing right after going to sleep and right before waking. Since growth hormone is associated not only with growth and differentiation but also tissue maintenance and repair, it makes sense that the peak of GH activity would occur during the nonactive period. In fact, the hypothalamic hormone that induces the release of GH (GH-releasing hormone) is a sleep inducer. Some researchers have suggested that the disappearance of deep sleep as we age and associated reduction of GH release may contribute to the physical decline that humans experience in old age.

GH represents about one-half the total hormone content of the **anterior** pituitary gland. GH stimulates the absorption of **amino acids** and **protein** synthesis necessary for development of skeletal muscle; stimulates breakdown of fat for energy utilization by cells of the body; stimulates the formation and maintenance of the epiphyseal plate in bone, and encourages lengthening of the long bones by stimulation of osteoblast cellular deposition of bone; and it stimulates the liver to make growth stimulating proteins, called insulin-like growth factors (IGF), which then affect the cellular metabolism of all cells in the body.

anterior toward the front

amino acid a building block of protein

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

Growth Disorders

Abnormal **secretion** of GH can lead to growth disorders. Oversecretion of GH can lead to gigantism, marked by extreme limb elongation especially in the terminal elements (hands and feet) and enlargement of the face, especially the chin, nose, and ears, a condition called *acromegaly* . This condition can occur either because of a tumor of specific cells that manufacture GH or GH-like proteins or because of insufficient regulation by the hypothalamic releasing factors that control GH release. Not only are body proportions distorted with acromegaly, but **hypersecretion** of GH causes excessive sweating and secretion by the skin, enlargement of the heart, and sometimes high blood pressure. As a result of the many physiological effects of excessive GH secretion, life expectancy is shortened.

secretion material released from the cell

hypersecretion excess secretion

In contrast, lack of sufficient GH, especially during early years of development, can produce short stature or dwarfism. However, short stature with normal body proportions can be found throughout the human population and is probably associated with deficient production of IGF from the liver. For example, African pygmies are short, but normally proportioned people who have normal GH levels, but exhibit low levels of one form of IGF. Low GH release after birth can result in retarded growth, and these individuals are at risk for hypoglycemia (low blood sugar) as well. This condition severely impairs normal development, and these individuals are not only short but exhibit greatly retarded maturation of all tissues. SEE ALSO BONE; DEVELOPMENT; FETAL DEVELOPMENT, HUMAN; HYPOTHALAMUS; INSECT; PITUITARY GLAND; SCALING.

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Gymnosperms

Gymnosperms are a group of plants that share one common characteristic: they bear seeds, but their seeds do not develop within an ovary. For this reason, gymnosperms were long thought to be an evolutionary precursor to the angiosperms, which are seed plants that enclose their seeds in an ovary and that are vastly more diverse than gymnosperms. Studies of their de-

A cycad. Most cycads superficially resemble ferns, but they differ in that they develop distinctive male and female cones.

oxyribonucleic acid (DNA) has shown that the gymnosperms consist of four major, related groups: conifers, cycads, ginkgo, and gnetophytes.

Conifers

With approximately 588 living species, this is the most diverse and by far the most ecologically and economically important gymnosperm group. Conifers grow in all climate zones and on all continents except Antarctica. They all bear their seeds within a cone or a structure **superficially** resembling a berry (true berries only exist among angiosperms). Most conifers are trees. Conifers appeared in the fossil record about 290 million years ago and have been an ecologically important, widespread group ever since then.

superficially on the surface; not deep

Cycads

The 220 species of cycads are widely distributed through the tropical and subtropical regions. Most of them superficially resemble ferns, having a cluster of long **pinnate** (rarely bipinnate) fronds growing from a central stalk, but they differ in developing distinctive male and female cones. Cycads are

pinnate featherlike

woody, long-lived, unisexual plants. All species have **coralloid** roots, which support symbiotic cyanobacteria that can fix atmospheric nitrogen. The cycads and ginkgo are unique among seed plants in having **motile** sperm; this is often taken as evidence of their evolutionary primitiveness. Cycads appeared in the fossil record about 230 million years ago and attained their greatest ecological importance during the Jurassic period, about 193 million to 136 million years ago, when they formed extensive forests.

coralloid resembling coral

motile able to move

Ginkgo

There is one surviving species of ginkgo. It is a tree, sometimes attaining large size, native to China but widely planted around the world. Ginkgo is often referred to as a "living fossil" because nearly identical plants are known from fossils nearly 200 million years old. The fossil record shows that they were formerly a widespread, abundant, and diverse group.

Gnetophytes

The gnetophytes are one of the most peculiar plant groups. They include three highly distinct groups totaling 68 species. One group, the genus *Ephedra*, is composed of shrubs native to deserts and semiarid areas. The second group, the genus *Gnetum*, is composed of climbing vines (and one tree species) native to tropical rainforests. The third group contains a single species, *Welwitschia mirabilis*. It lives in the desert of Southwest Africa, produces two leaves that grow throughout the life of plant, and lives an estimated two thousand years. Although the fossil record is virtually nonexistent, studies suggest that the Gnetales are a relatively young group that evolved from the angiosperms and thus are unrelated to the other gymnosperms. SEE ALSO CONIFERS; CYANOBACTERIA; NITROGEN FIXATION; PLANT

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Habitat

In its simplest sense, a habitat is where an organism lives and thus is a concrete physical location like a stand of trees or a pool of water. A broader concept of habitat encompasses the general set of living and nonliving features typical of a particular environment, for example, "desert habitat" or "coral reef habitat."

Ecologists can measure environmental conditions where a species normally occurs to define its habitat more rigorously. Appropriate habitat can be defined in terms of its temperature regime, the availability of light and water, the chemical environment (acidity, salinity), and the strength of physical forces (waves, wind). Species can vary substantially in the suite of

environmental conditions that they tolerate and can be classified as flexible habitat generalists or narrow habitat specialists.

Ecologist G. Evelyn Hutchinson developed the related concept of the species **niche**, which is a "living space" delineated by the entire range of environmental conditions that an organism can tolerate and by all the resources it requires for survival, growth, and reproduction. The niche of a species is where it lives and what it does. A cactus, tarantula, and roadrunner may share a common desert habitat, but each occupies a unique niche. SEE ALSO BIOME; COMMUNITY; ECOLOGY; ECOSYSTEM

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niche way an organism uses its environment

Hardy-Weinberg Equilibrium

The Hardy-Weinberg equilibrium is the fundamental concept in population genetics (the study of genetics in a defined group). It is a mathematical equation describing the distribution and expression of **alleles** (forms of a gene) in a population, and it expresses the conditions under which allele frequencies are expected to change.

allele a particular form of a gene

Mendelian genetics demonstrated that the phenotypic (observable) expression of some traits is based on a simple dominant-recessive relationship between the alleles coding for the trait. In Mendel's original work for instance, green pea pods were dominant to yellow pods, meaning that a heterozygote (an individual with one allele for green and one for yellow) would show the green trait. (A common misunderstanding is that a dominant allele should also be common. This is not the case. Frequency of an allele in a population is independent of its dominance or recessiveness. Either type of allele may be common or rare.)

Allele Frequencies

A significant question in population genetics, therefore, is determining the frequency of the dominant and recessive alleles in a population (for example, the frequency of blood type O allele in the United States), given the frequency of the **phenotypes**. Note that phenotypic and allelic frequencies are related but are not equal. Heterozygotes show the dominant phenotype, but carry a recessive allele. Therefore, the frequency for the recessive allele is higher than the frequency of the recessive phenotype.

phenotype observable characteristics of an organism

Early in the twentieth century mathematician Godfrey Hardy and physician Wilhelm Weinberg independently developed a model describing the relationship between the frequency of the dominant and recessive alleles (hereafter, p and q) in a population. They reasoned that the combined frequencies of p and q must equal 1, since together they represent all the alleles for that trait in the population:

$$p + q = 1$$

Hardy and Weinberg represented random mating in the population as the product $(p + q)(p + q)$, which can be expanded to $p^2 + 2pq + q^2$. This

corresponds to the biological fact that, as a result of mating, some new individuals have two p alleles, some one p and one q, and some two q alleles. P^2 then represents the fraction of the population that is **homozygous** dominant while $2pq$ and q^2 represent the **heterozygous** and homozygous recessive fractions, respectively.

Mathematically, since $p + q = 1$, $(p + q)^2$ must also equal 1, and so:

$$p^2 + 2pq + q^2 = 1$$

The usefulness of this final form is that q^2, the fraction of the population that is homozygous recessive, can be determined with relative ease, and from that value all of the other frequencies can be calculated. For instance, if 1 percent of the population is found to be homozygous recessive, $q2 = 0.01$, then $q = 0.1$, $p = 0.9$, $p^2 = 0.81$, and $2pq = 0.09$.

One value of the Hardy-Weinberg equilibrium equation is that it allows population geneticists to determine the proportion of each genotype and phenotype in a population. This may be useful for genetic counseling in the case of a genetic disease, for example, or for measuring the genetic diversity in a population of endangered animals.

Implications for Evolution

A significant implication of the Hardy-Weinberg relationship is that the frequency of the dominant and recessive alleles will remain unchanged from one generation to the next, given certain conditions. These conditions are: (1) a sufficiently large population to eliminate change due to chance alone; (2) random mating (the phenotypic trait being examined cannot play a role in mate selection); (3) no migration of individuals either into or out of the population under study; (4) the genes under consideration are not subject to mutational change; and (5) the dominant or recessive phenotype must not have an adaptive advantage; in other words natural selection must not be favoring one trait over another.

If any of these constraints are not satisfied then the Hardy-Weinberg equilibrium does not hold true. When a population geneticist finds a change in allele frequency over time, therefore, he or she may be confident that one or more of these factors is at work. In fact, one definition of evolution is a change in allele frequencies over time.

J. B. S. Haldane was the first person to adapt the Hardy-Weinberg relationship to model evolutionary change. He introduced a selection coefficient to represent a disadvantage for the homozygous recessive. His equation was later shown to successfully model the impact of industrial pollution on peppered moths in England. SEE ALSO ADAPTATION; EVOLUTION; GENETIC DISEASES; NATURAL SELECTION; POPULATION GENETICS

William P. Wall

homozygous containing two identical copies of a particular gene

heterozygous characterized by possession of two different forms (alleles) of a particular gene

DOBZHANSKY, THEODOSIUS (1900–1975)

Dobzhansky is a Ukrainian-born U.S. biologist and author who showed that ongoing change in gene frequencies in natural populations was the rule, not the exception. He also showed that individuals with two different versions of the same gene ("heterozygotes") could be better adapted than individuals with identical copies of a gene ("homozygotes").

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Harvey, William

English physician and physiologist
1578–1657

William Harvey (right) with Charles I (seated, left).

William Harvey was an English physician, a pioneer in the study of blood circulation and embryology, and the founder of experimental physiology. Educated in Cambridge, England, and Padua, Italy, he practiced medicine in London and was court physician to King James I and King Charles I.

The Roman physician Galen (129–c. 199 C.E.) had argued that the liver received food from the small intestine and converted it to blood, the heart pumped this blood to the other organs, and those organs consumed it. Harvey, refusing to accept this, measured the amount of blood pumped by the hearts of snakes and other animals. He concluded that (1) the heart pumps more blood in half an hour than there is in the entire body; (2) animals do not consume enough food to account for so much blood; and (3) the blood must be continually recirculated around the body, since the planets orbit the Sun and (he believed) the human body is modeled after the solar system. So for a mixture of scientific and superstitious reasons, Harvey correctly deduced that after blood leaves the heart it returns there rather than being consumed. He predicted that there must be a connection between the arteries and veins so blood could get back to the heart. Such connections, the capillaries, were first seen by Antony van Leeuwenhoek and Marcello Malpighi after Harvey's death.

Harvey published his conclusions in the book *Anatomical Studies on the Motion of the Heart and Blood in Animals* (a translation of its Latin title) in 1628. Harvey's contemporaries were so wedded to the ancient beliefs of Aristotle and Galen, however, that they ridiculed his conclusions. How could the blood serve any purpose, they argued, if the organs did not consume it? Harvey's reputation survived this skepticism, however, and he went on to do important work in embryology.

Harvey was forced to flee for his life in 1642, and his home was ransacked and his records destroyed in a rebellion against the British monarchy that ended with the beheading of his patron, King Charles. Depressed by this turn of events, Harvey gave up his medical practice and retired to the countryside. Nevertheless, at the urging of friends, he resumed work. Harvey rejected the belief that animals can arise from decaying flesh, and argued that every animal, including humans, arises from the union of sperm and egg. In 1651 he published this theory of animal development, with a detailed account of the embryology of the chick, as *Studies on the Generation of Animals.* The frontispiece of his book bore the inscription *ex ovo omnia*—everything [comes] from an egg.

Harvey died of a stroke in 1657, honored by his country and wealthy from the income on his books. SEE ALSO BLOOD VESSELS; CIRCULATORY SYSTEMS; HEART AND CIRCULATION; HISTORY OF MEDICINE

Kenneth S. Saladin

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Health

For many years, health was defined merely as the absence of disease. However, it has become clear that health is an active process that depends on the supportive interaction of all the body's systems. Reflecting this concept, the World Health Organization (WHO) defines health as "the state of complete physical, mental, and social well-being and not merely the absence of disease or infirmity." Many groups, such as the American Public Health Association, Worksite Health Promotion, and the National Wellness Association, have expanded the concept of health further to encompass wellness: the spiritual, social, mental, physical, and occupational needs for one to live life to the fullest.

The World Health Organization defines health as "the state of complete physical, mental, and social well-being and not merely the absence of disease or infirmity."

In either sense, health is a state of action that includes prevention, care, and individual responsibility to achieve optimal health. The U.S. Department of Health and Human Services (HHS), in *Healthy People 2010,* divides the ten leading factors affecting health into two major themes. The first, lifestyle challenges, includes physical activity, avoidance of excess weight and obesity, abstinence from tobacco use or substance abuse, and responsible sexual behavior. The second, system enhancement challenges, include mental health, freedom from injury and violence, good environmental quality, immunization, and equal access to health care.

Homeostasis

The state of health reflects the body's homeostasis, its attempt to maintain a relatively stable internal environment while confronted with changes in the external environment. One's ability to handle stress depends on the body's success in maintaining or returning to homeostasis. Failure to do so can result in abnormal function and disease.

Homeostasis involves negative **feedback** systems. The analogy to home heating and cooling systems is often made. When a house falls below a certain temperature, the system turns on to heat the house back to the set level. If it gets too warm, another system effects a change to cool the home off. Similarly, the human body senses changes from ideal conditions in variables, such as blood **glucose**, dehydration, blood calcium, carbon dioxide, heart rate, breathing rate, and fat deposition. The body also detects the presence of **pathogens** that alter homeostasis. When such factors disturb homeostasis, the body releases substances such as **hormones**, **neurotransmitters**, and antibodies to return conditions to normal.

Why is health important? The WHO states that it is fundamental to world peace and security as political strife can stem from inadequate food, medicine, or other resources. For the United States and other industrialized nations, the large increase in the older population calls for strategies to increase the number of quality years as people age. Living longer is not a positive goal if it means living longer with disease. HHS has made this one of two major goals in *Healthy People 2010.* The other is to eliminate disparities in health based on race or ethnicity. Too many segments of American society are not reaping the benefits from advances in medicine, technology, and health care.

Individual choices are important to health outcomes. Preventive medicine includes stress reduction, good nutrition, exercise, wearing seat belts and helmets, and having routine dental and physical screenings (for cholesterol level and blood pressure, for example). As science progresses in genetic engineering, important choices will be made about changing genes, thus altering the inheritance of many diseases. SEE ALSO ALCOHOL AND HEALTH; CARDIOVASCULAR DISEASES; DISEASE; ENVIRONMENTAL HEALTH; HISTORY OF MEDICINE; HOMEOSTASIS; PUBLIC HEALTH CAREERS; SEXUALLY TRANSMITTED DISEASES; SMOKING AND HEALTH

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feedback process in which the output or result influences the rate of the process

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

pathogen disease-causing organism

hormone molecule released by one cell to influence another

neurotransmitters molecules released by one neuron to stimulate or inhibit another neuron or cell

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The National Institutes of Health (NIH) is one of eight health agencies of the U.S. Public Health Service. The NIH was founded in 1887 with the goal to acquire new knowledge to help prevent, detect, diagnose, and treat diseases and disabilities. As one of the world's foremost medical research centers, the NIH conducts research, supports research elsewhere, helps train researchers, and fosters communication about medical and health sciences information.

Health and Safety Officer

Most companies, universities, and academic medical centers employ a health and safety officer (HSO). The HSO promotes the health and safety of employees and is in charge of the company's formal health and safety program. The HSO writes policies and procedures that the company and its employees must follow to assure a safe work environment. The program is based on state and federal regulations but may be stricter. Work includes measuring hazardous agents, observing workers accomplish their tasks, and making recommendations on ways to reduce injuries. Measurements may include chemicals in laboratory air, noise levels in production areas, and levels of radiation in facilities that use radiation or radioactive substances.

The HSO often observes workers to determine causes of injuries and recommends ways to avoid injuries or exposure to hazardous materials. The HSO provides personal protective equipment for eye and hearing protection, requires machine guards to prevent injuries, and requires protective clothing to guard against chemicals and bacteria. Sometimes the HSO works with a physician to determine the cause of a worker's illness. The HSO at a small company often has a biology or engineering background (depending on the company and hazards to employees). Usually a bachelor of science (B.S.) degree and a few years of experience in health and safety are adequate. Large companies and organizations often require formal graduate training in safety and certification, for example a Certified Safety Professional. The HSO at a large company often has a B.S. degree in a biological or physical science, plus a master's degree or doctorate, depending on the needs of the company. The best way to prepare to become an HSO is to obtain a B.S. degree in science or engineering and a graduate degree in a safety discipline such as safety engineering or industrial hygiene. SEE ALSO EPIDEMIOLOGIST

Richard J. Vetter

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Hearing

Hearing is the process by which humans, using ears, detect and perceive sounds. Sounds are pressure waves transmitted through some medium, usually air or water. Sound waves are characterized by frequency (measured in cycles per second, cps, or hertz, Hz) and amplitude, the size of the waves. Low-frequency waves produce low-pitched sounds (such as the rumbling sounds of distant thunder) and high-frequency waves produce high-pitched sounds (such as a mouse squeak). Sounds audible to most humans range from as low as 20 Hz to as high as 20,000 Hz in a young child (the upper range especially decreases with age). Loudness is measured in decibels (dB), a measure of the energy content or power of the waves proportional to amplitude. The decibel scale begins at 0 for the lowest audible sound, and increases logarithmically, meaning that a sound of 80 db is not just twice as loud as a sound of 40 db, but has 10,000 times more power! Sounds of 100
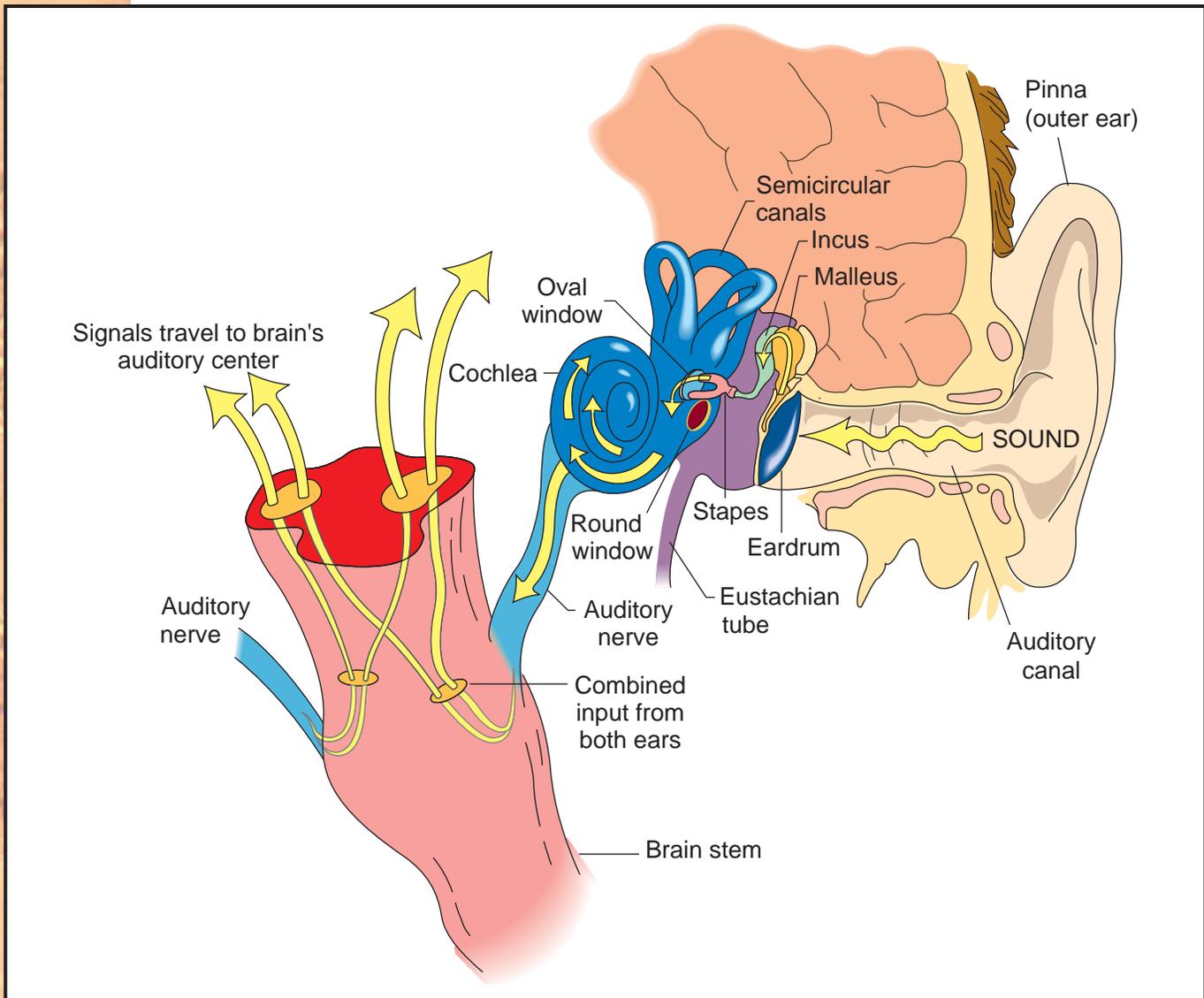
Anatomy of the human ear and the hearing process.

db are so intense that they can severely damage the inner ear, as many jackhammer operators and rock stars have discovered.

The ear is a complex sensory organ, divided into three parts: external (outer) ear, middle ear, and inner ear. The outer and middle ear help to protect and maintain optimal conditions for the hearing process and to direct the sound stimuli to the actual sensory receptors, hair cells, located in the cochlea of the inner ear.

Outer Ear and Middle Ear

The most visible part of the ear is the pinna, one of two external ear structures. Its elastic cartilage framework provides flexible protection while collecting sound waves from the air (much like a funnel or satellite dish); the intricate pattern of folds helps prevent the occasional flying insect or other particulate matter from entering the ear canal, the other external ear component. The ear (auditory) canal directs the sound to the delicate eardrum (tympanic membrane), the boundary between external and middle ear. The

ear canal has many small hairs and is lined by cells that secrete ear wax (cerumen), another defense to keep the canal free of material that might block the sound or damage the delicate tympanic membrane.

The middle ear contains small bones (auditory ossicles) that transmit sound waves from the eardrum to inner ear. When the sound causes the eardrum to vibrate, the malleus (hammer) on the inside of the eardrum moves accordingly, pushing on the incus (anvil), which sends the movements to the stapes (stirrup), which in turn pushes on fluid in the inner ear, through an opening in the cochlea called the oval window. Small muscles attached to these ossicles prevent their excessive vibration and protect the cochlea from damage when a loud sound is detected (or anticipated). Another important middle ear structure is the auditory (eustachian) tube, which connects the middle ear to the pharynx (throat). For hearing to work properly, the pressure on both sides of the eardrum must be equal; otherwise, the tight drum would not vibrate. Therefore, the middle ear must be connected to the outside.

Sometimes, when there are sudden changes in air pressure, the pressure difference impairs hearing and causes pain. In babies and many young people, fluid often builds up in the middle ear and pushes on the eardrum. The stagnant fluids can also promote a bacterial infection of the middle ear, called otitis media (OM). OM also occurs when upper respiratory infections (colds and sore throats) travel to the middle ear by way of the auditory tube. Sometimes the pressure can be relieved only by inserting drainage tubes in the eardrum.

Inner Ear

The inner ear contains the vestibule, for the sense of balance and equilibrium, and the cochlea, which converts the sound pressure waves to electrical impulses that are sent to the brain. The cochlea is divided into three chambers, or ducts. The cochlear duct contains the hair cells that detect sound. It is sandwiched between the tympanic and vestibular ducts, which are interconnected at the tip. These ducts form a spiral, giving the cochlea a snail shell appearance. Inside the cochlear duct, the hair cells are anchored on the basilar membrane, which forms the roof of the vestibular duct. The tips of the hair cells are in contact with the tectorial membrane, which forms a sort of awning. When the stapes pushes on the fluid of the inner ear, it creates pressure waves in the fluid of the tympanic and vestibular ducts (like kicking the side of a wading pool). These waves push the basilar membrane up and down, which then pushes the hair cells against the tectorial membrane, bending the "hairs" (stereocilia). When stereocilia are bent, the hair cell is excited, creating impulses that are transmitted to the brain.

How does the cochlea differentiate between sounds of different pitches and intensities? Pitch discrimination results from the fact that the basilar membrane has different vibrational properties along its length, such that the base (nearest the oval window) vibrates most strongly to high frequency sounds, and the tip to low frequencies. The hair cells along the length of the cochlea each make their own connection to the brain, just like the keys on an electric piano are each wired for a certain note. Loud (high-amplitude) sounds cause the basilar membrane to vibrate more vigorously than soft

(low-amplitude) sounds. The brain thus distinguishes loud from soft sounds by differences in the intensity of nerve signaling from the cochlea.

Hair cells themselves do not make the impulses that are transmitted to the **central nervous system** (CNS); they stimulate nerve fibers to which they are connected. These nerve fibers form the cochlear branch of the eighth **cranial** (vestibulocochlear) nerve. In the CNS, the information is transmitted both to the brainstem, which controls reflex activity, and to the auditory cortex, where perception and interpretation of the sound occur. By comparing inputs from two ears, the brain can interpret the timing of sounds from right and left to determine the location of the sound source. This is called binaural hearing. SEE ALSO BRAIN; NEURON

Harold J. Grau

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central nervous system brain and spinal cord

cranial related to the cranium, or brain cavity

Heart and Circulation

"It is absolutely necessary to conclude that the blood in the animal body is impelled in a circle, and is in a state of ceaseless motion; that this is the act or function which the heart performs by means of its pulse." William Harvey's description of the circulation of the blood and the motive force of the heart in *de Motu Cordis* (1628) is considered the beginning of modern physiology. In the adult human body, the heart beats about 70 times per minute, or approximately 100,000 beats per day. During exercise or intense emotion the human heart rate can increase to 200 beats per minute. Thus, in a life span of seventy-five years, with everyday stresses and emotions, a human heart may beat more than 3 billion times.

The heart pumps approximately 100 milliliters per beat. In seventy-five years, this amounts to 300 million liters of blood. The pumping action of the heart and the changes in its activity in response to body needs are necessary for life, so much so that up to one-third of all deaths in the United States result from heart disease.

In humans and other mammals, the heart consists of two pumps. The right side of the heart pumps blood to the lungs, where the blood is oxygenated and then returns to the heart. This circuit is called the pulmonary circulation. The left side of the heart receives oxygenated blood from the lungs and pumps it to the rest of the body. Then, as was first described by Harvey in 1628, blood is pumped throughout the body and returns to the heart, to be pumped again to the lungs. The circuit of blood from the left side of the heart, to the periphery, and then back to the heart is known as the **systemic** circulation.

Contraction of the heart underlies its pumping action. Most heart cells are muscle cells. Contraction of the muscle cells and coordination of their pumping action is controlled by electrical activity in the heart cells.

systemic throughout the body

Left common carotid artery

Left subclavian artery

Brachiocephalic trunk

Superior vena acva

Aorta

Right pulmonary artery

Trunk of left pulmonary artery

Right pulmonary veins

Left pulmonary veins

Left atrium

Semilunar valve

Semilunar valve

Atrioventricular valve

Left ventricle

Atrioventricular valve

Right ventricle

Septum

Apex of heart

Inferior vena cava

Oxygen-rich blood to the body

Oxygen-rich blood from the lungs

Oxygen-poor blood to the lungs

Oxygen-poor blood from the upper part of the body

oxygen-poor blood from the lower part of the body

ventricles relaxed

ventricles contracted

Heart Structure

Anatomy of the human heart.

The heart is located in a lubricated sac (the pericardium) in the left center of the thorax (chest). Blood returning from the body enters the right side of the heart from the superior vena cava, which carries blood from the head and other parts of the body above the heart, and the inferior vena cava, which carries blood from parts of the body below the heart. These veins merge as they enter the upper chamber on the right side of the heart, the right atrium, which acts as a "receiving room" for blood entering the heart.

ventricle lower chamber of the heart

Blood in the right atrium flows into the right **ventricle**, the lower chamber on the right side of the heart, through the tricuspid valve, a one-way valve.

The tricuspid valve allows blood to flow into the right ventricle but prevents its return to the right atrium when the ventricle contracts. Instead, ventricular contraction pumps blood out through another one-way valve, the pulmonary valve, into the pulmonary artery, which carries blood to the lungs. All of the blood that is pumped to the lungs by the right side of the heart returns to the heart through four pulmonary veins that empty into the upper chamber on the left side of the heart, the left atrium.

From the left atrium, blood flows into the lower chamber on the left side of the heart, the left ventricle, through another one-way valve, the mitral valve. Similar in function to the tricuspid valve on the right side, the mitral valve prevents blood from reentering the left atrium and pulmonary veins when the ventricle contracts. Contraction of the left ventricle pumps blood out of the heart through the one-way aortic valve, into the largest artery of the body, the aorta. As the aorta curves over the top of the heart, large arteries branch off to the head, arms, and upper thorax.

The aorta descends through the lower part of the thorax and abdomen, where arteries branch off carrying blood to the liver, spleen, intestine, kidneys, gonads, and legs. After passing through smaller arteries and then capillaries, the blood returns to the heart through the veins. Also branching off the aorta as it leaves the heart is a pair of coronary arteries. These arteries supply blood to the heart and are considered part of the systemic circulation. After passing through capillaries in the heart, blood in the coronary circuit returns to the right side of the heart through veins that empty directly into the right atrium. Heart attacks are caused by clots in coronary arteries, depriving the heart muscle of oxygen.

The Cardiac Cycle

When the heart is relaxed, blood pressure in the veins is higher than the **atria**, which in turn are higher than the pressures in the ventricles. Hence, blood flows from the veins into the atria and from the atria into the ventricles.

atria two upper chambers of the heart (singular, atrium)

Contraction of the heart (systole) begins first with the atria. As atria contract on both sides of the heart, atrial pressures increase, pushing more blood into the ventricles; however, after a delay of about 0.1 second, the ventricles begin to contract. When the blood pressure in the ventricles becomes greater than in the atria, the tricuspid and mitral valves close. Contraction continues, increasing pressure in the ventricles still further until it exceeds the blood pressure in the exit artery (the pulmonary artery for the right side, the aorta for the left side), at which point the arterial valves open, and blood flows into the arteries.

As contraction of ventricles continues, blood pressure in the pulmonary artery and aorta reaches a maximum, the systolic blood pressure. Blood pressure then falls slowly as blood flows away from the heart into the lungs and periphery, respectively. Diastole begins when the heart relaxes, and the blood pressure continues to fall. The lowest blood pressure reached in the arteries before the next contraction is the diastolic pressure. For a healthy young adult, an aortic systolic pressure of 120 mil-

limeters of mercury (mm Hg) and a diastolic pressure of 70 mm Hg are normal. Since blood pressures in the aorta and the arteries in the arm are approximately the same, measurement of blood pressure using an arm cuff is a reasonably accurate method of estimating the aortic systolic and diastolic blood pressures. Pressures in the pulmonary circulation are lower than in the systemic circulation.

Electrical Activity

Contraction of heart muscle cells is caused by the movement of **ions** into and out of the muscle cells. This movement of ions is an electric current that can be observed by placing electrodes on the skin. Measurement of the electrical activity of the heart is known as an electrocardiogram.

ion an electrically charged particle

The inside of relaxed muscle cells is negatively charged. When channels permeable to sodium open up, sodium rushes into heart muscle cells, making the inside more positive. This causes calcium channels to open, and calcium rushes in. Calcium causes contractile **proteins** (actin and myosin) to attach and pull on one another, producing force. Calcium is the most important ion for activating contraction. Potassium going out of the cell makes the muscle cell negative again and terminates the contraction. This cycle of electrical activity, going from negative to positive to negative again, is called an action potential.

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

Action potentials in one muscle cell can excite adjacent muscle cells. This process spreads and coordinates contraction over the entire heart. Some muscle cells are adapted for conducting the electrical activity from one part of the heart to another. Other muscle cells initiate action potentials spontaneously and are known as pacemaker cells.

Pacemaker cells in the sinoatrial node, located over the right atrium, initiate the cardiac cycle. Systole begins when excitation spreads over both atria, activating atrial contraction. Excitation spreads to the atrioventricular node, near the atrioventricular border, from which excitation is conducted by the bundle of His and the Purkinje system (groups of specialized muscle cells) to the bottom of the ventricles. Excitation spreads upward in the ventricles, contracting them from the bottom up, like squeezing a toothpaste tube from the bottom. When the action potentials end, diastole (relaxation) begins, until excitation is again initiated by the pacemaker cells of the sinoatrial node.

Electrical activity of the heart is recorded in an electrocardiogram. Here, one complete cycle is shown, comprising contraction and relaxation of the atria and the ventricles.

Five waves in the normal electrocardiogram correspond to the movement of ions into and out of muscle cells and the direction of conduction over the heart. P is due to activation of atrial cells. Q, R, and S waves correspond to activation of ventricular muscle cells. (The positive or negative direction of QRS waves depends on whether activity is spreading towards the electrode or away from it.) The T wave corresponds to the end of the ventricular action potential. No wave for the end of the atrial action potential is seen because it occurs at the same time as QRS. Abnormalities in the size or duration of the electrocardiogram waves can be used to diagnose heart attacks and other forms of heart disease. In abnormal hearts, waves may be missing or out of sequence. SEE ALSO BLOOD; BLOOD VESSELS; CARDIOVASCULAR DISEASES; CIRCULATORY SYSTEMS

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Herbal Medicine

Using medicines derived from plants is a practice probably as old as humankind itself. Prehistoric peoples likely noted when consuming a particular plant part provided relief, such as willow bark "tea" lowering a fever. Sumatran clay tablets engraved forty centuries ago list plant-based remedies for common ills, as do ancient writings from Egypt and China. In nineteenth-century United States, St. John's wort and *Echinacea* were just two of many commonly used herbal remedies.

Many modern medicines are synthetic versions of plant-derived "natural products." A compound from a periwinkle plant, for example, served as the basis for a powerful drug that fights leukemia. Poppies provide alkaloids such as morphine that are potent painkillers.

In the U.S. today, one-third of all adults have tried herbal treatments, creating a multibillion-dollar market. The resurgence of interest in herbal medicine is largely due to the Dietary Supplements Health and Education Act (DSHEA) of 1994, which expanded the definition of "dietary supplement" beyond essential nutrients to include "herbs and botanicals," thus removing them from regulation as drugs. This designation means that labels can only mention ways that the herbal product can promote health, not cure disease. For example, valerian root "promotes restful sleep," St. John's wort "may help enhance mood," and *Echinacea* and goldenseal "may help support the immune system." Table 1 lists some herbal products marketed as food supplements that are currently being tested for efficacy in treating specific illnesses. Many physicians and biochemists argue that active ingredients in many herbal remedies are indeed drugs, and should be regulated as such.

The U.S. Food and Drug Administration does not require food supplements to be tested for safety and efficacy in treating illness, or even that a product be consistent in concentration of the active ingredient, or the plant part from which it is derived. Two-thirds of individuals who take herbal supplements do so without consulting a physician, which can be dangerous. St. John's wort, for example, interacts with **enzymes** that control blood levels of many drugs, including anesthetics and drugs that transplant recipients must take. Some herbal supplements may be dangerous if taken in large

enzyme protein that controls a reaction in a cell

Herbal Supplements and Conditions They Treat	
Product	**Condition**
Cannabis	migraine
Echinacea	respiratory infection
Garlic	cardiovascular disease
Ginger root	nausea and vomiting
Ginkgo biloba	memory impairment intermittent claudication glaucoma tinnitus altitude sickness
Horse chestnut	chronic venous insufficiency
Kava	anxiety
Oregon grape	psoriasis
Red clover	elasticity of large arteries
Red grape juice	coronary artery disease
Saw palmetto	frequent urination due to enlarged prostate
Valerian root	insomnia
Willow bark	lower back pain

doses or by individuals with particular illnesses. For example, *Ginkgo biloba* has been linked to intracranial bleeds, and *Ephedra* to seizures, hypertension, stroke, and death.

Studies to test effects of herbal substances may be flawed or yield inconsistent results. Some reports are actually studies of studies, selected in a way that prejudices the results. Many trials are too small or not well enough controlled to yield meaningful conclusions. Consider an investigation on whether fruits of the chastetree can prevent symptoms of premenstrual syndrome. For three months, 1,634 women took two capsules a day of the extract, and reported their symptoms before and after the trial period—with no control group not receiving the drug. For St. John's wort, one large investigation found it to be just as effective as a standard antidepressant drug, yet another large study published a few months later found it to be useless.

Not all herbal remedies lack scientific backing due to the peculiarities of regulatory law or variations in experimental design. For example, people have drunk cranberry juice to ease symptoms of urinary tract infections for many years. The effect was thought to be due to increasing acidity of urine, but a 1998 study found that compounds called proanthocyanidins prevent bacterial outgrowths from adhering to the wall of the uterine tract.

It is wise to consult a physician when considering use of an herbal product. Even for a well-understood remedy such as cranberry extract, additional therapy may be required, or drug interactions a possibility. The law may not currently consider herbal ingredients to be drugs, but science indicates

otherwise. SEE ALSO CLINICAL TRIALS; ETHNOBOTANY; PSYCHOACTIVE DRUGS; SECONDARY METABOLITES IN PLANTS

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Herbivory and Plant Defenses

Herbivory is the consumption of plant tissues by animals. This usually has a negative impact on plant growth and reproduction, and so imposes natural selection on plants, thereby favoring the evolution of traits that reduce losses (defenses).

Terrestrial plants generally lose less than 10 percent of annual production to herbivores. Fish can consume 100 percent in some shallow-water marine systems in days or weeks, and single-celled algae are often eaten as fast as they reproduce. A few terrestrial herbivores (gypsy moths or locusts, for example) occasionally experience population explosions during which they may totally defoliate their preferred food plants over wide areas A loss of even 15 percent of annual production can reduce plant growth and fitness.

The fact that some herbivores occasionally can consume most or all vegetation suggests that something prevents this most of the time. Two dominant opposing hypotheses are that "top-down" forces (predators, **parasites**, disease) limit herbivore populations so all plants are not consumed, or that "bottom-up" forces (plant quality) prevent herbivores from eating some plant tissues. In reality both forces combine to limit herbivores and herbivory. Herbivore damage is greater in simplified managed systems, reflecting the loss of these interactions.

Plants have developed numerous physical (spines, thorns, tough tissues, sticky resins, and hairs) and chemical defenses that may reduce herbivory. Some of these are fixed (constitutive), whereas others are only produced (induced) when the plant is attacked. A tremendous diversity of plant biochemicals are toxic, repellent, or antinutritive for herbivores of all types. Many of these chemicals have been called "secondary **metabolites**" because roles have not been found for them in primary plant functions like growth and reproduction. Examples include alkaloids (such as caffeine and nicotine), terpenoids (terpene and pinene), glucosinolates (sinigrin), and phenolics (tannin and chlorogenic acid).

Although many of these compounds appear to have specific activity in animal systems, such as interfering with neurotransmission, recent research suggests that they may have other functions in plants. Nonetheless, it is

Plants have developed physical defenses that reduce the likelihood of herbivory.

parasite organism living in close association with another from which it derives most of its nutrition

metabolite molecule involved in a metabolic pathway

clear that plant chemistry is a major barrier to herbivory. It is also exploited by humans in medicinal plant use and pharmaceutical development.

While all plants produce chemical defenses continuously, all plants so far studied also change or increase production of both physical and chemical defenses when attacked by herbivores. Defenses can be induced throughout a plant, even in unattacked tissues or tissues produced after the attack, producing **systemic** resistance. New physical and chemical defenses may be synthesized, **enzymes** may activate preexisting defenses, or tissues may be dropped (abscised) to remove pests. This requires detection, coordination, and response. Plants can discriminate among and respond differentially to wounding (such as wind damage) and herbivores, or even among herbivores.

systemic throughout the structure

enzyme protein that controls a reaction in a cell

Chemicals found in insect regurgitant (mouth juices) trigger plant responses; these cues may be produced by the insect or by bacteria living in their guts. Fatty acid signals made by the plant (especially jasmonic acid) in response to attack circulate widely, stimulating defense **gene expression** and providing systemic resistance. Methyl jasmonate is **volatile** and escapes wounded plants, triggering defense responses in nearby unwounded plants.

gene expression use of a gene to create the corresponding protein

volatile easily vaporized

Because producing defenses requires materials (such as carbon and nitrogen) and energy that presumably could be used for growth or reproduction, many believe that defense may be costly for plants. Clear evidence of this is difficult to obtain, but some plants grow or reproduce less when producing maximum defenses, providing indirect support. The types of defenses employed by fast-growing versus slow-growing, or early- versus late-successional plant species differ in consistent ways, but why this is so is not clear. One benefit of induced defenses could be cost-saving, since they are only produced when needed. Induced or **constitutive**, plant defense chemistry influences litter quality, decomposition and nutrient cycling in **ecosystems**.

constitutive at a constant rate or continually

ecosystem an ecological community and its environment

Herbivores, especially insects, have developed behavioral and biochemical mechanisms that reduce the effects of plant defenses. Plant evolution includes ongoing development of new defenses, which is thought to favor the evolution of new herbivore adaptations and promote speciation in both plants and herbivores. This kind of reciprocal evolutionary impact is called coevolution. While all plants gain some protection from defenses, no plant escapes herbivory by at least some adapted herbivores. Plant defenses and consumer adaptation can limit consumption, and thus can determine the length and shape of **food webs**. SEE ALSO HERBAL MEDICINE; HORMONES, PLANT; PLANT PATHOGENS AND PESTS; POISONOUS PLANTS; SECONDARY METABOLITES IN PLANTS

food web set of feeding relations in an ecosystem

Jack C. Schultz

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High School Biology Teacher

Those with a broad knowledge of life science, strong interpersonal and decision-making skills, and an understanding of human development can become high school biology teachers. To prepare for this career, a student should have four years each of science and mathematics coursework, pursue outside interests in science and nature, and spend considerable time working with young people.

Biology teachers work independently and with others to select the material to be taught, apply effective teaching methods for conveying that material to adolescents, and evaluate students' knowledge of the subject. Responsible for the production of scientifically literate citizens and future scientists, they should be able to inspire and instruct.

Teaching generally requires a bachelor of science degree in biology and an additional year of college preparation to learn how students acquire knowledge as well as ways that are effective for promoting learning. Once prepared, individuals seek approval from the state's certifying body, which will attest that the candidate has met the content and pedagogical requirements to teach biology to high school students. Having a criminal-free background, completing a period of supervised practice teaching, and passing a licensure exam are among the requirements. Certified teachers are employed by public school districts and private schools throughout the state of licensure. SEE ALSO COLLEGE PROFESSOR

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History of Agriculture

Agriculture is the raising of domesticated animals and the planting, cultivation, and preservation of crops. Agriculture entails selective breeding of organisms with combinations of inherited characteristics that benefit humans (and not necessarily the organisms themselves), and so these practices have over time greatly influenced the course of evolution of these animals. Agriculture arose thousands of years ago in different parts of the world. The steps were similar in different places, but the types of organisms that were raised or cultivated differed. Underlying all of agriculture is human control of the environment.

From Hunting and Gathering to Intentional Intervention

Preparing a feast today is as easy as visiting the local supermarket, farm stand, or garden. However, fifteen thousand years ago, conditions were quite different. Isolated bands of people hunted and gathered on the parts of the earth not covered in ice, seeking wild game and edible plants. They had to find food, or starve.

Cultivation of plants may have arisen accidentally. According to the "dump heap hypothesis," wandering peoples discarded remains of plant

foods in piles in cleared areas, then returned to the sites and discovered that the same types of plants they had eaten the year before grew again. Eventually, people connected the leaving of seed one season to finding of edible plants the next. Farming began when people intentionally saved and planted seeds of their favorite plants.

By selecting characteristics that make a plant a good crop, early farmers altered the genetic makeups of plant populations. Corn, for example, is a product of human intervention. Corn's ancestor, a grass called teosinte, had small ears with sparse kernels. As humans selected teosinte ears bearing the most plump kernels, they gradually edged evolution towards forming a new species, corn. A reminder today of this ancient intervention is that the jackets formed by the leaves covering an ear of corn (husks) are so tight that the plant cannot naturally release its seed. Other plant species were also changed by humans selecting variants that held onto seeds more tightly, a trait that would not benefit a plant in the wild.

Multiple Origins of Agriculture

Some of the earliest archeological evidence for agriculture comes from the Yellow River region of China, where the people raised rice and millet some fifteen thousand years ago. By thirteen thousand years ago, when warmer and wetter weather followed the end of the Pleistocene ice age, people in the Fertile Crescent, an area that today includes Iran, Iraq, Turkey, Syria, Israel, and Lebanon, cultivated wild grasses, which were the ancestors of barley and emmer and einkorn wheat, as well as lentils and chickpeas. The fields of grasses supported grazing animal populations.

Striking evidence of early agriculture is a ten thousand-year-old farming village in Jericho in the Jordan Valley built over the remains of a hunter-gatherer settlement. The farm was larger and supported more people, and included permanent homes and evidence of irrigation, including walls to hold back floods and ditches. Barley flourished in nearby fields.

By eight thousand years ago, farming settlements and villages ringed by crop fields had spread from the Middle East to Eastern Europe. People raised wheat, barley, legumes, goats, sheep, pigs, cattle, and many other species. By seven thousand years ago, people in central Europe and the western Mediterranean region were actively farming, and by four thousand years ago, the change came to the British Isles. Tombs, mummy wrappings, and paintings and hieroglyphics from Assyria and Egypt from this time herald a diet, at least among the well-to-do, that included figs, dates, grapes, olives, pomegranate, and several cereals. Meanwhile, agriculture was spreading in the Americas. By eight thousand years ago, people there were eating kidney beans, peanuts, lima beans, cocoa, avocados, pumpkins, squashes, tomatoes, chili peppers, and corn. Potatoes were a staple in settlements in the Andes Mountains in South America about four thousand years ago. On the African continent, cassava, yams, coffee, cotton, millet, and sorghum were among the first crops, grown about five thousand years ago.

Modern Agriculture and Biotechnology

The work of Charles Darwin and Gregor Mendel in the late nineteenth century, in evolution and genetics, respectively, revealed the biological
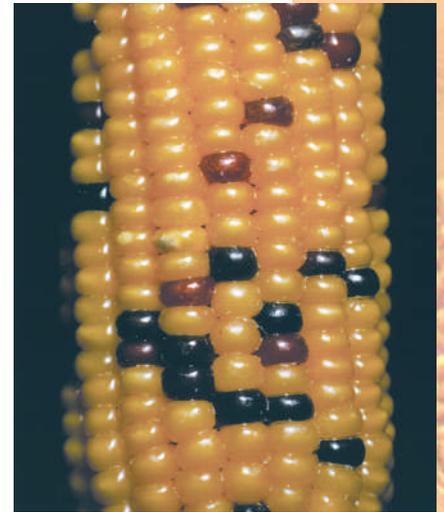
Genetically engineered corn. Humans have intervened with the growth of corn since ancient times.

inbred repeatedly bred with close relatives, creating organisms with very little genetic variation

hybrid combination of two different types

monoculture cultivation of a single type of crop in a large area

pathogen disease-causing organism

transgenic characterized by presence of one or more genes from a different organism

genetic code relationship between triples of RNA nucleotides and the amino acids they code for during protein synthesis

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

basis of the selective breeding that is agriculture. Cultivation approaches could therefore become more directed. For example, in the early twentieth century, George Shull, at the Station for Experimental Evolution in Cold Spring Harbor, New York, crossed highly **inbred** strains of corn, and produced very robust **hybrids**. Use of hybrids ushered in a new era in agriculture, with many fields planted with the same strains of crop plants (**monocultures**). But this set the stage for disaster, such as arrival of a **pathogen** to which all of the plants were equally vulnerable. In the twenty-first century, farmers plant several varieties of the same crop to avoid the weakness of monocultures.

Traditional agriculture selects valuable variants among individual organisms, and breeding is between members of the same or very closely related species. Conventional breeding therefore mixes up many traits at a time. In contrast is agricultural biotechnology, in which addition or modification of specific genes creates valuable variants. Specifically, a **transgenic** plant or animal has an added gene in each of its cells. The transgene can come from a different type of organism, which is possible because all species use the same **genetic code** to manufacture **protein**. To return to the example of corn, plants that are transgenic for a gene from the bacterium *Bacillus thuringiensis* produce a protein that kills certain caterpillars, including the devastating European corn borer. Use of such "bt corn" enables a farmer to avoid using chemical pesticides, but has potential consequences of its own, such as promoting selection of borers resistant to the poison, and harm to nearby insect populations.

Agricultural biotechnology began in the 1970s, and people in the United States have been eating genetically modified foods since the mid-1990s. The goals of agricultural biotechnology are the same as traditional agriculture: improved appearance, flavor, and nutritional content of foods, and ease of cultivation. SEE ALSO AGRICULTURE; AGRONOMIST; GRAIN; ORGANIC AGRICULTURE; PLANT PATHOGENS AND PESTS

Ricki Lewis

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History of Biology: Biochemistry

Biochemistry as a recognizably distinct discipline emerged at the beginning of the twentieth century. Initially it focused on the chemical changes of cellular **metabolism**.

metabolism chemical reactions within a cell

Roots of Biochemistry

Biochemistry had its roots in nineteenth-century physiological chemistry, animal chemistry, and the chemistry of biological materials. The earliest

views on the chemistry of life posited that it was fundamentally different from nonliving chemistry. From around 1835, the view had developed that **protoplasm**, seen as a jellylike single homogeneous form of matter within organisms, carried out all the processes of **intracellular** breakdown of foods, respiration, and biosynthesis. Despite this general belief, neither Justus Liebig nor Ernst Hoppe-Seyler, two eminent chemists, accepted this view. Hydrolytic enzymes such as amylase, maltase, and pepsin were known in the nineteenth century, but were not thought to act within cells.

Probably the single most important experiment that initiated the study of biochemistry was the preparation by Eduard Buchner in 1897 of a cell-free extract of yeast, called zymase, which fermented **glucose** and produced carbon dioxide and ethanol. Buchner regarded zymase as a single enzyme, although others soon showed that it contained several. This work confirmed fermentation as a chemical process and discredited the protoplasm theory. Furthermore, the distinction between **catalysis** by hydrolytic extracellular enzymes and by intracellular enzymes disappeared.

Enzymes

The nature of catalysis began to be explored early in the twentieth century with the realization that enzymes bind their **substrates** during the reaction. At the beginning of the twentieth century, Emil Fischer proposed that a substrate fits its enzyme like a key fits a lock. Mathematical analysis of enzyme action enabled Leonor Michaelis and Maud Menten to formulate the classic equations for enzyme action in 1913. The chemical nature of enzymes as proteins remained uncertain until James Sumner crystallized urease from Jack bean meal in 1926. Several other enzymes were crystallized in the following years and were all shown to be proteins. In 1959, Sanford Moore and William Stein determined the first primary sequence (the **amino acid** sequence) of an enzyme, ribonuclease. The path was now open, using X-ray crystallography to reveal the catalytic process in three-dimensional models of enzymes.

Metabolism

Part of the significance of Buchner's work lay in initiating the study of fermentation as a metabolic pathway. Otto Meyerhof demonstrated that muscle juice had similar properties, although producing lactic acid rather than ethanol. Thus, the glycolytic pathway, associated with the names of Gustav Embden, Meyerhof, and Otto Warburg, was elucidated over the first four decades of the twentieth century.

In the first years of the twentieth century, Franz Knoop and also Henry Dakin outlined the basis of fatty acid **oxidation**, although this pathway was not fully formulated until the 1950s. The cyclical nature of some metabolic pathways became apparent to Hans Krebs in his study of the synthesis of urea, which led to the description of the urea cycle in 1931. In 1937, building on much work on cell oxidation reactions, Krebs formulated the citric acid cycle (often called the **Krebs cycle** in his honor). Identification of acetyl coenzyme A in the early 1950s facilitated the understanding of **pyruvate** oxidation, fatty acid oxidation, and the citric acid cycle.

During the 1930s, biochemists began to use radioactive **isotopes** such as deuterium (^{2}H), ^{32}P, and ^{35}S in studies of metabolism. After World War

Eduard Buchner, whose experiments with zymase initiated the study of biochemistry.

protoplasm fluid portion of a plant cell within the cell wall

intracellular within a cell

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

catalysis aiding in the reaction of

substrate the molecule acted on by an enzyme

amino acid a building block of protein

oxidation reaction characterized by loss of electrons, or reaction with oxygen

Krebs cycle central metabolic pathway in mitochondria

pyruvate the ionized form of pyruvic acid, a key intermediate in cell metabolism

isotopes forms of an atom that differ by the number of neutrons in the nucleus

II, ^{14}C became readily available, and together with the use of microbial mutants, enabled researchers to elucidate metabolic pathways, particularly from 1945 to 1975.

Bioenergetics and Membranes

The importance of adenosine triphosphate (**ATP**) emerged slowly from a study of the cofactors necessary for **glycolysis** in yeast and muscle. In 1939, Vladimir Engelhardt and Militsa Lyubimova showed ATP to be a substrate for myosin that participates in muscular contraction. In 1941, Fritz Lipmann set out the essential role of ATP as the energy currency of the cell. Initially ATP synthesis was thought to be associated only with glycolysis, but during the 1930s a number of studies showed that much of ATP production was associated with oxygen uptake, linking oxygen consumption with **phosphorylation**.

During the 1920s and 1930s, David Keilin outlined the steps of the respiratory chain, through which oxygen is consumed in the mitochondrion. By the 1950s, it was clear that the respiratory chain was coupled to the synthesis of ATP. In 1961, Peter Mitchell formulated the chemiosmotic theory of ATP production, based on a **gradient** of H^+ **ions** and **membrane potential**. This not only resolved the issue of **oxidative phosphorylation** but also gave a firm foundation for studies of transport across membranes. Jonathon Singer and Garth Nicholson resolved problems of membrane structure by proposing in 1972 the fluid mosaic model in which proteins are embedded in a fluid **lipid bilayer**.

At the beginning of the twentieth century, the basic process of photosynthesis had already been defined. From 1954 to 1956, Melvin Calvin and Andrew Benson formulated the metabolic pathway for carbon dioxide fixation, which would be named the Calvin-Benson cycle in their honor. In 1937, Robin Hill and others had progressively elaborated the workings of the electron transport chain of the chloroplast. In the second half of the 1950s, Daniel Arnon showed that the electron transport chain drives ATP synthesis in the chloroplast. Many researchers in the twentieth century explored the basic photochemistry of photosynthesis, but the determination of the structure of a bacterial reaction center complex by Johann Deisenhofer in 1984 has helped to clarify the field.

Proteins

The theory that proteins were composed of linear chains of amino acids had been enunciated at the beginning of the twentieth century, while the amino acid constituents of proteins were still being identified. However, it was not until Fred Sanger obtained the first complete primary structure of a protein, insulin, in 1955 that the theory was confirmed. A model of the three-dimensional structure of a protein (whale myoglobin) was determined by John Kendrew and colleagues between 1958 and 1960 based on X-ray analysis. Concurrently Max Perutz described the structure of **hemoglobin**. Among other issues, these achievements confirmed the predictions made in 1950 by Linus Pauling and Robert Corey that the amino acid chain could coil into a spiral staircase-like structure called the alpha helix. Researchers have described the three-dimensional structures of many proteins since that time.

ATP adenosine triphosphate, a high-energy nucleotide used by cells to power most energy-requiring reactions

glycolysis initial stages of sugar breakdown in a cell

phosphorylation addition of the phosphate group PO_4^{3-}

gradient difference in concentration between two places

ion an electrically charged particle

membrane potential electrical and chemical differences across a membrane leading to storage of energy and excitability

oxidative phosphorylation use of oxygen to make ATP

lipid fat or waxlike molecule, insoluble in water

bilayer composed of two layers

hemoglobin oxygen-carrying protein complex in red blood cells

Improved techniques of crystallography, X-ray analysis, and other skills in protein chemistry are bringing new insights to many areas of classical biochemistry, including enzymology. For example, the elucidation of the structure and mechanism of the bacterial **mitochondrial** and chloroplast ATP synthase (ATPase) in the 1990s, based on the work of Paul Boyer and John Walker, has revealed an enzyme that involves a rotating core to carry out ATP synthesis. This molecule is used by both mitochondria and chloroplasts to make ATP.

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

DNA and Protein Synthesis

Work on bacteria led Oswald Avery to suggest in the 1940s that deoxyribonucleic acid (DNA) was the genetic material of the cell. Francis Crick and James Watson elucidated the structure of DNA in 1953. The structure they proposed suggested immediately the way in which genes might be replicated. More importantly, Crick suggested that the sequence of bases determines the sequence of amino acids in proteins, and that the amino acid sequence in itself determined the three-dimensional structure of these proteins. By 1960, it was believed that a sequence of three DNA bases encodes an individual amino acid. Marshall Nirenberg, Severo Ochoa, and Gobind Khorana "cracked" the **genetic code**—the specific DNA base triplets that specify particular amino acids—in a series of experiments conducted in the 1960s.

genetic code relationship between triples of RNA nucleotides and the amino acids they code for during protein synthesis

In 1961, François Jacob and Jacques Monod introduced the concept of regulatory genes, which control the expression of structural genes that encode for proteins. Other methods of control were discovered later. By the 1970s, it was possible to synthesize proteins *in vitro*.

in vitro "in glass"; in lab apparatus, rather than within a living organism

Manipulation of DNA and Elucidation of Protein Structure

The sequencing of significant lengths of DNA remained a problem until in 1977 Fred Sanger sequenced a bacteriophage **genome** of 5,375 **nucleotides**. This achievement led the way to Sanger's sequencing of the DNA of the human mitochondrial genome of more than 16,000 nucleotides in 1981. These early sequencing successes contributed to the idea that arose in the mid-1980s to sequence the human genome, which researchers expect to complete in 2003 (a draft sequence was published in 2001).

genome total genetic material in a cell or organism

nucleotide the building block of RNA or DNA

Parallel to DNA sequencing efforts was the use of **restriction enzymes**, which cut DNA at specific sequences. Restriction enzymes made possible DNA sequencing, recombinant DNA technology, **transgenic** technology, and other tools, giving rise to the rapid development in the 1990s of biotechnology based on gene splicing. SEE ALSO CRICK, FRANCIS; ENZYMES; GLYCOSIS AND FERMENTATION; HISTORY OF BIOLOGY: CELL THEORY AND CELL STRUCTURE; HISTORY OF BIOLOGY: INHERITANCE; KREBS CYCLE; METABOLISM, CELLULAR; MUSCLE; OXIDATIVE PHOSPHORYLATION; PROTEIN STRUCTURE; WATSON, JAMES

restriction enzyme enzyme that cuts DNA at a particular sequence

transgenic characterized by presence of one or more genes from a different organism

John Prebble

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Robert Hooke's microscope. Hooke first described cells in 1665.

History of Biology: Cell Theory and Cell Structure

All living organisms are composed of cells, and all cells arise from other cells. These simple and powerful statements form the basis of the cell theory, first formulated by a group of European biologists in the mid-1800s. So fundamental are these ideas to biology that it is easy to forget they were not always thought to be true.

Early Observations

The invention of the microscope allowed the first view of cells. English physicist and microscopist Robert Hooke (1635–1702) first described cells in 1665. He made thin slices of cork and likened the boxy partitions he observed to the cells (small rooms) in a monastery. The open spaces Hooke observed were empty, but he and others suggested these spaces might be used for fluid transport in living plants. He did not propose, and gave no indication that he believed, that these structures represented the basic unit of living organisms.

Marcello Malpighi (1628–1694), and Hooke's colleague, Nehemiah Grew (1641–1712), made detailed studies of plant cells and established the presence of cellular structures throughout the plant body. Grew likened the cellular spaces to the gas bubbles in rising bread and suggested they may have formed through a similar process. The presence of cells in animal tissue was demonstrated later than in plants because the thin sections needed for viewing under the microscope are more difficult to prepare for animal tissues. The prevalent view of Hooke's contemporaries was that animals were composed of several types of fibers, the various properties of which accounted for the differences among tissues.

At the time, virtually all biologists were convinced that organisms were composed of some type of fundamental unit, and it was these "atomistic" preconceptions that drove them to look for such units. While improvements in microscopy made their observations better, it was the underlying belief that there was some fundamental substructure that made the microscope the instrument of choice in the study of life.

In 1676 the Dutch microscopist Antony van Leeuwenhoek (1632–1723) published his observations of single-cell organisms, or "little animalcules" as he called them. It is likely that Leeuwenhoek was the first person to observe a red blood cell and a sperm cell. Leeuwenhoek made numerous and detailed observations on his microorganisms, but more than one hundred years passed before a connection was made between the obviously cellular structure of these creatures and the existence of cells in animals or plants.

The Development of the Cell Theory

In 1824 Frenchman Henri Milne-Edwards suggested that the basic structure of all animal tissues was an array of "globules," though his insistence on uniform size for these globules puts into question the accuracy of his observations. Henri Dutrochet (1776–1847) made the connection between plant cells and animal cells explicit, and he proposed that the cell was not just a structural but also a physiological unit: "It is clear that it constitutes the basic unit of the organized state; indeed, everything is ultimately derived from the cell" (Harris 1999, p. 29). Dutrochet proposed that new cells arise from within old ones, a view that was echoed by his contemporary François Raspail (1794–1878). Raspail was the first to state one of the two major tenets of cell theory: *Omnis cellula e cellula*, which means "Every cell is derived from another cell." However, despite this ringing and famous phrase, his proposed mechanism of cell generation was incorrect. Raspail was also the founder of cell biochemistry, making experiments on the chemical composition of the cell and their response to changing chemical environments.

In 1832 Barthelemy Dumortier (1797–1878) of France described "binary fission" (cell division) in plants. He observed the formation of a midline partition between the original cell and the new cell, which, Dumortier noted, "seems to us to provide a perfectly clear explanation of the origin and development of cells, which has hitherto remained unexplained" (Harris 1999, p. 66) These observations led him to reject the idea that new cells arise from within old ones, or that they form spontaneously from noncellular material. The discovery of cell division is usually attributed to Hugo von Mohl (1805–1872), but Dumortier proceeded him in this regard. Von Mohl did coin the word "protoplasm" for the material contained in the cell.

The first unequivocal description of the cell **nucleus** was made by a Czech, Franz Bauer, in 1802 and was given its name in 1831 by Robert Brown (1773–1858) of Scotland, who is best remembered for discovering the random "Brownian" motion of molecules. The first accurate description of the nucleolus was made in 1835.

Schleiden and Schwann, who are usually given credit for elucidating the cell theory, made their marks in 1838 and 1839. In 1838 Matthais Schleiden (1804–1881) proposed that every structural element of plants is composed of cells or the products of cells. However, Schleiden insisted on priority for several ideas that were not his and clung to the idea that cells arise by a crystallization-like process either within other cells or from outside, which Dumortier had dispensed with some years earlier. (In Schleiden's defense, it should be remembered that drawing incorrect conclusions from limited observations is a risk inherent in science, especially when working on the frontier of a new field.)

In 1839 a fellow German, Theodor Schwann (1810–1882), proposed that in animals too every structural element is composed of cells or cell products. Schwann's contribution might be regarded as the more groundbreaking, since the understanding of animal structure lagged behind that of plants. In addition, Schwann made the explicit claim that the fundamental laws governing cells were identical between plants and animals: "A common principle underlies the development of all the individual elementary subunits of all organisms" (Harris 1999, p. 102).

nucleus membrane-bound portion of cell containing the chromosomes

cytologist scientist who studies cells

A special word should be said here about the Czech Jan Purkyně (1787–1869), or Purkinje, as his name is usually given. Purkinje was the premiere **cytologist** of his day, and one of the most influential formulators of the cell theory. He gave his name to structures throughout the body, including the Purkinje cells of the cerebellum. Purkinje, in fact, deserves much of the credit that usually goes to Schwann, for in 1837 he proposed not only that animals were composed principally of cells and cell products (though he left room for fibers) but also that the "basic cellular tissue is again clearly analogous to that of plants" (Harris 1999, p. 92). Unfortunately, Schwann did not credit Purkinje in his influential publication.

Reproduction and Inheritance

Despite the work of Dumortier, the origins of new cells remained controversial and confused. In 1852 a German, Robert Remak (1852–1865), published his observations on cell division, stating categorically that the generation schemes proposed by Schleiden and Schwann were wrong. Based on his observations of embryos, Remak stated instead that binary fission was the means of reproduction of new animal cells. This view was widely publicized not by Remak but by Rudolf Virchow (1821–1902), unfortunately without crediting Remak. Virchow is also usually given the credit for the phrase *Omnis cellula e cellula*, indicating the importance of cell division in the creation of new cells.

chromosomes "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

mitosis separation of replicated chromosomes

endoplasmic reticulum network of membranes within the cell

cytoskeleton internal scaffolding in a cell, composed of protein

The understanding of the central importance of **chromosomes** lagged well behind their discovery. In 1879 Walther Flemming (1843–1905) noted that the chromosomes split longitudinally during **mitosis** (a term he introduced). Wilhelm Roux (1850–1924) proposed that each chromosome carried a different set of hereditable elements and suggested that the longitudinal splitting observed by Flemming ensured the equal division of these elements. This scheme was confirmed in 1904 by Theodor Boveri (1862–1915). Combined with the rediscovery of Gregor Mendel's 1866 paper on heritable elements in peas, these results highlighted the central role of the chromosomes in carrying genetic material. The chemical nature of the gene was determined in a series of experiments over the next fifty years, culminating in the determination of the structure of deoxyribonucleic acid (DNA) in 1953 by James Watson and Francis Crick.

Modern Advances

The modern understanding of cellular substructure began with the use of the electron microscope. Keith Porter (1912–1997) was a pioneer in this field and was the first to identify the **endoplasmic reticulum** and many elements of the **cytoskeleton**. The explosion of knowledge brought about by improvements in microscopy, biochemistry, and genetics has led to a depth of understanding of cell structure and function undreamed of by the earliest cell biologists. SEE ALSO Cell; Electron Microscopy; Leeuwenhoek, Anton Von; Light Microscopy; Porter, Keith

Richard Robinson

WILSON, EDMUND B. (1865–1939)

Premier cell biologist of the early twentieth century, Wilson described how a fertilized egg divides up into hundreds of cells to form an embryo and which parts of the body develop from which cells. His student Walter Sutton discovered the role of chromosomes as the units of heredity.

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History of Biology: Inheritance

Heredity (colloquially synonymous with "inheritance") refers to the process by which certain features (heritable characteristics) are transmitted from parent to offspring. This process has long been a source of intense interest to scientists. Just why do children look like their parents, but not exactly? This question can be separated into two parts: (1) In sexually reproducing organisms, how do the features of the parents get combined and transmitted to the offspring? (2) What actually gets transmitted? To ask these questions requires the materialist belief that some physical substance is transmitted that corresponds to particular traits, an assumption that was not widely held before the late nineteenth century.

From Aristotle to Weismann

Before the nineteenth century, questions about offspring looking like their parents were asked within a conceptual framework that embraced very different assumptions than scientists do today. The contributions of the parents to the offspring were not necessarily assumed to be equal, or even to be purely material. The ancient Greek philosopher Aristotle, for example, thought that the male semen contributed the "active element" to the offspring, bringing it to life, while the female contributed only nutritional material for the offspring.

Theorists who did think both parents contributed some material elements generally assumed that *blending inheritance* held true: the parental contributions were believed to blend together so that the offspring's characteristics were usually intermediate between those of the parents. If one parent had a short nose and another a long one, the child could be expected to have a nose somewhere in between. Moreover, in this conceptual framework, heredity was not separated sharply from environment; it was "common sense" that environmental effects on parental characteristics could reappear in their offspring. (This would later be called "the inheritance of acquired characters," or "Lamarckism," after the early-nineteenth-century biologist Jean-Baptiste Lamarck.) Thus, if parents were well educated, it was assumed that their children would be smart.

In the late nineteenth century, this framework was gradually abandoned. Two shifts in outlook were especially important. First, spurred on by new observations, scientists came to view hereditary transmission as a purely material process (possibly exempt from the effects of the environment). Starting in the 1860s, biologists developed new microscopic techniques to study the physical processes of the cell (a branch of biology called **cytology**). In 1875, the German anatomist Oscar Hertwig was the first to observe a sperm penetrating an egg (of a sea urchin), thereby lending credence to the idea that a material substance was actually physically transferred via the sperm.

In the 1870s, new structures in the **nucleus** were discovered, called **chromosomes** (which means "colored bodies") because they absorbed dyes more intensely than the surrounding nuclear material. Although their function was mysterious, the fact that they came in pairs (perhaps one from each parent) suggested a possible role in heredity. As cytologists raced to sort out the complex and confusing cell-division events of **mitosis** and **meiosis** from
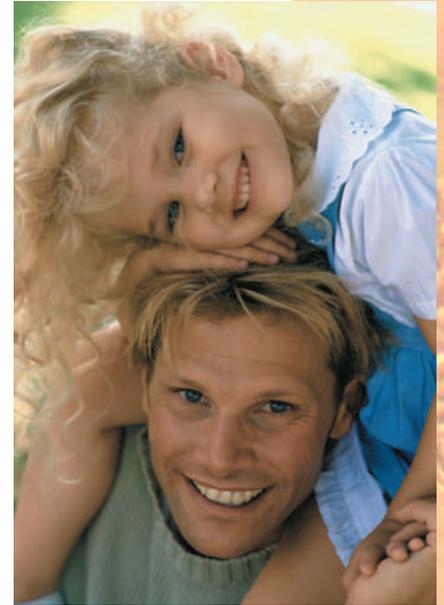
Heredity refers to the process by which certain features are transmitted from parents to offspring.

cytology study of cells

nucleus membrane-bound portion of cell containing the chromosomes

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

mitosis separation of replicated chromosomes

meiosis cell division that forms eggs or sperm

fertilization union of sperm and egg

Why do children look like their parents, but not exactly? Heredity refers to the process by which certain features (heritable characters) are transmitted from parent to offspring.

the late 1870s to the early 1900s, they constructed innovative theories of heredity to accommodate these new observations. In contrast with earlier work, most of these theories postulated that some physical substance carried by the sperm and egg combined during **fertilization** to produce the offspring.

August Weissmann. At the same time, theorists began to challenge a second fundamental assumption of the old framework: blending inheritance. Instead, they suggested that inheritance was *particulate:* each parent contributed to the offspring its own share of discrete units corresponding to some hereditary trait (such as height or eye color), which were somehow then combined and sorted in the offspring. In the 1880s and 1890s, the German zoologist August Weismann influentially combined the two new concepts (material transfer and particulate inheritance), postulating a substance called the "germ plasm" that was carried in the chromosomes of the reproductive cells from generation to generation, and that was made up of invisible particles corresponding to particular body structures. Though Weismann's theory was highly speculative, by the early 1900s studies of chromosomal action during fertilization and early development seemed to confirm important parts of it, especially the role of the chromosomes as bearers of particulate hereditary material.

Weismann was not the only theorist to propose that the hereditary material was made up of discrete particles: Charles Darwin had conceived of heredity as particulate in the late 1860s (though his theory of heredity was not well regarded), and the Dutch plant breeder Hugo de Vries theorized a hereditary particle he called the "pangene." Thus, in 1900 scientists were already thinking about hereditary particles when de Vries and the German botanist Carl Correns rediscovered an obscure paper published in 1865 by the Austrian monk Gregor Mendel.

Gregor Mendel. Describing his breeding experiments on the common garden pea, Mendel developed his basic concept of paired, discrete hereditary "factors" (he did not call them "genes" or "alleles"). Each parent contributed one factor for each trait, and each trait came in one of two forms, dominant or recessive. Although only the dominant form would be visible in any combination of dominant and recessive, the recessive factor was still there, hidden, and could be passed to the next generation. If two recessives combined together, then the recessive form would be "expressed." Mendel's results also supported the idea that traits such as height and seed texture were not generally linked but recombined randomly during reproduction, showing independent assortment. A tall pea plant could thus have either smooth or wrinkled seeds; so could a short pea plant. In 1909, the Danish Mendelian Wilhelm Johannsen named these presumed hereditary particles "genes."

Mendel's ideas commanded immediate, widespread interest. His pea-breeding experiments, which ran over many generations of plants to yield impressively stable statistical ratios of hereditary traits, provided biological theorists with compelling new evidence for the hypothesis of paired hereditary characters that sorted independently. Mendel's results appeared to offer practical guidance as well. Animal and plant breeders believed that they would help them develop rational systems for combining desirable traits in livestock and agriculturally important plants. Eugenicists, who sought to improve the human race through breeding "the best" traits together (such as

strength and intelligence), thought Mendelism would provide rules for rational human breeding.

Thomas Hunt Morgan.   By the early 1900s, then, the existence of discrete genes that governed heredity seemed plausible to most biologists. However, the location and the physical nature of these theoretical entities was still uncertain. In particular, the relation between genes (which seemed to come in pairs) and chromosomes (which also came in pairs) was still a matter of some debate. Then in the 1910s, Thomas Hunt Morgan at Columbia University united the cytological focus on chromosome activity with the Mendelian breeding approach.

Combining breeding experiments on fruit flies (*Drosophilia*) with microscopic study of their chromosomes, Morgan and his students established beyond any doubt that hereditary material was carried on the chromosomes and that the theoretical entity known as the gene corresponded to particular identifiable traits. They also refined the theory of the gene substantially, developing explanations for "linked" traits that did not sort randomly (genes near each other on the same chromosome), positing the existence of more than two forms of a gene (multiple **alleles**), and developing the idea that some genes could act as modifiers on others, changing their effect.

allele a particular form of a gene

Morgan's student Alfred H. Sturtevant combined breeding experiments, statistical analysis, and the study of chromosomes under the microscope to draw up chromosome "maps" that showed how far apart the genes for various traits must be on the chromosome. Although some scientists outside Morgan's powerful circle—especially in Europe—contested the view that the chromosomal gene was the sole bearer of hereditary material (arguing, for example, that the **cytoplasm** surrounding the nucleus might also play a role in heredity), the views established by Morgan and his school in the 1910s and 1920s largely prevailed, and have come to be known as classical genetics.

cytoplasm material in a cell, excluding the nucleus

Biochemistry.   Biologists in the Morgan tradition, however, were unequipped to answer the question, What is the gene made of? Answering this question required attention to biochemistry. In the 1930s and 1940s, the leading candidate was **protein**, though a minority view held that it might be deoxyribonucleic acid, or DNA. In 1944, Oswald Avery, Colin MacLeod, and Maclyn McCarty published results of their experiments with the pneumonia-causing bacterium *Streptococcus pneumoniae* that indicated that DNA was the right pick, and in 1952 this view gained strong verification by the famous "Waring blender" experiments of Alfred Hershey and Martha Chase, which showed that the protein of the bacteriophage virus was a mere protective coating, while the stuff that created genetic transformation was DNA.

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

In 1953, James Watson and Francis Crick went further, postulating a double-helical structure for DNA, arguing that the four **nucleotide** bases guanine, cytosine, thymine, and adenine were its building blocks. The parallel structure of the helices suggested the possibility that it "unzipped" in replication, such that each side of the zipper, each helix, could then act as a **template** for the synthesis of a **complementary** strand of DNA, thus creating a perfect replica, ideally suited for passing on to offspring. Finally, in the early 1960s, scientists interpreted the sequence of nucleotides along the chromosome as a code for the sequence of **amino acids** in protein. This insight illuminated the means by which the gene dictates the physical characteristics

nucleotide the building block of RNA or DNA

template master copy

complementary matching opposite

amino acid a building block of protein

of the organism possessing it. Although many details needed to be resolved, it seemed to many that the most basic keys to heredity had been discovered.

By the late twentieth century, then, biologists had come to view the gene from two directions. Working from the "outside in," organismal and population biologists continued to operate with the classical concept that a gene (or some combination of genes) corresponds to a trait (as in "a gene for X"). Working from the "inside out," biochemists and molecular biologists defined the gene as the amount of DNA that codes for one protein or one **polypeptide**. Since a protein is not the same as a trait, much work continues to aim at unravelling the complex nature of **gene expression**. As research continues to develop, and the field of genomics continues to expand, the idea of the gene continues to evolve. SEE ALSO CRICK, FRANCIS; DNA; GENE; GENOMICS; HISTORY OF BIOLOGY: CELL THEORY AND CELL STRUCTURE; MENDEL, GREGOR; WATSON, JAMES

Lynn K. Nyhart

polypeptide chain of amino acids

gene expression use of a gene to create the corresponding protein

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History of Evolutionary Thought

Although Charles Darwin's name is virtually synonymous with the word evolution, he was not the first person to recognize the phenomenon of species change nor did he even use the word "evolution" in the original theory he set forth in *On the Origin of Species* (1859). In fact, only the very last word of his book was *evolve* The word *evolution* was introduced after Darwin published his book and by commentators like English biologist Thomas Henry Huxley (1825–1895) who borrowed the term from **embryology**.

embryology study of development

Antiquity

The history of evolution long predates Darwin and his theory. The belief in a changing or dynamic universe can be first seen in ancient Greek philosophy. Heraclitus (c. 500 **B.C.E.**), also known as the "flux philosopher," believed that change was a fundamental property of the universe. His successor, Empedocles (c.. 392–432 **B.C.E.**), first articulated a crude but dynamic theory that postulated that the origin of life had taken place in a manner that suggested evolution.

B.C.E. before the Common Era, equivalent to BC

From Aristotle to Linnaeus

However, beginning with the philosophical worldview established by Aristotle (384–322 B.C.E.), the belief in a changing universe fell into disfavor. Aristotle and his numerous medieval and Renaissance translators, commentators, and supporters, instead believed in a static universe which held that living organisms were created initially and then remained essentially unchanged. These ideal types or species were arranged hierarchically in what came to be known as the "scala naturae," or the ladder of creation. Like rungs on a ladder, each species took its place with lower forms of life on the bottom and higher forms of life on the top.

During the Renaissance, the ladder of creation gave way to the popular metaphor of the "great chain of being," which referred to a progression of living forms linked in an orderly chainlike arrangement. Extinction, the sudden disappearance of a species, in such a scheme, was unthinkable since it meant that the chain would lose a vital link. Belief in the fixity of species, therefore dominated biological thought and was most clearly demonstrated in the modern classification scheme that originated with Carolus Linnaeus (1707–1778).

Buffon, Lamarck, and Transmutationism

Belief in species change, or transmutationism, slowly began to emerge during the **Enlightenment**. This period saw the emergence of the belief in a progressive world, both scientific and social. It also saw the beginnings of the new science of geology. Geological theories suggested that fossils were of **organic** (once-living) origin and that uniform or constant processes rather than catastrophic or one-time events had shaped Earth's history.

The French naturalist Comte de Buffon (Count Buffon, 1707–1788) was one of the first to question the fixity of species and to suggest a transmutationist theory with a startling resemblance to Darwinian evolution. Although he was a respected naturalist, his theoretical explanations for the origin of life and of species change were not accepted during his time. Buffon's transmutationist ideas were also not accepted because they opposed the philosophical teachings of his French colleague Georges Cuvier, the great comparative anatomist and the father of modern paleontology. Cuvier upheld the fixity of species despite fossil evidence of species change. Ironically, though he opposed transmutationism strongly, Cuvier was the first to recognize the phenomenon of extinction, or the view that species had disappeared from the biological record.

The first to suggest a viable theory of species change was Frenchman Jean-Baptiste Lamarck. Lamarck was interested in adaptation, or the manner and process by which organisms are able to adapt physiologically and morphologically to their environment. He was especially interested in how well-adapted organs like the neck of the giraffe had originated. According to Lamarck, the use or, in many cases, disuse of such a vital organ could lead to the development of novel but well-adapted traits. The cumulative effect of these adaptations could eventually lead to a new species. Lamarck never provided a cogent mechanism by which this physical transformation took place, however, though he did draw on contemporary theories from

Georges Léopold Cuvier opposed evolutionary theories, even though he was the first to recognize the phenomenon of extinction.

Enlightenment
eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

organic composed of carbon, or derived from living organisms

animal physiology to suggest that the body heat generated by physical exercise could lead to structural transformation.

Sometimes called "the inheritance of acquired characters," Lamarckian transmutationism, also later called Lamarckian evolution, was subsequently shown to be erroneous because changes acquired as a result of use and disuse were shown to be not heritable. Lamarck's ideas were, however, very popular throughout much of the nineteenth century and well into the twentieth century. Darwin himself relied heavily on the inheritance of acquired characters to explain many adaptations that he later outlined in laying out his own transmutationist theory.

Transmutationism itself became increasingly acceptable by the early nineteenth century. It captured the interest of Darwin's own grandfather, Erasmus Darwin (1731–1802), who suggested that life had originated from "one living filament." Other transmutationists included French anatomist Isidore Geoffroy Sainte Hilaire (1805–1861), who studied birth defects. He suggested that through such "monstrous births" new species might suddenly arise.

In 1844 the work of one transmutationist in particular drew the attention of a wide audience. Writing anonymously at first, Robert Chambers (1802–1871) outlined a transmutationist theory under the title *Vestiges of the Natural History of Creation.* The book drew such heavy criticism that it dissuaded Charles Darwin from setting forth his own controversial transmutationist views for nearly fifteen years.

Darwin and *On the Origin of Species*

Charles Darwin was the leading transmutationist of the nineteenth century. Darwin had developed the major features of his theory as early as 1837 after returning from his five year voyage of the HMS *Beagle* and after reading the famous *Essay on the Principle of Population* by Thomas Malthus (1766–1834). However, Darwin did not make his work public until much later. He felt that he needed to collect solid evidence to his support what he knew would be a contentious theory. He was finally forced into joint publication of an abbreviated version of his theory in 1858, shortly after English naturalist Alfred Russel Wallace (1823–1913) independently formulated his own nearly identical theory.

It took Darwin less than a year to outline in book form his theory of species change that he called "descent with modification" by means of the mechanism of natural selection. The full title of his famous book was *On the Origin of Species or the Preservation of Favored Races in the Struggle for Life.* The book appeared in bookstores on November 24, 1859, and sold out on the first day. It went through six editions as Darwin modified his theory in response to his many critics. It is generally thought that the first edition is a more accurate account of the workings of evolution because subsequent editions included a watered-down version of his original theory.

Darwin thought "descent with modification" took place primarily through the mechanism he termed natural selection. Natural selection occurs when an organism with a favorable variation in some trait reproduces more as a result, thereby increasing the frequency of the variation in the next generation. In addition to this mechanism for driving species change, Darwin included

some four of five other mechanisms that he thought could account for species change including the inheritance of acquired characters. Though he did not address human evolution in this book, Darwin's readers quickly made the connection between humans and other primates. Darwin eventually turned to the human evolution in 1871 when he wrote *The Descent of Man*. In this book, Darwin corrected earlier misconceptions of his work and made it clear that humans had not evolved from modern-day monkeys, but that both had shared a common ancestor.

Criticisms and Controversies

Darwin's theory did face notable criticism in his day. One problem had to do with the absence of any viable mechanism of inheritance in Darwin's work. This led to the criticism that novel characters would be diluted out in subsequent generations. This problem was not solved until the particulate nature of heredity was elucidated during the "rediscovery of Mendel" in 1900. Another problem was the age of the earth, which was then thought to be only about 400 million years old. This was an insufficient amount of time to account for the slow, gradual process that Darwin envisioned. This problem was solved after the discovery of radioactivity in the late nineteenth century which showed the age of the earth to be nearly 5 billion years, an estimate of time long enough to account for evolution.

Yet another difficulty was that Darwin had no direct proof for a process that took place over such a long stretch of time. This proof of evolution by means of natural selection was finally provided beginning in the1920s, with the example of industrial melanism in the peppered moth, *Biston betularia*.

More difficult to resolve were the theological and philosophical questions that followed from the mechanism of natural selection. Even though Darwin had only one line in his 1859 book on human evolution, the theory implied that humans were subject to the same mechanistic process as plants and animals. Because natural selection provides a means to develop highly complex structures without divine intervention, it challenged one argument for God's existence (namely that complex designs require a complex creator).

The Evolutionary Synthesis

Despite a storm of controversy over the mechanism, the fact of evolution was rapidly accepted by scientists. Only after the mechanism of heredity was understood and only after the science of genetics was integrated with natural history was the debate over the mechanism of natural selection extinguished. This took place between 1920 and 1950 and was part of the event called the "evolutionary synthesis." The evolutionary synthesis drew on the work of genetics, systematics, botany, paleontology, **cytology**, and **morphology** to create what contemporary scientists call the "synthetic theory of evolution" or the "Neo-Darwinian theory of evolution."

cytology study of cells

morphology related to shape and form

The evolutionary synthesis drew on the work of twentieth-century biologists like Theodosius Dobzhansky (1900–1975), Ernst Mayr (b. 1904), Julian Huxley (1887–1975), George Ledyard Stebbins (1906–2001), and George Gaylord Simpson (1902–1984). It endorses the view that natural selection is the dominant mechanism that drives evolutionary change. In 1975,

Dobzhansky stated the important fact that "nothing in biology makes sense except in the light of evolution." In stating this, he was stressing the fact that evolution by means of natural selection serves as the central, unifying principle of the modern science of biology. SEE ALSO ADAPTATION; BUFFON, COUNT (GEORGES-LOUIS LECLERC); DARWIN, CHARLES; EVOLUTION; EVOLUTION, EVIDENCE FOR; LAMARCK, JEAN-BAPTISTE; LINNAEUS, CAROLUS; MENDEL, GREGOR; NATURAL SELECTION; PALEONTOLOGY

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History of Medicine

Medical history reflects a gradual transition from supernatural to natural explanations of human diseases and disorders. Speculation with few facts characterized prehistoric medicine; that is, "supernatural" medicine men blending magic, religion, and social customs with variably effective herbal medicines. The earliest "medical text" (1550 B.C.E.), containing spells, incantations, and herbal remedies, was found in a tomb in Thebes on the Nile. Many rules of hygiene and health, some with bases in science and others in tradition, are in the Hebrew Torah (1200 B.C.E.). Medical advances came as technology and social beliefs permitted; for example, cellular biology required the development of the compound microscope, and anatomy could not develop until dissecting the human body was no longer considered a sacrilege.

Hippocrates (460–377 B.C.E.) is known for his writings and the founding of a Grecian "medical school." Physicians today still take the Hippocratic oath, an ethical code for care of the ill and dying. Greek "medicine" was mostly caring for and comforting the ill and appealing to gods. Aristotle (384–324 B.C.E.) inherited the traditions of Socrates, Plato, and Hippocrates, and perpetuated a theory of disease based on four humors and four qualities. This theory was accepted for almost two thousand years. Alexander the Great spread Grecian teachings as far as Afghanistan and Egypt.

During Roman dominance, Galen (C.E. 131–201), dissected animals (such as pigs and monkeys) because human dissection was forbidden. His experiments defined many neurological deficits, but he based his physiology on natural, vital, and animal "spirits" that reflected his religious views. Roman engineering contributed greatly to hygiene and sanitation with sewer systems and aqueducts.

Many eminent universities were founded during the Middle Ages, notably in Paris (1110), Bologna (1158), Oxford (1167), Montpellier (1181),

B.C.E. before the Common Era, equivalent to BC

C.E. Common Era, equivalent to AD

Cambridge (1209), Padua (1222), and Naples (1224). In London, St. Bartholomew's hospital (1123) and St. Thomas's hospital (1215) opened. With the human body less sacrosanct, **postmortem** examinations and dissections occurred. Medicine grew to be based on a better knowledge of anatomy, recorded in accurate drawings by Vesalius (1514–1564) and others during late Middle Ages and early Renaissance.

William Harvey's studies (1628) functionally defined the cardiovascular system, although he lacked a knowledge of capillaries. Zacharias Jansen (1590) introduced the compound microscope and subsequent improvements by Galileo Galilei and Antony van Leeuwenhoek accelerated microscopic study. Marcello Malpighi (1661) described capillaries and Leeuwenhoek described spermatozoa (1679) and bacteria (1683). Robert Boyle's chemical studies (1661) finally dispelled Aristotelian concepts of elements.

The Hunter brothers founded the Hunter School of Anatomy in London (1770). Crawford Long and William Morton invented ether anesthesia for surgery and Robert Liston amputated patients' limbs under ether anesthesia in 1846. Surgery blossomed thanks to anesthesia, but surgeons still depended on daylight and lacked sterile technique. The "golden age of surgery" began when such limitations were overcome in the twentieth century. Later highlights include heart-lung machines (1951), heart valve replacement (1952), kidney transplantation (1954), liver transplantation (1964), and heart transplantation and coronary bypass surgery (1967). Noninvasive imaging, ultrasound (1950s), and computerized axial tomography (CAT, 1972), followed later by nuclear magnetic resonance (NMR) tomography, dramatically reduced exploratory surgery.

In 1858 Rudolf Virchow published his renowned *Cellular Pathology* and Louis Pasteur proved there was no spontaneous generation of life. By 1879, Pasteur grew streptococci from a case of puerperal (childbed) fever and vaccinated sheep for anthrax (1881) while Robert Koch discovered the tuberculosis bacillus (1882). Alexander Fleming (1928) noted that *Penicillium* mold killed staphylococci, however, it took Howard Florey and Ernst Chain until 1938 to purify it. It was in general use by 1944. Viruses were first isolated and chemically defined in the 1950s and Albert Sabin's polio virus vaccine appeared in 1957. The U.S. Centers for Disease Control recognized HIV (human immunodeficiency virus) and AIDS (acquired immunodeficiency syndrome) in 1981.

In the nineteenth century, the **central nervous system** was believed to be a syncytium with all **neurons** structurally continuous. Proponents of the "neuron doctrine" (especially Santiago Ramon y Cajal) challenged this (1890s), believing the nervous system contained individual nerve cells, distinct anatomically and functionally. Ramon y Cajal and Camillo Golgi (a supporter of the syncytial theory) shared the 1906 Nobel Prize. Charles Scott Sherrington (1906) published *Integrative Action of the Nervous System* and shared the Nobel Prize with Edgar Douglas Adrian for nerve impulse work (1932). Electron microscopic studies (1960s) demonstrated points of "near contact" between neurons called synapses, final proof for the neuron doctrine.

Hormones were described by William Bayliss and Ernest Starling (1902), and Earl Sutherland described their molecular mechanisms of action in

postmortem after death

central nervous system brain and spinal cord

neuron nerve cell

SEMMELWEIS, IGNAZ PHILIPP (1818–1865)

Hungarian physician who discovered that doctors were the cause of childbed fever, which killed up to 30 percent of women who delivered a baby in a hospital. Semmelweiss showed that the fever was an infection spread by doctors who did not wash their hands. The doctors and their students dissected the bodies of women who had died of the disease, then moved directly to examine and infect healthy mothers.

the 1950s. James Watson and Francis Crick discovered deoxyribonucleic acid (DNA) structure in 1953, but the Human Genome Project wasn't initiated until 1986. Human genetic sequencing is expected to be complete in 2003 (a draft of the human genome was completed in 2001). Genetic engineering and cloning are ethical issues for the twenty-first century. SEE ALSO CRICK, FRANCIS; HARVEY, WILLIAM; HUMAN GENOME PROJECT; IMAGING IN MEDICINE; HORMONES; NEURON; PASTEUR, LOUIS; TRANSPLANT MEDICINE; LEEUWENHOEK, ANTON VON; VESALIUS, ANDREAS; WATSON, JAMES

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History of Plant Physiology

Plant physiology is concerned with the life processes of plants, and from the beginning has been focused largely on the higher green terrestrial plants, the autotrophic (self-feeding) plants that feed us animals. In part, plant physiology has roots in agriculture.

The central question of plant physiology is how do plants grow, develop, and reproduce? When primitive humans collected seeds and began raising food plants they must have noted that plants need sunlight, warmth and moist (but not wet) soil of good tilth, and that seeds from vigorous plants produced vigorous plants. They observed the beneficial effects of manuring (mentioned in the Bible; Luke 13:8). Centuries of agricultural practice produced improved varieties and cultural practices, and early studies of physiology drew on this basic knowledge of plant growth and gross anatomy.

Early Experiments on Growth

An early physiological question was where a plant gets the material with which it grows. In the early 1600s, Jan van Helmont, a Belgian physician, decided the source must be water alone. Van Helmont grew a willow seedling in 200 pounds of soil, and only added rainwater. A 164-pound tree was produced with only 57.1 grams (2 ounces) of soil lost. He knew of carbon dioxide but never dreamed that a diffuse gas could produce willow wood.

organic composed of carbon, or derived from living organisms

In the next century Antoine Lavoisier found **organic** matter to be largely formed of carbon and oxygen. Joseph Priestley, Jan Ingenhousz, and Jean Senebier demonstrated that plant leaves in light take up carbon dioxide and emit equivalent amounts of oxygen. Later, Nicholas de Saussure noted that water was involved in the process. The reverse occurred in the dark—plants **respired** like animals, taking up oxygen and emitting carbon dioxide. J. R. Mayer observed that the process converted light energy into the chemical energy of organic carbon. Thus growth of seedlings in the dark or of roots in the soil was at the expense of this energy. Therefore, by the nineteenth century, photosynthesis, although not understood bio-

respire use oxygen to burn cellular fuel

chemically, was established as the primary and essential synthetic process in plant growth.

Nutrition and Transportation

In his experiment, van Helmont assigned no importance to the two ounces of soil lost. However, starting in the late 1700s and extending into the mid 1800s, Julius Sachs and others used chemical assays to establish that quantitatively minor soil constituents of nitrogen, potassium, phosphate, sulfur, and other elements had major importance in plant growth. The long-recognized importance of manure lay with its content of these **inorganic** nutrients, especially nitrogen. It was discovered these could be added to the soil as inorganic salts, such as potassium nitrate. The organic material of manure, or the residue of its decay, contributed to improved tilth, or soil structure, but did not provide nutrients. From these discoveries came the modern agricultural use of chemical fertilizers.

What about the extensive loss of water from the soil? Van Helmont had to continuously water his willow tree with many more pounds of water than were ultimately incorporated by the tree. In 1727 an English clergyman and amateur physiologist, Stephen Hales, published *Vegetable Staticks*, an account of his pioneering studies on the transpiration, growth, and gas exchanges of plants. Hales demonstrated that water from the soil moves up the stems to the leaves where it is lost as water vapor, a process called transpiration. Subsequent research of the nineteenth and early twentieth centuries showed that the water diffuses out through **stomata** (singular stoma), pores in the leaf epidermis (outer layer of leaf cells).

With light and adequate water the two cells bounding the stoma inflate, opening the pore to gas diffusion; under dry conditions the cells grow flaccid and the pore closes, conserving water. Capillary forces originating in the microscopic pores of the leaf mesophyll (internal green photosynthetic cells), with some contribution from **osmosis**, pull columns of water up the open vessels and tracheids of the **xylem** (wood) carrying nutrient salts from the roots. The coherence between water molecules and their adherence to cell walls prevents the taut water columns from breaking even in trees of great height. This scheme was first proposed in 1895 by Henry Dixen and John Joly. Numerous researchers in the twentieth century confirmed and refined this "cohesion-tension" theory of transportation.

Hales also measured the root pressure (forced bleeding) of decapitated plants. Subsequent work showed that under conditions of good soil moisture and aeration, roots actively secrete high concentrations of salt into the root xylem creating a high osmotic pressure that forces water up the stem and out pores at the tips of leaves (guttation). In 1926, E. Munch proposed a similar mechanism for **translocation**, the movement of sugars from leaves to roots and other plant parts. This mechanism is known as the pressure-flow model.

Cellular and Molecular Plant Physiology

By the twentieth century, plant physiologists increasingly turned to chemistry and physics for assistance with fundamental questions. They also

Stephen Hales conducted pioneering experiments on the transpiration, growth, and gas exchanges of plants.

inorganic not bonded to carbon

stomata openings in leaves for gas exchange, surrounded and regulated by guard cells

osmosis passage of water through a membrane in response to concentration differences

xylem water-transporting system in plants

translocation movement of sugars and other nutrients throughout a plant
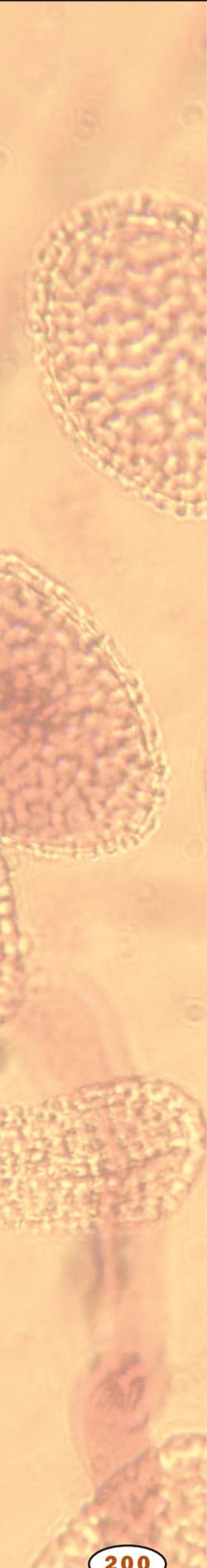
ion an electrically charged particle

hormone molecule released by one cell to influence another

enzyme protein that controls a reaction in a cell

abscission shedding of leaves; falling off

circadian related to a day or daylength

organelle membrane-bound cell compartment

carbohydrates sugars, starches, and other molecules combining carbon, hydrogen, and oxygen and serving as fuel or structural components

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

established their own societies with journals to publish their findings, which had a catalytic effect in increasing the level and amount of research. A great deal of the fundamental biochemistry of cell growth and function, known from the more extensive medical, animal, and microbiological research, was found to apply to plant cells. Anatomical studies gave structural details to support physiological findings, and submicroscopic cell structure was revealed by the electron microscope.

All the mineral nutrients required for plant growth were established. The key to their selective uptake from the soil and transport into the root xylem proved to lie with an energy-requiring proton (hydrogen **ion**) pumping mechanism in the cell membranes.

Environmental, hormonal, and genetic controls on growth and development have been extensively explored, but there is still more to learn. Ethylene, a simple two-carbon gas generated by plants initiates fruit ripening and regulates aspects of seed germination. Phototropisms (bending in response to unilateral light, investigated by Charles Darwin), and geotropisms (root growth down, stem growth up) were found to be due to displacement of a cell growth **hormone**, or auxin. In some circumstances, auxins could also elicit cell division (root formation in stem cuttings). Other hormones, the gibberellins, regulate cell division at the stem apex and activate **enzyme** formation in seed germination.

Attempts to culture plant tissues led to discovery of more cell division hormones, the cytokinins. Another type of hormone, abscisic acid, initiates the senescence and **abscission** of leaves in the fall, and causes the stomata to close under water stress. Additional growth regulating compounds are being found and investigated but a coordinated picture of hormone interaction is lacking.

Photoperiodism, the regulation of flowering by day length was discovered. Sleep movements, such as the drooping of bean leaves in the evening, were found to be controlled by a biological "clock," a **circadian** rhythm, not by the onset of darkness. In 1952, phytochrome was discovered and found to be the pigment at the center of photoperiodism.

In recent years there has been a major shift to molecular genetics in attempts to locate the genes responsible for physiological processes. In photosynthesis chlorophyll structure was determined and localized in the internal membranes of the chloroplasts of the mesophyll cells. Red and blue portions of the light spectrum were found effective, leading to the discovery that two light reactions are required. In the 1930s, C. B. van Neil used radioactive water to show that water, not carbon dioxide, was the source of oxygen released during photosynthesis. Sugar was found to be synthesized in the stroma (fluid part) of the chloroplast, and the molecular details of its creation were worked out by Melvin Calvin and Andrew Benson. All plant cells were found to respire, an energy-yielding process essentially the same as that in animals, involving another membranous **organelle**, the mitochondrion, and yielding metabolic energy available for transport reactions and synthesis of cell substance.

The formation of fats and oils from **carbohydrates** was found to be similar to that in animals, but plants had the added ability to transform oils in germinating seeds into carbohydrates such as the **glucose** used in **cellu-**

lose wall formation. The symbiotic relationships of plants and microorganisms was explored, notably in the cases of reduced nitrogen formation from atmospheric nitrogen by nodule bacteria.

At the end of twentieth century, the small mustard plant *Arabidopsis thaliana* took center stage in the attempt of scientists to understand plant **genomes**. The full sequence of this genome was elucidated in 2000 by an international consortium of plant geneticists. SEE ALSO C4 AND CAM PLANTS; DE SAUSSURE, NICOLAS THÉODORE; HORMONES, PLANT; INGENHOUSZ, JAN; PHOTOPERIODISM; RHYTHMS OF PLANT LIFE; WATER MOVEMENT IN PLANTS

John Hanson

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

genome total genetic material in a cell or organism

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Homeostasis

Living cells can function only within a narrow range of such conditions as temperature, **pH**, **ion** concentrations, and nutrient availability, yet living organisms must survive in an environment where these and other conditions vary from hour to hour, day to day, and season to season. Organisms therefore require mechanisms for maintaining internal stability in spite of environmental change. American physiologist Walter Cannon (1871–1945) named this ability homeostasis (*homeo* means "the same" and *stasis* means "standing or staying"). Homeostasis has become one of the most important concepts of physiology, physiological ecology, and medicine. Most bodily functions are aimed at maintaining homeostasis, and an inability to maintain it leads to disease and often death.

The human body, for example, maintains blood pH within the very narrow range of 7.35 to 7.45. A pH below this range is called acidosis and a pH above this range is alkalosis. Either condition can be life-threatening. One can live only a few hours with a blood pH below 7.0 or above 7.7, and a pH below 6.8 or above 8.0 is quickly fatal. Yet the body's metabolism constantly produces a variety of acidic waste products that challenge its ability to maintain pH in a safe range.

Body temperature also requires careful homeostatic control. On a spring or fall day in a temperate climate, the outdoor Fahrenheit temperature may range from the thirties or forties at night to the eighties in the afternoon (a range of perhaps 4 to 27 degrees Celsius). In spite of this environmental fluctuation, our core body temperature is normally 37.2 to 37.6 degrees Celsius (99.0 to 99.7 degrees Fahrenheit) and fluctuates by only 1 degree or so over the course of 24 hours. Indeed, if core body temperatures goes below 33 degrees Celsius (91 degrees Fahrenheit) a person is likely to die of **hypothermia**, and if it goes above 42 degrees Celsius (108 degrees Fahrenheit), death from hyperthermia is likely.

pH measure of acidity or alkalinity; numbers below 7 are acid, above are basic

ion an electrically charged particle

hypothermia subnormal temperature of the body
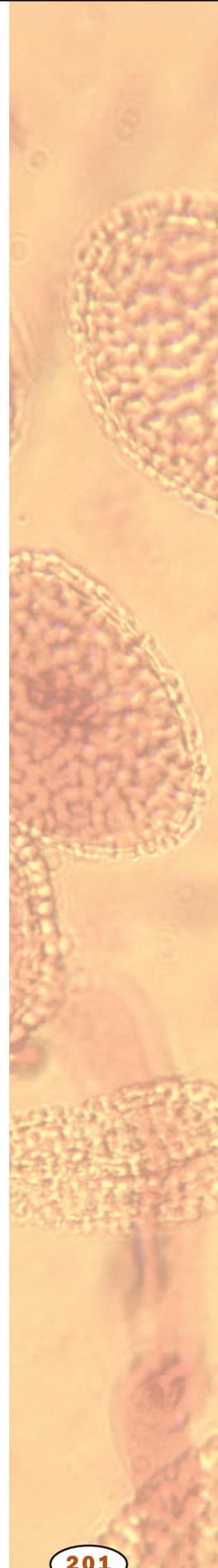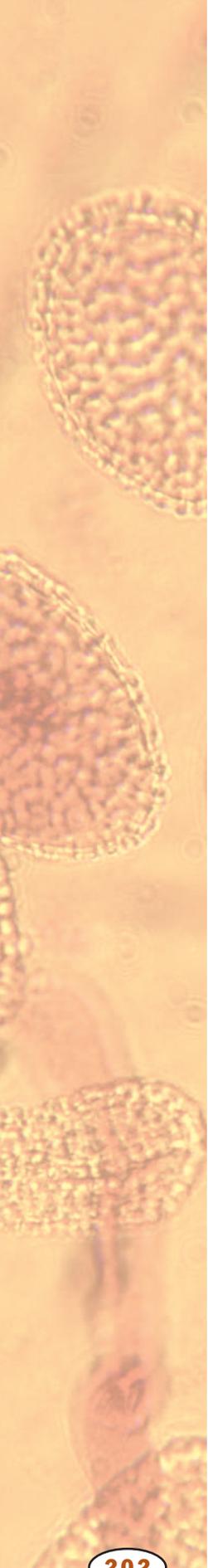
Internal conditions are not absolutely stable but fluctuate within a narrow range around an average called the set point. The set point for core body temperature, for example, is about 37.4 degrees Celsius, but the temperature fluctuates within about ($\pm$0.5 degrees Celsius. Thus, it is more accurate to say the body maintains an internal dynamic equilibrium than to say it maintains absolute stability.

Negative Feedback and Stability

The usual means of maintaining homeostasis is a general mechanism called a negative **feedback** loop. The body senses an internal change and activates mechanisms that reverse, or negate, that change.

An example of negative feedback is body temperature regulation. If blood temperature rises too high, this is sensed by specialized neurons in the hypothalamus of the brain. They signal other nerve centers, which in turn send signals to the blood vessels of the skin. As these blood vessels dilate, more blood flows close to the body surface and excess heat radiates from the body. If this is not enough to cool the body back to its set point, the brain activates sweating. Evaporation of sweat from the skin has a strong cooling effect, as we feel when we are sweaty and stand in front of a fan.

If the blood temperature falls too low, on the other hand, this is also sensed by the hypothalamus and signals are sent to the cutaneous arteries (those supplying the skin) to constrict them. Warm blood is then retained deeper in the body and less heat is lost from the surface. If this is inadequate, then the brain activates shivering. Each muscle tremor in shivering releases heat energy and helps warm the body back toward its 37 degrees Celsius set point.

In both cases, specialized neurons sense the abnormal body temperature and activate corrective negative feedback loops that return the temperature to normal. As a result, body temperature seldom goes more than 0.5 degrees Celsius above or below its set point. Other negative feedback loops regulate blood sugar concentration, water balance, pH, and countless other variables. Many such loops are regulated by the nervous system, and others by the hormones of the endocrine system.

Positive Feedback and Rapid Change

The counterpart to negative feedback is the positive feedback loop, a process in which the body senses a change and activates mechanisms that accelerate or increase that change. This can also aid homeostasis, but in many cases it produces the opposite effect and can be life-threatening.

An example of its beneficial effect is seen in blood clotting. Part of the complex biochemical pathway of clotting is the production of an **enzyme** that forms the matrix of the blood clot, but also speeds up the production of still more thrombin. That is, it has a self-**catalytic**, self-accelerating effect, so that once the clotting process begins, it runs faster and faster until, ideally, bleeding stops. Thus, this positive feedback loop is part of a larger negative feedback loop, one that is activated by bleeding and ultimately works to stop the bleeding.

Another example of beneficial positive feedback is seen in childbirth, where stretching of the uterus triggers the secretion of a **hormone**, oxytocin,

feedback process in which the output or result influences the rate of the process.

enzyme protein that controls a reaction in a cell.

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

catalytic aiding in the reaction of

hormone molecule released by one cell to influence another

which stimulates uterine contractions and speeds up labor. Yet another is seen in protein digestion, where the presence of partially digested protein in the stomach triggers the secretion of hydrochloric acid and pepsin, the enzyme that digests protein. Thus, once digestion begins, it becomes a self-accelerating process.

Often, however, positive feedback produces the very opposite of homeostasis: rapid loss of internal stability with potentially fatal consequences. For example, if the death of a small area of heart tissue triggers a heart attack (myocardial infarction), the heart pumps an inadequate amount of blood. Thus, the heart muscle itself is deprived of blood flow, and still more begins to die. This can lead to a rapid worsening of cardiac function until a person dies. Many diseases involve dangerous positive feedback loops.

Homeostasis, while described here with examples from human physiology, is a fundamental property of life and a necessity for survival of all living things—not just humans but all other animals as well as bacteria, plants, fungi, and protists. It enables all living organisms to maintain internal stability in spite of a ceaselessly changing and challenging environment. SEE ALSO BLOOD CLOTTING; BLOOD SUGAR REGULATION; BRAIN; ENDOCRINE SYSTEM; HORMONES; HYPOTHALAMUS; NERVOUS SYSTEMS; OSMOREGULATION; PHYSIOLOGICAL ECOLOGY; TEMPERATURE REGULATION

Kenneth S. Saladin

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Hormones

Hormones are molecules released by a group of cells in the body that influence the behavior of another group of cells. Hormones are the chemical signals of the **endocrine** system, the group of glands that, along with the nervous system, controls the body's responses to internal and external stimuli. Hormones are carried to their target cells in the bloodstream.

All hormones bind at the target cell to a specific receptor, a **protein** made by the target cell. When the hormone binds to the receptor, it causes a change in the receptor's **conformation**, or shape. This conformation change allows the receptor to fit with other cell molecules in a way it could not before, thus triggering new activities in the cell. While a hormone such as testosterone (produced in the testes) reaches all cells in the body, only some cells have testosterone receptors, and therefore only those cells are sensitive to testosterone's effects. Similarly, different receiving cells make different sets of molecules to interact with the testosterone receptor, and this controls the exact response the target cell exhibits.

endocrine related to the system of hormones and glands that regulate body function

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

conformation three-dimensional shape

adrenaline, noradrenaline, or peptide

membrane receptor (unique to hormone)

cAMP

AMP

cell-specific proteins activated by cAMP

steroid

steroid receptor

thyroxine

thyroxine receptor
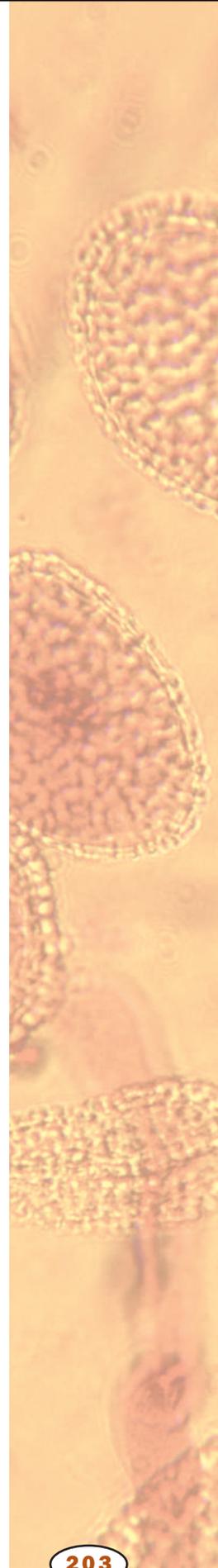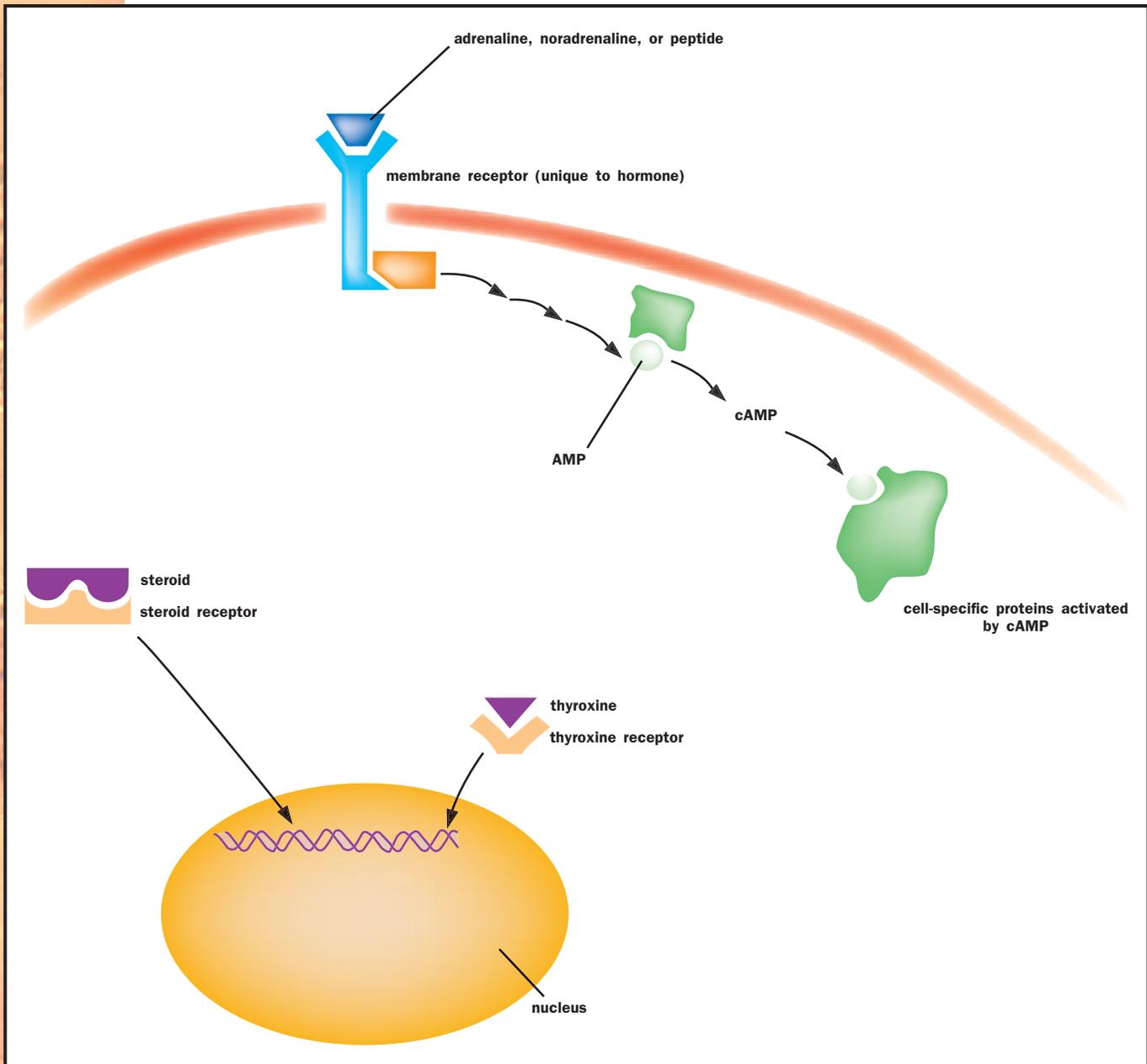
nucleus

Hormones differ in where their receptors are found in the target cell. Some are located in the nucleus, some in the cell cytoplasm, and still others bind to a receptor on the membrane surface.

amino acid a building block of protein

Hormones are classified based on their chemical structures. Peptide hormones are chains of **amino acids**. Insulin and glucagon, which help control blood sugar, are peptide hormones, as are the hormones of the hypothalamus and the pituitary gland. **Steroid hormones** are **lipids** (fatlike molecules) whose structures are derived from cholesterol. Hormones of the sex organs and the adrenal cortex (part of the adrenal gland) are steroids. Monoamine hormones are made by modifying amino acids. These hormones include adrenaline and noradrenaline made by the adrenal medulla, thyroid hormone (thyroxine), and melatonin from the pineal gland in the brain.

Hormones also differ in where their receptors are found in the target cell, and the type of effect they cause when they bind to their receptors.

The receptor for thyroxine is located in the **nucleus**, while the receptors for steroid hormones are found in the cell's **cytoplasm**. In both cases, the hormone binds to the receptor to form a complex, and then the hormone-receptor complex activates specific **genes** within the nucleus, leading to synthesis of new proteins.

Adrenaline, noradrenaline, and the peptide hormones do not enter the target cell. Instead, they bind to a receptor on the membrane surface. The receptor extends through the membrane, and when the outside portion binds to the hormone, the inside portion of the receptor undergoes a conformation change. This change sets off a cascade of reactions inside the cell, ultimately leading to an increase in concentration of one or another internal messenger molecules. The most common of these so-called "second messengers" (the hormone is the "first messenger") are calcium **ion** and cyclic **AMP** (cAMP), a type of **nucleotide**. The second messenger then triggers other activities in the cell, depending on the cell type. In muscle, adrenaline causes cAMP buildup, which causes breakdown of **glycogen** to release **glucose**, which the muscle cell uses to support increased activity.

Hormones that bind to external receptors and work through second messengers affect pre-existing proteins within the cell. Because of this, they typically cause much faster effects than those that bind to internal receptors, which influence creation of new proteins. For example, adrenaline's effects last from minutes to hours at the most, while testosterone's effects last from days to months or more. SEE ALSO ADRENAL GLAND; AMINO ACID; BLOOD SUGAR REGULATION; ENDOCRINE SYSTEM; FEMALE REPRODUCTIVE SYSTEM; HOMEOSTASIS; HYPOTHALAMUS; MALE REPRODUCTIVE SYSTEM; NUCLEOTIDES; PANCREAS; PITUITARY GLAND; THYROID GLAND; TRANSCRIPTION

Richard Robinson

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Hormones, Plant

Plant hormones are chemical messengers that are produced in one part of the plant and have a physiological effect on a target tissue that may be distant from the site of production. When hormones reach the target tissue they can: (1) have a direct effect on the target tissue causing a rapid metabolic response; (2) involve the use of a second messenger within target cells; and/or (3) affect **transcription** of nuclear deoxyribonucleic acid (DNA). Unlike animals, plants have no specialized organs designed solely for hormone synthesis and **secretion**. Leaves, stem tips, root tips, flowers, seeds, and fruits all produce hormones. Most plant hormones are functional at very low concentrations.

Auxins, cytokinins, gibberellins, abscisic acid, and ethylene are the best known plant hormones. All are in some way involved in regulating plant growth and development. Some promote growth by stimulating cell enlargement or division while others inhibit growth by inducing dormancy or promoting senescence. Recently brassinolides, jasmolates, and salicylic acid have been shown to have hormonal function.

steroid hormone group of hormones that include estrogen, testosterone, and progesterone

lipid fat or waxlike molecule, insoluble in water

nucleus membrane-bound portion of cell containing the chromosomes

cytoplasm material in a cell, excluding the nucleus

gene portion of DNA that codes for a protein or RNA molecule

ion an electrically charged particle

AMP adenosine monophosphate, form of ATP after removal of two phosphate groups

nucleotide the building block of RNA or DNA

glycogen complex carbohydrate used as storage in animals and some other organisms

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

transcription messenger RNA formation from a DNA sequence

secretion material released from the cell

Principles of Hormone Function

Often two or more hormones work synergistically. In a classic 1957 experiment, Skoog and Miller provided evidence that auxins and cytokinins work together in the differentiation of plant organs. Using tobacco tissue culture, they showed that when a tissue culture medium contains low concentrations of auxin *and* optimal cytokinin levels, then formation of shoots is favored. In contrast, when the culture medium is supplied with optimal concentrations of auxin combined with low concentrations of cytokinins, root formation is favored.

apical at the tip

lateral side-to-side

Hormones sometimes work antagonistically. **Apical** dominance is a process in which **lateral** buds of stems remain dormant as long as the stem apex remains intact. It has been shown that auxin produced in the stem apex is responsible for maintaining lateral bud dormancy by causing cells in the lateral buds to produce another hormone, ethylene, which is a growth inhibitor. During early spring, rapidly growing root tips will generate a high concentration of cytokinin that counteracts the effect of ethylene on the lateral buds of the stem. The lateral buds released from dormancy by cytokinins can then begin growth on their own.

Auxins

Auxins were the first class of plant hormones to be identified. Many auxins, both natural and synthetic, are now known and all have similar effects on plant growth and development. The most widely studied naturally occurring auxin is indol-3-acetic acid (IAA), which is chemically related to the **amino acid** tryptophan. IAA can be synthesized from tryptophan in intact cells but other synthetic pathways are available. Because auxins can have an effect in very low concentrations, plants regulate synthesis and disassembly of auxin very precisely. Auxins are produced in young shoots and always travel downward in the plant from shoot to root. This polar movement of auxin is not well understood but requires calcium **ions** (Ca^{2+}) and most likely involves special carriers in cell membranes. Naturally occurring auxins promote cell enlargement, are important in tropisms, prevent **abscission**, promote fruit development, and are involved in apical dominance. Synthetic auxins such as naphthalene acetic acid are used as rooting hormones. Other synthetic auxins include 2,4-D (2,4-dichlorophenoxyacetic acid) and 2,4,5-T (2,4,5-trichlorophenoxyacetic acid) that are used as weed killers.

amino acid a building block of protein

ion an electrically charged particle

abscission shedding of leaves; falling off

pH measure of acidity or alkalinity; numbers below 7 are acid, above are basic

enzyme protein that controls a reaction in a cell

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

plasticity change form

endoplasmic reticulum network of membranes within the cell

kinase enzyme that adds a phosphate group to another molecule, usually a protein

The effect of IAA on cell enlargement has been well studied. IAA stimulates special pumps in the cell membrane of target cells to release H^+ ions into the cell wall, resulting in a **pH** drop to approximately 5.0 in the cell wall. **Enzymes** that are pH-dependent then break down important structural bonds between **cellulose** microfibrils causing an increase in cell wall **plasticity**. As the cell wall becomes more plastic, water is able to flow in and the cell enlarges. Auxin also may have an effect on transcription of nuclear DNA that can contribute to cell enlargement.

Calcium acts as a second messenger in processes involving auxin. Auxin stimulates the release of $Ca2^+$ from the vacuole and **endoplasmic reticulum** in target tissues which affects Ca-dependent enzymes, including **kinases**, phophatases, and phospholipases.

Plant Hormones: Roles

Hormone	Role
Auxins	Involved in differentiation of vascular tissue, control cellular elongation, prevention of abscission, involved in apical dominance and various tropisms, stimulate the release of ethylene, enhance fruit development
Cytokinins	Affect cell division, delay senescence, activate dormant buds
Gibberellins	Initiate mobilization of storage materials in seeds during germination, cause elongation of stems, stimulate bolting in biennials, stimulate pollen tube growth
Abscisic Acid	Maintains dormancy in seeds and buds, stimulates the closing of stomata
Ethylene	Causes ripening of climacteric fruits, promotes abscission, causes formation of aerenchyma tissue in submerged stems, determines sex in cucurbits
Jasmonates	Involved in response to environmental stresses, control germination of seeds
Brassinolides	Promote of elongation, stimulate flowering, promote cell division, can affect tropic curvature
Salicylic Acid	Activates genes involved with plant's defense mechanisms

Auxins are involved in tropisms, which are growth responses to directional environmental stimuli such as light, gravity, and touch. In phototropism, unidirectional light will cause auxin to move toward the darkened side of the organ and stimulate enlargement of cells on the darkened side. This causes the organ to bend toward the light. This effect is often seen in potted plants growing in windowsills.

Other Plant Hormones

Cytokinins (for example, zeatin, isopentenyl adenine) have an effect on cell division. As previously mentioned, cytokinins work synergistically with auxin in the control of tissue and organ differentiation. Cytokinins are produced in root tips and may be transported in the **xylem** toward the shoot.

Gibberellins are a very large class of compounds, all with a similar chemical makeup. There have been as many as eighty-four gibberellins identified (named GA1 through GA84), but GA3, called gibberellic acid, has been the most studied. Gibberellins promote cell elongation, overcome genetic dwarfism, stimulate **bolting** in biennials, and are involved in seed germination. During the germination of grass seeds the imbibition (intake) of water stimulates the production of gibberellins by the embryo that diffuse throughout the seed. A **protein**-rich layer just internal to the seed coat, the aleurone layer, responds to gibberellins by synthesizing hydrolytic enzymes that aid in mobilization of stored food in the **endosperm** for use by the embryo.

Abscisic acid (ABA), is a growth inhibitor that, despite its name, is probably not involved in leaf or fruit abscission. One role of ABA is the stimulation of **stomatal** closure. When ABA binds to receptors on guard cell membranes, chloride ion channels open, letting chloride ions move out of the **guard cells**. The resulting depolarization of the membrane stimulates the movement of potassium ions (K+) ions out of guard cells, which then lose water, causing the stomata to close.

Ethylene is the only plant hormone that is a gas. Ethylene is also considered a growth inhibitor as it may have a role in causing bud dormancy, and it is involved with leaf abscission, causes fruit ripening, may determine

xylem water-transporting system in plants

bolting sudden spurt of growth

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

endosperm nutritive tissue within a seed

stomata openings in leaves for gas exchange, surrounded and regulated by guard cells

guard cells paired cells on leaves that control gas exchange and water loss

steroids hormones such as testosterone or estrogens that control many aspects of physiology

sex in cucurbits (melon family), and stimulates formation of aerenchyma (gas transport tissue) in submerged roots and stems.

Brassinolides are plant **steroids** (many animal hormones are steroids) that may be involved in the light-induced expression of genes. SEE ALSO CELL WALL; MERISTEMS; PLANT DEVELOPMENT; SENESCENCE

George Wittler

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Horticulturist

Horticulturists find work in two distinct areas: agriculture and landscape design. The training for both of these specialties is the same but the day-to-day activities are different. People with a Bachelor of Science degree in botany, biology, or agriculture may find employment as horticulturists after college. A strong training in the basic sciences, especially chemistry and biology, is necessary.

An agricultural horticulturist is responsible for investigating the best techniques for managing the aboveground aspects of agriculture. These include pruning, mulching, trellising, plant spacing, and pollination. His or her partners in this endeavor are the agronomist, who is concerned with fertilization, irrigation, and drainage, and the integrated pest manager who is concerned with plant **pathogens** and pests. Each must know the essentials of the others' fields and all must work together to produce profitable food and fiber crops.

pathogen disease-causing organism

The landscape horticulturist is concerned with all aspects of plant growth: aboveground aspects and fertilization, irrigation, and drainage. The landscape horticulturist must also have training in art and architecture. It is essential to know the requirements of decorative plants. Horticulturists work for commercial nurseries; schools or businesses with a "campus" or landscaped grounds; entertainment centers such as theme parks; and local, state, and federal governmental agencies (such as public works departments) for the creation of green spaces and color spots along highways, in city parks, or in residential areas. SEE ALSO AGRICULTURE; AGRONOMIST; PROPAGATION

Dennis Carnes

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Human Evolution

It is remarkable that the unique qualities of humans—language, advanced thought, and culture—evolved through the same processes that shaped the adaptations of all other creatures on earth: natural selection. How this came

Sites of early civilizations.
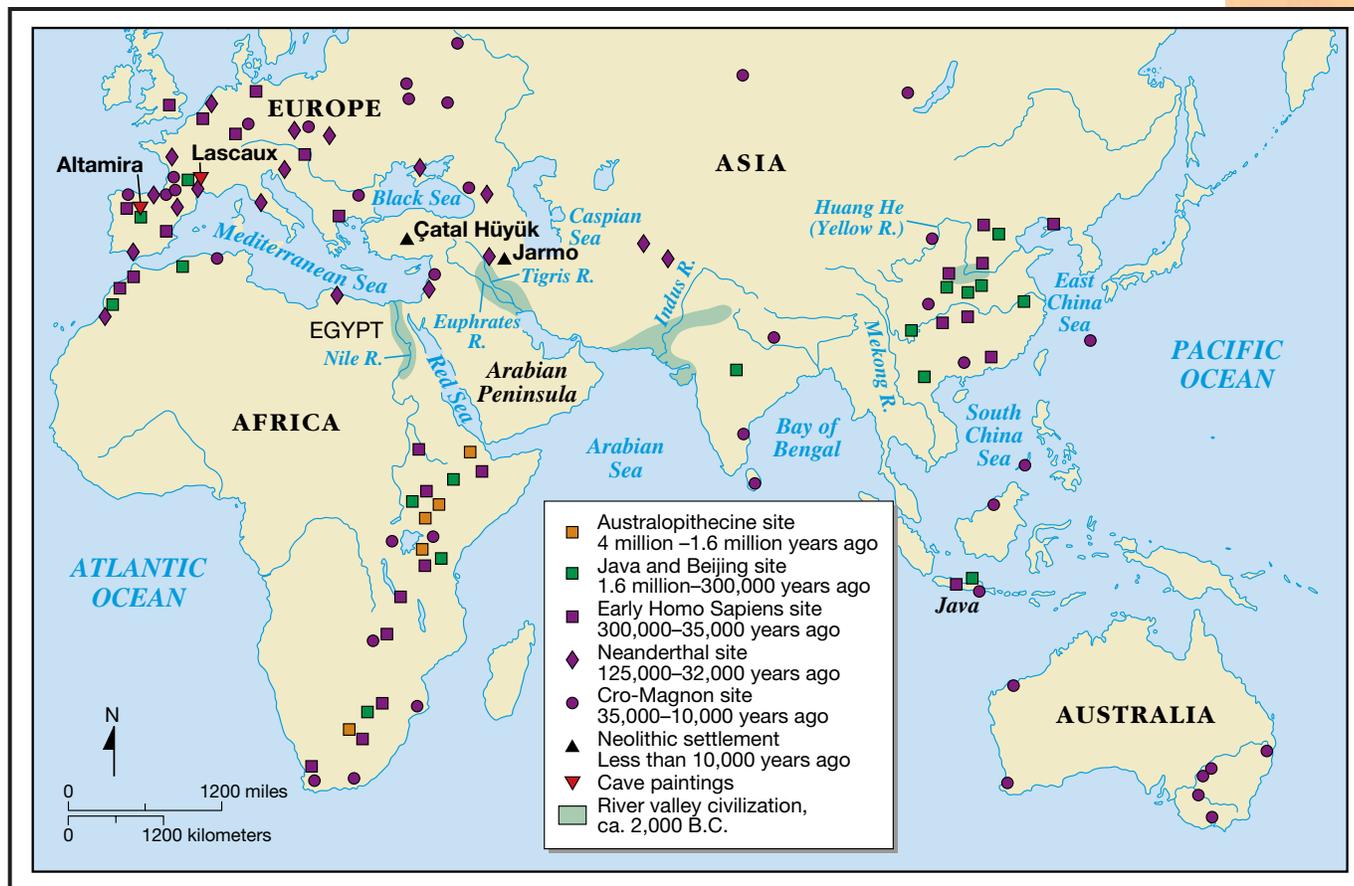
about is perhaps the most fascinating question of all time. The direct evidence for human evolution has increased enormously since the early 1990s via the discovery of hundreds of new fossils, including three new genera and even more new species; and via the comparisons of modern and ancient deoxyribonucleic acid (DNA). Great leaps forward are being made in science because of this proliferation of information.

Humans and our ancestors are called hominins, going back to the time of the split from the **lineage** of human's closest relatives, the chimpanzees. (Until recently the term hominid was used, but based on genetic relatedness and the rules of zoological nomenclature, the word hominid should apply to *both* the chimpanzee and human clades [lineages].) Humans have evolved various traits that have diverged from the typical great ape collection of characters; notable is human's commitment to standing on two legs (bipedalism) rather than four, increased fine motor dexterity making possible extensive use of tools, prolonged period of infancy and childhood, increased brain size, language, great cultural complexity and economic interdependence.

lineage ancestral line

Ape Ancestors

During the Miocene epoch (23 to 5 million years ago), when our superfamily, the Hominoidea (apes) flourished and speciated, more than twenty genera and about twice that number of species in the Hominoidea family. Many of these species went extinct, and today there are only five genera of apes: gibbons, orangutans, gorillas, chimpanzees/bonobos, and humans. The

origins of the hominins remain obscure. Genetic comparisons and the molecular clock suggest that the human-chimp lines split in the late Miocene about 6 million years ago. The fossil record is very incomplete at this time, and neither fossils of ancestral chimpanzees nor fossils that are clearly ancestral to both lines are known. However, field research since the mid-1990s has resulted in several fossils from this time period, and researchers hope that this trend of discovery will continue and scientists' understanding of the origin of hominins will improve over the twenty-first century.

Scientists do know this: Hominins evolved from an ape that was similar to the living African apes, and the human lineage did not spread beyond Africa into Eurasia until about 1.8 million years ago. The early hominins lived in an array of habitats, but most evidence points to wooded **savannas** (a type of grassland) as a principal one. There is solid evidence that significant amounts of bipedal behavior preceded other major events such as increased brain size or tool use.

savanna open grassland with sparse trees

Earliest Hominins

The earliest named hominin, *Orrorin tugenensis*, was discovered in 2000 in eastern Kenya, and is believed to have lived 6 million years ago. Thigh bones suggest that this species spent a significant amount of time bipedally. In the 5-million-year time range there are several fragmentary fossils from East Africa, but they are difficult to associate with particular species. At 4.4 million years ago, another genus and species, *Ardipithecus ramidus*, is present. This species has many traits, especially in the teeth, that are between chimpanzees and later hominins (australopithecines) in size and character (for example canine size, enamel thickness, and size of the cheek teeth). Discovery of a third new early hominin, *Kenyanthropus platyops*, was published in 2001 by Meave Leakey and colleagues.

The newly discovered *Kenyanthropus platyops* dates from the same era as the *Australopithecus* but belongs to a previously unknown species. The new skull has a more humanlike face with much smaller teeth. Its name means "the flat-faced human from Kenya."

Between 3.9 and 2.0 million years ago there was a proliferation of australopithecine species, including the "gracile" australopithecines of the genus *Australopithecus*, with five commonly recognized species, and the robust australopithecines of the genus *Paranthropus*, with three commonly recognized species. These australopithecine species are variable, but general trends include: significant amounts of terrestrial bipedalism, with some species also retaining significant arboreal adaptations; brains still very close to chimpanzees' in size; tool use generally minimal; very large grinding cheek teeth and chewing muscles, consistent with a largely vegetarian diet including many tough foods; canine teeth reduced in size; and male body size much larger than females (that is, high degrees of sexual dimorphism).

Origins of *Homo*

The origins of the human genus *Homo* is also being reexamined in the early twenty-first century. There are many fossils in the 2.4- to 1.6-million-year time range in Africa that have variously been assigned to *Homo habilis*, *Homo rudolfensis*, or *Homo* species, but many still have large cheek teeth, smallish brains, and faces shaped like australopithecines. Some of these fossils even retain many arboreal adaptations. Thus the majority of these specimens will probably be moved into the genus *Australopithecus*; reserving the genus *Homo* to include only those specimens which are clearly more closely related to humans.

Considered this way, the human genus evolved nearly 2 million years ago with the appearance of *Homo ergaster*. *Homo ergaster*, personified by the amazingly well-preserved West Turkana skeleton of a twelve-year-old boy, is a markedly different creature than australopithecines, though still not modern. They were tall, lanky, long-legged with body proportions nearly the same as modern humans, committed to efficient terrestrial bipedalism at the expense of arboreality, and larger—about the size of modern humans. This increase in body size was accompanied by an increase in brain size— the largest examples having **cranial** capacities (brain cavities) of about 900 cubic centimeters (cc), the smaller examples closer to 650 cc. (Modern human brains are about 1300 cc, chimpanzees are about 400 cc.) Because of the increase in body size, this is not a large relative increase in brain size over earlier hominids. The trend toward increasingly large cheek teeth is reversed in our lineage: There is a reduction in cheek tooth size, generally thought to reflect consumption of higher quality foods and/or more food preparation.

cranial related to the cranium, or brain cavity

Homo ergaster also used tools. The earliest archaeological sites, which contain the debris of stone tool manufacture and animal bones eaten by hominins, date to 2.6 million years ago in Ethiopia. The earliest stone tools are simply sharp flakes broken off rocks that were used as cutting tools. It is difficult to say which species made and used these earliest tools, in fact it probably included some of the australopithecine species. By 1.5 million years ago the stone tool industries include more elaborate, symmetrically flaked rocks, called Acheulian hand axes.

Spread Beyond Africa

Immediately after the evolution of *Homo ergaster* there was an initial, but probably short-lived, spread beyond Africa into the Near East, Far East (Java), and southern Spain. Either something about *H. ergaster* or the environment must have facilitated this spread. Was it the increase in body size? Did their ecological position shift up as they became more successful at acquiring meat, and therefore their home ranges needed to increase to encompass more and more space? Was it learning to control fire? Or changes in social organization? More research will focus on these questions, but whatever caused this initial spread, there is very little evidence for *Homo* outside of Africa again for about 1 million years, when more sites are found around Europe and Asia.

The populations in the Far East (China and Indonesia) evolved into a local species called *Homo erectus*, which may have survived until into the Late Pleistocene (approximately 50,000 years ago). These fossils have long low skulls with thick brows and cranial capacities near 1000 cc. Interestingly, *H. erectus* seems to have been contemporary with other species of archaic *Homo*, specifically species that evolved into *Homo neanderthalensis* in Europe and the Near East, and another that evolved into anatomically modern humans (AMH) in Africa. All of these species have long, low skulls, big faces, and large brow ridges, but differ in details of the cranial anatomy, and some have larger cranial capacities. They are robust with massive skeletons and muscles, reflecting a large dependency on brawn to cope with the world. Archaeological evidence for accomplished hunting in the form of wooden spears is clear by 400,000 years ago.
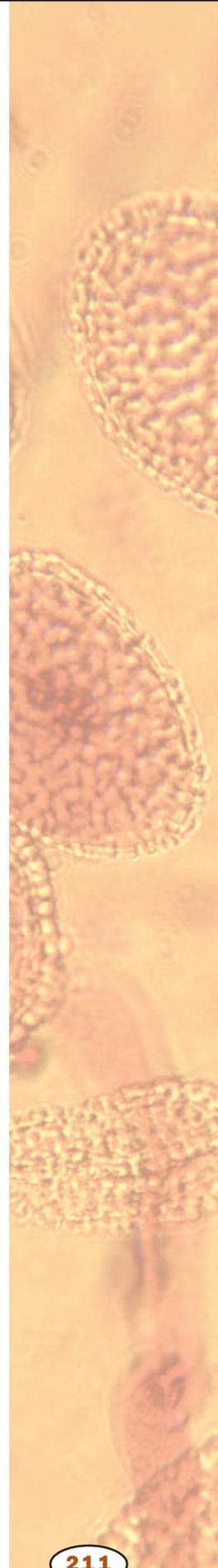
In Europe Neanderthals evolve into their classic form: extremely strong, stocky, and robust, with large eyes and noses and jutting faces; their bodies seem well adapted to the cold Pleistocene. Their tool kit was more elaborate, including stone-tipped spears, and archeological and isotopic evidence indicates a great reliance on meat in the diet. Nonetheless, except in a very few instances when Neanderthals were contemporary with modern humans, there is little to no evidence for art. For this reason, many anthropologists believe Neanderthals did not have modern language.

Anatomically Modern Humans

Meanwhile, archaic *Homo* evolved into anatomically modern humans in Africa. Throughout this time range (between 200,000 and 100,000 years ago) there are increasing bits of evidence for art and symbolism in the form of red ochre, beads, and composite tools in Africa while they are still absent in Europe, and it is during this period that genetic evidence from modern humans suggests that anatomically modern humans evolved. Indeed, the earliest anatomically modern humans fossils come from Africa and the Near East, just over 100,000 years ago. Anatomically modern humans are characterized by a reduction in skeletal robustness and strength, probably related to greater reliance on technology and culture rather than brute strength. Cranial capacity remains about the same as in the more robust predecessors, but the face and teeth are smaller, the forehead becomes high and the chin juts out. Cultural elaboration is evident in increased number of tools types, regional variation in style, more composite tools, and notably, art.

There is a minority of anthropologists who consider all the *Homo* specimens to be from one diverse species. In the early twenty-first century, the majority of anthropologists believe that the fossil, archaeological, and genetic evidence concur that anatomically modern humans evolved in Africa about 200,000 to 150,000 years ago, and spread out from there to Europe and Asia as recently 100,000 to 25,000 years ago (depending on where), replacing the archaic *Homo* species, for example, Neanderthals and *Homo erectus*, and these later species may have contributed relatively little genetic diversity to the human gene pool. The information scientists have thus suggests that all humans across the globe today are very closely related to one another. SEE ALSO BIOLOGY OF RACE; EVOLUTION; GRASSLAND; LEAKEY FAMILY; NATURAL SELECTION; POPULATION GENETICS; PRIMATE

Martha Tappen

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nucleotide the building block of RNA or DNA

base pair two nucleotides (either DNA or RNA) linked by weak bonds

Human Genome Project

The Human Genome Project (HGP), the determination of the complete **nucleotide** sequence of all of the more than three billion **base pairs** of de-

oxyribonucleic acid (DNA) in the **nucleus** of a human cell, is one of the greatest scientific undertakings in the history of humankind. The project reached an important milestone in 2001 with the completion of the "first draft" of the entire sequence. The HGP promises to bring unprecedented scientific rewards in the discovery of disease-causing **genes**, design of new drugs, understanding developmental processes, and determining the origin and evolution of the human race. It has also raised many ethical issues.
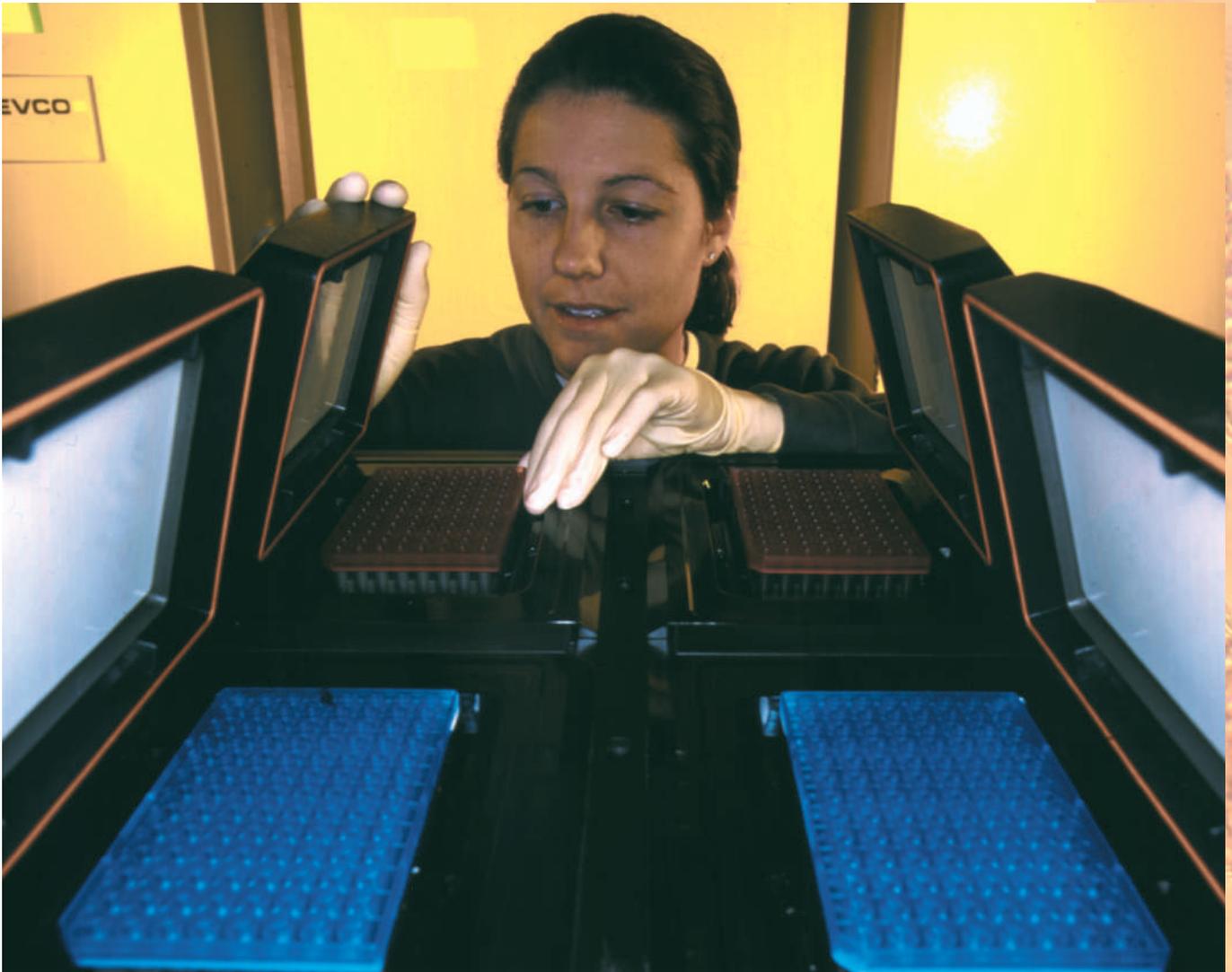
nucleus membrane-bound portion of cell containing the chromosomes

gene portion of DNA that codes for a protein or RNA molecule

Origins

The original impetus for the HGP came from the U.S. Department of Energy (DOE) shortly after World War II. In 1945 there were many survivors of the atomic bombs dropped on Hiroshima and Nagasaki who had been exposed to high levels of radiation. In 1946 geneticist and Nobel Prize winner H.J. Müller opined in the *New York Times* that "if they could foresee the results [mutations among their descendants] 1,000 years from now . . . they might consider themselves more fortunate if the bomb had killed them." Müller, who had studied the biological effects of radiation on the fruit fly *Drosophila melanogaster*, had firsthand experience with the devastating effects

of radiation. The survivors of the bomb were considered poor marriage prospects, because of the potential of carrying mutations and were often ostracized by Japanese society. Thus the Atomic Energy Commission (AEC) of the DOE set up an Atomic Bomb Casualty Commission in 1947 to address the issue of potential mutations among the survivors. The problem they faced, though, was how to experimentally determine such mutations. It would be many years before the technology was developed to do so.

During the mid-1970s, molecular biologists developed techniques for the isolation and cloning of individual genes. In 1977 Walter Gilbert and Fred Sanger independently developed methods for the sequencing of DNA, for which they received the Nobel Prize. In 1980, the polymerase chain reaction (PCR) was invented by a scientist at Cetus Corporation. This technique allowed one to take minute samples of DNA and amplify them a billionfold for analysis. In 1986, an automated DNA sequencer was developed, increasing the number of bases sequenced per day. Thus, by the mid-1980s, there was a feeling among molecular biologists that it might now be feasible to sequence the entire human genome. The first major impetus came in June 1985 when Robert Sinsheimer, chancellor of the University of California at Santa Cruz, called a meeting among leading scientists to discuss the possibility of sequencing the human genome. Meanwhile, the DOE, led by Charles Delisi, was a strong supporter of the initiative, for the DOE had a continuing interest in identifying radiation-caused mutations. Sequencing the entire genome would clearly provide the best way to analyze such mutations.

Many biologists were interested in this "Holy Grail of Molecular Biology." Most notably was Walter Gilbert who, through his interest, personality, and academic ties, developed enormous enthusiasm for the project. The initial goals were to develop:

- genetic linkage maps

- a physical map of ordered clones of DNA sequences

- the capacity for large-scale sequencing, as faster and cheaper machines and great leaps in technology would be necessary.

By 1990 the Human Genome Project had received the endorsement of the National Academy of Sciences, the National Research Council, the DOE, the National Institutes of Health (NIH), the National Science Foundation, the U.S. Department of Agriculture, and the Howard Hughes Medical Institute. Sequencing of the human genome was now officially begun. Nobel Prize winner James Watson agreed to head the project at the NIH. It was estimated to cost $3 billion and be completed by September 30, 2005. However, Watson resigned as the director of the HGP over the issue of patenting the genome. Francis Collins succeeded him as director. Just as important was the establishment of projects seeking to sequence several model organisms, that is, those organisms of genetic, biochemical, or medical importance.

Rapid Progress

Thousands of scientists, in more than one hundred laboratories in nineteen different countries around the world, are contributing to the HGP. The sequencing progressed well ahead of schedule and well under budget, a rare
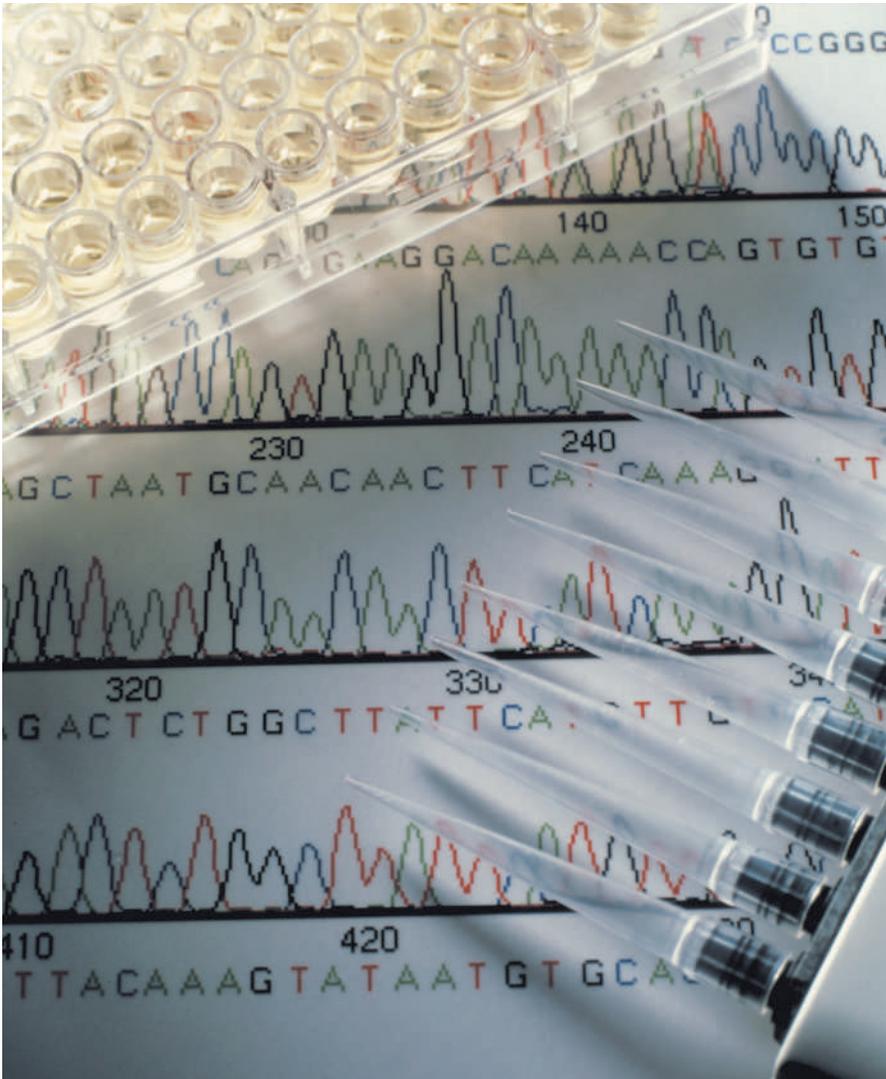
A computer printout of a DNA sequence.
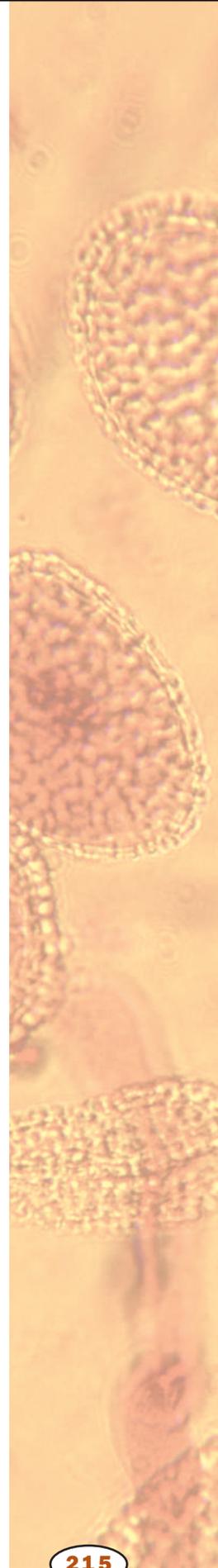
phenomenon in government-sponsored endeavors. In 1995, the first complete genome, that of the bacterium *Haemophilus infuenzae*, was published by the biotech company TIGR (The Institute for Genome Research). Several of the model organisms have subsequently been completed, including the yeast *Saccharomyces cerevisiae*, the first eukaryote sequenced.

The human genome consists of twenty-two pairs of **chromosomes** plus the X and Y sex chromosomes. On December 2, 1999, more than one hundred scientists working together in laboratories in the United Kingdom, Japan, United States, Canada, and Sweden announced the complete sequence of the first human chromosome, chromosome #22, the smallest of the autosomes. In 1998, J. Craig Venter, along with Perkin Elmer (PE) Corporation, founded the private biotech company Celera Genomics with the goal of privately sequencing the human genome, in direct competition with the public efforts supported by the NIH and DOE. Celera had available three hundred of the world's fastest PE automatic DNA sequencers along with one of the world's most powerful supercomputers. With remarkable speed Celera sequenced several of the model genomes and, in April 2000,

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

announced that it had preliminary sequence of the human genome. In February 2001 Celera and the public consortium jointly announced completion of the draft human sequence.

Whose Genome?

To assure the accuracy of the sequence, each segment will be sequenced at least ten times. Although all humans share a 99.99 percent or more of their sequences, each human is unique. Geneticists estimate that each person carries many, perhaps hundreds or thousands, mutations. Moreover, it is anticipated that there will be distinct differences among different populations. No single person's genome will be identical to that in the databank as "the human genome." The Human Genome Diversity Project was proposed in 1997 to catalog such variations among racial and/or geographic groups. Samples from four thousand to eight thousand individuals in dozens of populations are to be analyzed. Similarly, a Human Cancer Genome Anatomy Project was initiated in 1997 to catalog all genes expressed in cancer cells to aid in the detection and treatment of cancers.

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

Most of the genome does not code for **proteins**. Indeed, perhaps only 5 percent of the DNA will be found to encode a gene. Estimates by scientists of the number of genes in the human genome have ranged from 35,000 to 140,000. Using the sequence data already available, scientists can anticipate that the final number will be approximately 120,000.

Patenting the Genome

From the outset there has been considerable debate among scientists, politicians, and entrepreneurs as to whether the human gene sequences can or should be patented. As of the year 2000, the U.S. Patent and Trademark Office is granting patents to genes that have been identified, rather than just random sequenced fragments. The data will be an invaluable resource, particularly in the area of developing new medical treatments. This has given rise to the new field of genomics (the study of gene sequences), and is resulting in the "mining of the genome" for valuable sequence data. Similarly, proteomics (the study of protein sequences) is a new, rapidly expanding field, as protein sequences can be predicted from the gene sequence. The folding of the proteins (secondary and **tertiary** structures) can be predicted by computers as well, leading to a three-dimensional view of the protein encoded by a particular gene.

tertiary third level

Ethical Issues

From the outset, many have been concerned with ethical issues raised by the HGP, which need to be addressed by society as a whole. These including the following:

- confidentiality of an individual's DNA information
- insurance denial for pre-existing conditions if a person carries a gene that predisposes one to a particular disease
- stigmatization due to carrying certain genes
- genetic testing required for employment
- prenatal testing and abortion issues

- genetic manipulation

- challenges to self-understanding, given the knowledge of one's genes

- psychological burdens resulting from the knowledge that one carries a detrimental gene.

SEE ALSO BIOINFORMATICS; DNA SEQUENCING; GENOME; GENOMICS

Ralph Meyer

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Human Nutrition

Nutrition is a broad topic that includes the components of food, food intake, what happens to the food once in the body, elimination of the residue, and how nutrients are related to health and disease. Research, education, and advertising combine to bombard the public with massive amounts of information or misinformation on what to eat, how much, and when. A strong understanding of nutrition will help people make better and healthier choices about nutrition.

Nutrients

A nutrient is an ingested chemical that is absorbed and made part of the human tissues. Substances in the food that are not absorbed are not considered nutrients, but may nevertheless be essential to one's health, such as dietary fiber. A chemical need not be digested (chemically modified) to be considered a nutrient. Water, vitamins, minerals, and cholesterol are all important nutrients, for example, that are absorbed into the tissues without requiring chemical breakdown. Foods can confer health benefits beyond their nutritional value. For example, fiber helps prevent colon cancer, and cranberries and blueberries promote urinary tract health.

Nutrients include macronutrients (carbohydrates, **lipids**, proteins, and water) that are consumed in large quantities and micronutrients (vitamins

Foods can confer health benefits beyond their nutritional value.

lipid fat or waxlike molecule, insoluble in water

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

complex carbohydrate molecules formed by linking simpler carbohydrates such as sugars

polysaccharide carbohydrate composed of many individual units of sugar

glycogen complex carbohydrate used as storage in animals and some other organisms

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

carbohydrates sugars, starches, and other molecules combining carbon, hydrogen, and oxygen and serving as fuel or structural components

steroid hormone group of hormones that include estrogen, testosterone, and progesterone

amino acid a building block of protein

connective tissue one of four types of body tissue, characterized by few cells and extensive extracellular material

hormone molecule released by one cell to influence another

enzyme protein that controls a reaction in a cell

excrete deposit outside of

electrolytes ions in body fluids

dissociate break apart

osmosis passage of water through a membrane in response to concentration differences

hemoglobin oxygen-carrying protein complex in red blood cells

and minerals) that are consumed in much smaller quantities, although they are no less essential to health. The macronutrients provide raw material for building tissues, as well as energy. The energy stored in the nutrient is measured in kilocalories (simply called calories in dietetics). A positive energy balance means one is consuming more kilocalories than one is using; the excess stored mostly as fat. A negative energy balance means that one is "burning" more calories than are being eaten; this results in weight loss.

Macronutrients

Carbohydrates are the most important source of quick energy, but they also function in cell-membrane structure. They include the simple sugars **glucose**, fructose, and galactose; the disaccharides maltose, lactose, and sucrose; and the **complex carbohydrates** or **polysaccharides**, which are **glycogen** in human tissues and **cellulose** (fiber) and starch in plant tissues.

Lipids provide the body with more stored energy than **carbohydrates** do. They are also important as cell membrane components, **steroid hormones**, and visual pigments. Adipose tissue, which is mostly stored lipid, provides insulation and protection for the organs. About 95 percent of the body's lipid is in the form of triglycerides (fats).

Proteins are chains of **amino acids**. They are important structural components of cell membranes and the extracellular materials of bones, tendons, and other **connective tissues**, and all muscle contraction results from the action of proteins. Proteins also function as **hormones**, **enzymes**, and antibodies.

Water makes up most of the body. It is the body's major solvent, and it serves in lubrication, temperature control, and waste removal. A water deficiency can kill more quickly than a deficiency of any other nutrient.

Micronutrients

Vitamins serve a wide variety of functions in enabling enzymes to work (thus contributing to the synthesis of the body), and in vision, immunity, protection from harmful free radicals, and absorption of other nutrients. The fat-soluble vitamins (A,D,E, and K) are absorbed with dietary fat and stored mainly in the liver. Water-soluble vitamins (vitamin C and the B vitamins) are not stored in the body (except for vitamin B12), since they mix freely with the body fluids and are quickly **excreted** by the kidneys.

Minerals are chemical elements such as sodium, potassium, chlorine, calcium, iron, magnesium, manganese, and phosphorus. They come ultimately from the soil and pass up the food chain from plants to humans. Some minerals serve as **electrolytes**—salts that **dissociate** in water to from charged particles (ions), whose movements through cell membranes produce nerve signals and muscle contractions (including the heartbeat). Minerals have a major effect on **osmosis** and thus strongly affect the body's water balance. They act as co-factors that enable many enzymes to function.

Calcium and phosphorus are important components of bones and teeth. Phosphorus is also a part of deoxyribonucleic acid (DNA), ribonucleic acid (RNA), adenosine triphosphate (ATP), and the phospholipids that compose cell membranes. Iodine is needed to make thyroid hormone, and iron to make **hemoglobin**.

Good nutrition hinges on the senses of hunger and thirst, which are both controlled by centers in the hypothalamus of the brain. Thirst is triggered by dehydration and hunger by a low blood glucose concentration. Long-term satiety (satisfaction) of thirst and hunger results when the water and glucose content of the blood return to normal. The hypothalamus thus regulates eating and drinking patterns, although these are also subject to factors such as habit, stress, time of day, social obligations, and availability of food and drink. The food pyramid is a chart of the relative amounts of different food categories recommended for a healthy daily diet. SEE ALSO CARBOHYDRATES; DIGESTION; LIPIDS; VITAMINS AND COENZYMES

Richard Robinson

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Human Population

Human population refers to the number of people living in a particular area, from a village to the world as a whole. A secondary meaning of population is the inhabitants themselves, but in most uses population means numbers.

No one knows the population of the earliest humans, but there may have been only a few tens of thousands of individuals when the species *Homo sapiens* first emerged 200,000 years ago. Today more than 6 billion human beings inhabit the earth. Three-fifths of them live in one continent, Asia, with the rest occupying every continent except Antarctica.

The overwhelming bulk of human population growth has occurred since the Industrial Revolution began, more than half since 1950. All but a small percentage of the roughly 80 million people added to world population each year live in the world's developing countries, which are home to 80 percent of humanity and more than 95 percent of world population growth. In Europe and Japan, small average family size and relatively modest immigration levels are leading to a leveling of, and even decreases in, population. In the United States, Canada, and Australia, slightly larger families and higher levels of immigration make for continued population growth.

World population grows because births significantly outpace deaths on average. This imbalance occurs not because women are having more children than they once did—quite the reverse—but because improved sanitation and health mean that many more children than in the past survive to become parents themselves. Human reproduction is such a success story that some analysts believe that today's large and ever-increasing population growth threatens the earth's support systems and contributes to global poverty.

Debate on this question has raged since at least the 1800s. Some economists and other social scientists argue that higher populations provide more human resources for solving problems and producing wealth. Most physical and biological scientists, by contrast, argue that key natural resources—fresh water, cropland, forests, and fisheries, for example—are increasingly strained by burgeoning human demands. Rising natural resource consumption by individuals also boosts these demands. The long-term growth of human population clearly has been an especially significant factor in human-induced climate change, species extinction, the loss of forests, and other environmental problems. But scientists and other analysts have been unable to agree on population's exact role in environmental change. Many other factors, from consumption patterns to government policies to the unequal distribution of power and wealth, also influence the environment.

One clear trend in human population is that its growth is slowing down. Women and men increasingly want to have later pregnancies and smaller families than did their own parents. Governments increasingly provide the health services that allow couples to plan their families. For some countries, this trend raises questions about how societies will cope with lower proportions of young and working people. For the world as a whole, however, births are likely to outnumber deaths for decades to come, and human population will continue to grow. SEE ALSO BIODIVERSITY; DESERTIFICATION; EXTINCTION; GLOBAL CLIMATE CHANGE

Robert Engelman

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Hybridization

complementary matching opposite

base pair two nucleotides (either DNA or RNA) linked by weak bonds

Hybridization is a technique in which molecules of single-stranded deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) are bound to **complementary** sequences of either single-stranded DNA or RNA. Complementary **base pairs** are adenine (A) with thymine (T) or uracil (U) and vice versa, and guanine (G) with cytosine (C) and vice versa. Although the DNA double helix is relatively stable at body temperatures, high temperatures can split, or "melt," the double helix into single, complementary strands. After disrupting the double helix in this way, lowering the temperature then causes the single-stranded DNA to base-pair, or anneal, to other single strands that have complementary sequences.

Single-stranded DNA can hydridize to either single-stranded DNA or single-stranded RNA. Two complementary single-stranded DNA molecules can reform the double helix after annealing. In DNA-RNA hybridization, the RNA base uracil pairs with adenine in DNA. Single-stranded RNA that is complementary to a messenger RNA (mRNA) sequence is called "antisense" RNA. Antisense RNA and mRNA form a double helix that is slightly different from a DNA double helix.

Researchers use hybridization for many purposes. Overall genetic relatedness of two species can be determined by hybridizing their DNA. Due to sequence similarity between closely related organisms, higher temperatures are required to melt such DNA hybrids when compared to more distantly related organisms. In **forensic** DNA testing, a variety of different methods use hybridization to pinpoint the origin of a DNA sample, including the polymerase chain reaction (PCR). PCR produces many copies of a particular nucleic acid sequence and is also used to clone genes. In another technique, short DNA sequences are hybridized to cellular mRNAs to identify expressed genes. Pharmaceutical drug companies are exploring the use of antisense RNA to bind to undesired mRNA, preventing the **ribosome** from translating the mRNA into **protein**. SEE ALSO DNA; POLYMERASE CHAIN REACTION; RNA

Mary Beckman

forensic related to legal proceedings

ribosome protein-RNA complex in cells that synthesizes protein

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

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Hybridization, Plant

Hybridization is the process of interbreeding between individuals of different species (interspecific hybridization) or genetically divergent individuals from the same species (intraspecific hybridization). Offspring produced by hybridization may be fertile, partially fertile, or sterile.

Plants hybridize much more frequently and successfully than animals do. Pollen from flowering plants disperses widely and may land on flowers of other species. Chromosomal doubling (polyploidy) occurs more frequently in plants and facilitates the fertility of the hybrid offspring. Finally, plant forms are less stringently controlled than animal forms, and so the intermediate form of a plant hybrid is more likely to be physiologically successful.

One of the first persons to study plant hybridization was Josef Kölrueter, who published the results of his experiments on tobacco in 1760. Kölrueter concluded that **interspecific** hybridization in nature is rare unless humans disturb the habitat. Since that time, many instances of hybridization among various plant species have been documented.

One good example of plant hybridization involves hybridization between the elegant sego lily (*Calochortus selwayensis*) and a mariposa lily (*C. apiculatus*) in western Montana. The sego lily, with purple-spotted petals, lives in dry sites at mid-elevations in the Rocky Mountains under the somewhat open canopy of ponderosa pine forests. The mariposa, with its cream-colored petals, lives in moister sites at higher elevations under the more closed Douglas-fir canopies. Interspecific hybrids between the elegant sego and mariposa lilies are found in great abundance on ski slopes where Douglas-fir canopies have been opened and kept clear of trees and tall shrubs.

The ski slope is a habitat that is too dry and too open for the mariposa to thrive and too moist for the elegant sego, but just right for the hybrids.
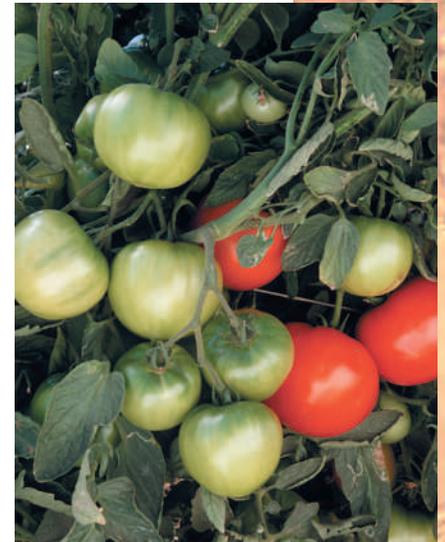
Crop yields increase dramatically when hybridization is used to exceed one or more of the parents in size and reproductive potential.

interspecific between different species

Such an intermediate habitat is called a hybrid habitat. Human disturbance can generate hybrid habitats of many types and thus can foster interspecific hybridization.

Backcrossing, which is the interbreeding between hybrids and their parental species, can transfer **alleles** from one parent to the other using the interspecific hybrids as a genetic bridge in a process called introgression. Introgression increases the genetic variation of one or both of the parents. In the previous example, there is extensive backcrossing between the hybrids and mariposa lily. The result of this introgression is that some mariposa lilies now display petals with some of the purple spotting characteristic of the elegant sego, and theoretically they can live in slightly drier habitats.

Often interspecific hybrids are sterile or for some other reason cannot interbreed with the parental species. Occasionally sterile interspecific hybrids can undergo a doubling of their **chromosome** set and become fertile tetraploids (four sets of chromosomes). For example, the bread wheats that humans use today are a result of two hybridizations each followed by chromosome doubling to produce fertile hexaploids (six sets of chromosomes). In such instances the hybrids can become new species with characteristics different from either of the parents.

Humans have used intraspecific hybridization, hybridization between strains of a single species, to develop high-yielding crops. In corn, continually **inbred** varieties will often exhibit inbreeding depression, which is a reduction in vitality and yield. Hybridization between inbred lines can result in hybrids that exceed one or more of the parents in size and reproductive potential. This increased vitality is called hybrid vigor and has been studied since the time of English naturalist Charles Darwin. Crop yields increase dramatically (as much as 100 percent) when hybridization is used in this way. In the twenty-first century, over 90 percent of the corn grown is of hybrid origin. SEE ALSO GRAIN

George H. Wittler

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Hypothalamus

The hypothalamus is a tiny part of the brain of vertebrate animals; in humans it weighs about four grams in a brain that weighs on average 1,400 grams (49 ounces). Despite its small size, the hypothalamus plays a pivotal role in an astounding number of functional and behavioral activities that are essential for day-to-day survival of the individual animal (or person) and for continuing survival of its species. Its overall role is to collect and integrate a huge variety of information from the body and to organize **neural** and **endocrine** responses that maintain homeostasis (constant internal environment).

allele a particular form of a gene

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

inbred repeatedly bred with close relatives, creating organisms with very little genetic variation

neural related to nerve cells or the nervous system

endocrine related to the system of hormones and glands that regulate body function

Carrying out this single overriding task requires coordinating the activity of the **autonomic** nervous system and the endocrine system, and ultimately influences several important behaviors. Thus energy **metabolism** is regulated by control of feeding, drinking, and digestion. Body temperature is monitored and maintained at a constant level (37 to 38°C [98.6 to 100.4°F] in humans) by a complex interplay of behavior and activity in several body systems, and reproductive behavior is coordinated with endocrine regulation of the reproductive organs. Blood pressure and composition of the blood plasma are regulated by hypothalamic mechanisms. The expression of emotions such as fear, rage, and anger are partly controlled by the hypothalamus, and it even helps regulate sleep and levels of consciousness.

Location/Anatomy

The hypothalamus is a thin (3 to 4 millimeters [.118 to .157 inches] in thickness) plate of neural tissue found along either side of the front end of the third **ventricle** (one of the fluid-filled cavities inside the brain). Deeply buried in the brain, near the center of the **cranial** cavity, it lies just below the thalamus (a relay center for sensory and motor pathways in the brain). It is almost completely hidden by the overlying cerebral hemisphere, although when a brain is removed for study, the hypothalamus is visible on the **basal** surface.

The hypothalamus has a special structural and functional relationship with the pituitary gland, which dangles below it, attached by a thin stalk of nerve fibers. Important information passes along both the nerve fibers and the blood vessels of this stalk.

Working Principles

About ten or eleven small, indistinct nuclei (nerve cell groups) are packed into the hypothalamus. Reflecting their complex and highly specialized functions, the cells here use several unusual means of cell-to-cell communication.

Some hypothalamic cells are specialized to detect the presence and the concentration of large molecules such as **hormones** circulating in the blood and tissue fluids. They are able to do this because even the capillaries here are specialized. Unlike other brain vessels, they permit large molecules like hormones to leak into the tissues and carry signals to the **neurons**.

Hypothalamic neurons also receive information from other body and brain areas by way of electrical impulses conducted from many sensory sources (signaling pain, vision, and blood pressure, for example) scattered through the body. Other hypothalamic neurons respond by changing their firing pattern when there are changes in the desired values of variables such as blood (body) temperature, **glucose** concentration, or salt concentrations in the body fluids.

When the hypothalamus, using signals like those just described, establishes a need for response, hypothalamic cells influence other cells in two ways. Like other neurons, they send electrical signals (action potentials) to stimulate or inhibit cells in other regions of the brain and body. In addition, some release chemicals (hormones), usually small **proteins** called peptides, into the bloodstream so they can act on target cells at a considerable distance.

autonomic independent; regulating involuntary actions

metabolism chemical reactions within a cell

ventricle fluid-filled chamber

cranial related to the cranium, or brain cavity

basal lowest level

hormone molecule released by one cell to influence another

neuron nerve cell

glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

Anatomic location of the hypothalamus, in relation to the thalamus and pituitary gland.
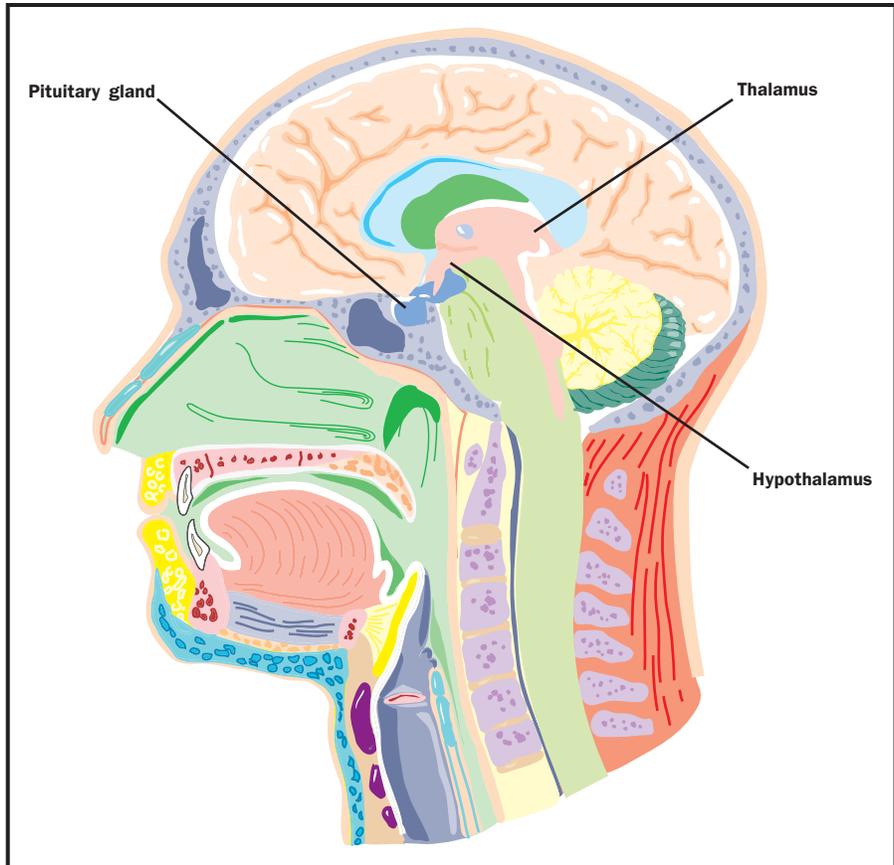
Localized Hypothalamic Functions

nucleus cluster of cell bodies in the central nervous system

Two of the most prominent hypothalamic nuclei (because their neurons are large) are the paraventricular **nucleus** and supraoptic nucleus. Upon appropriate stimulation, cells in these nuclei secrete (release) two hormones into the bloodstream. Oxytocin causes uterine contraction during birth and induces milk release in females with young. Antidiuretic hormone (ADH) travels to the kidneys to help the body retain water by decreasing urinary output.

anterior toward the front

Several other hypothalamic nuclei, mostly located in the **anterior** area, respond to several different hormones circulating in the body. When hormone levels change, cells in these nuclei release peptide signaling molecules into a special system of blood vessels that carry them to the anterior lobe of the pituitary. These peptides cause pituitary cells to either increase or decrease the **secretion** of one of about eight specific hormones into the bloodstream. This basic mechanism regulates blood levels of growth hormone, adrenocorticotropic hormone (for response to stress), thyrotropin (regulating basal metabolism), and the several hormones that regulate the reproductive organs and sexual behavior.

secretion material released from the cell

Also in the anterior hypothalamus, the tiny suprachiasmatic nuclei sit atop the optic chiasm. A few optic nerve fibers from the eyes end here, informing these cells about cycles of light and darkness. Through their expansive projections to other brain areas, especially the pineal organ, these cells evoke release of the hormone melatonin into the bloodstream and thus

help to regulate the body's **circadian** rhythms. Circadian rhythms are the cyclic, often subtle, fluctuations in many body functions that reoccur at intervals of about twenty-four hours.

Cells in the anterior and posterior hypothalamic areas detect blood temperature and have connections that allow them to adjust abnormal body temperature. Neural activity in the anterior area activates systems for heat loss, dilating blood vessels of the skin and causing sweating and panting. Neurons in the posterior hypothalamus help to preserve heat by constricting blood vessels of the skin, causing shivering and slowed breathing. Still other hypothalamic nuclei work together to balance food intake. Activity in the **lateral** hypothalamic area encourages eating while the ventromedial nucleus (VMN) suppresses food intake. Damage to the VMN results in animals (and humans) that overeat to excess and become obese.

In the preoptic area at the front end of the hypothalamus are cells that use several of the hormonal mechanisms already described to drive and regulate the menstrual cycles and other aspects of reproductive organ function and behavior. Finally, a range of behaviors characterized as rage or aggression represent physiological responses to stress; these can be seen following experimental stimulation of the dorsomedial nucleus of animals. Blood pressure and heart rate are elevated, muscles are tensed, the animals show signs of strong internal, emotional feeling. SEE ALSO BRAIN; CENTRAL NERVOUS SYSTEM; ENDOCRINE SYSTEM; FEMALE REPRODUCTIVE SYSTEM; HOMEOSTASIS; HORMONES; MALE REPRODUCTIVE SYSTEM; PITUITARY GLAND; TEMPERATURE REGULATION; THYROID GLAND

James L. Culberson

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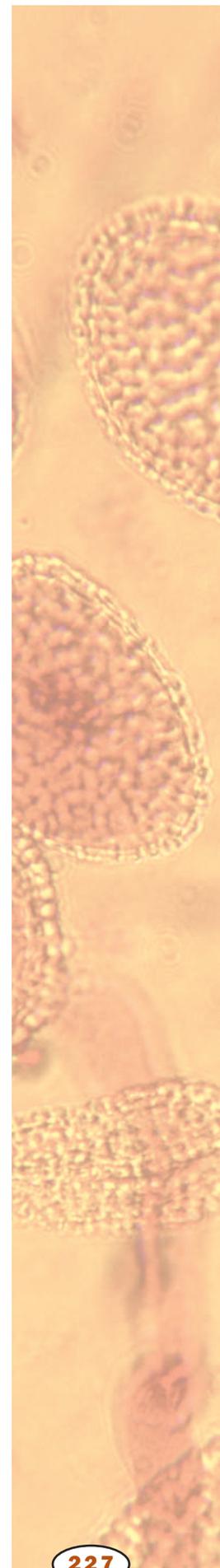
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Glossary

abiotic nonliving

abscission shedding of leaves; falling off

acetylation addition of an acetyl group, CH_3-CHOO-

acidic having an excess of H^+ ions and a low pH

acinus one of the small divisions of a fruit such as a raspberry

action potential wave of ionic movement down the length of a nerve cell

active site surface region of an enzyme where it catalyzes its reaction

adaptive radiation diversification of a group of organisms into several different forms that adapt to different environments

adhesion attachment; sticking to the surface of

ADP adenosine diphosphate, the low-energy form of ATP

adventitious growing from a nonstandard location

aerobe organism that needs oxygen

aerobic with oxygen, or requiring it

aestivating remaining dormant for the summer

affinity attraction

aflatoxin toxic compound produced by a mold fungus

agar gel derived from algae

agnosia "not knowing"; loss of ability to recognize familiar objects

agroecosystem agricultural ecosystem

alkaline chemically basic, with an excess of OH- ions

allele a particular form of a gene

allelopathy inhibition of one plant's growth by another plant

amino acid a building block of protein

amoeba a single-celled protist that moves by crawling

amoeboid like an amoeba, especially in movement via extension of portions of the membrane

AMP adenosine monophosphate, form of ATP after removal of two phosphate groups

amphipathic having both polar and nonpolar regions

anabolic characteristic of a reaction that builds complex molecules from simpler ones, and requires energy

anadromous describes fish that return to the rivers where they were born in order to breed

anaerobe organism not needing oxygen

anaerobic without oxygen, or not requiring oxygen

anemia lack of oxygen-carrying capacity in the blood

aneurysm bulging of the wall of a blood vessel

antagonism working against

antagonist muscle muscle that works against the action undertaken

anterior toward the front

anterograde forward

anthocyanins colored compounds made by plants

anthropogenic of, or relating to, the influence of human beings or nature

antibody immune system protein that binds to foreign molecules

antigen foreign substance that provokes an immune response

antioxidant substance that prevents damage from oxidation

antitoxin molecule used to inactivate a toxin

aphasia loss of the ability to form ideas into words

apical at the tip

apical meristem growing tip from which all plant tissues arise

appendage attached organ or structure

aqueous watery or water-based

areolar related to a small space within a tissue

aromatic compound including a double-bonded carbon ring

arterioles any of the small, terminal twigs of an artery that ends in capillaries

arthropods organisms with jointed appendages and exoskeletons, including insects, spiders, and crustaceans

asymptomatic without symptoms

ATP adenosine triphosphate, a high-energy nucleotide used by cells to power most energy-requiring reactions

atria two upper chambers of the heart (singular, atrium)

attenuation lessening over time

autoimmune disease disease in which the immune system attacks the body's own tissues

autonomic independent; regulating involuntary actions

autonomic nervous system one of the branches of the motor system, controlling involuntary muscles and glands

autosomal dominant pattern of inheritance in which inheritance of a single allele from either parent results in expression of the trait

avian concerning birds

axon long extension of a nerve cell down which information flows

B lymphocyte white blood cell that makes antibodies

B.C.E. before the Common Era, equivalent to B.C.

basal lowest level

base pair two nucleotides (either DNA or RNA) linked by weak bonds

basic having an excess of OH⁻ ions and a high pH

bilaterally symmetric symmetric, or similar, across a central line

bilayer composed of two layers

bioaccumulate build up within organisms

bioluminescence production of light by biochemical reactions

biopharmaceuticals drugs produced by and harvested from living organisms

biosynthetic forming a complex molecule from simpler ones

biotic living

bolting sudden spurt of growth

boreal of, relating to, or located in northern regions

brood parasite organism of one species that lays its eggs in the nest of another species

C4 and CAM plants plants that employ accessory systems for trapping carbon for photosynthesis

cadherins family of calcium-dependent adhesion proteins

carbohydrates sugars, starches, and other molecules combining carbon, hydrogen, and oxygen and serving as fuel or structural components

cardiomyopathy heart muscle disease

catalysis aiding in the reaction of

catalyst substance that aids in a reaction without being used up
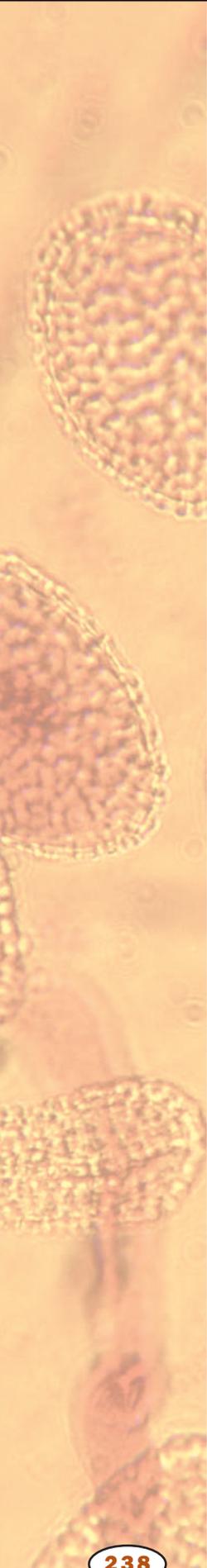
catalyze aid in the reaction of

caudate toward the tail

C.E. Common Era; equivalent to AD

cell cycle sequence of growth, replication, and division that produces new cells

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

central nervous system brain and spinal cord

centromere region of the chromosome linking chromatids

cerebral cortex outermost wrinkled portion of the brain

chemiosmosis use of proton gradients to make ATP

chitin nitrogen-containing carbohydrate found in arthropod exoskeletons and fungus cell walls

chromatid a replicated chromosome before separation from its copy

chromatin complex of DNA, histones, and other proteins making up chromosomes

chromosomal analysis staining, banding, and other techniques for detection of chromosomal abnormalities

chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

cilia short, hairlike cell extensions of the cell membrane formed by the cytoskeleton

ciliated possessing cilia, which are short, hairlike extensions of the cell membrane

circadian related to a day or daylength

clavicle collar bone

cloaca common exit cavity for intestinal, genital, and urinary tracts

codon sequence of three mRNA nucleotides coding for one amino acid

cognition mental processes of thought and awareness

cognitive related to thought or awareness

communicable transmissible from person to person

complementary matching opposite

complex carbohydrate molecules formed by linking simpler carbohydrates such as sugars

condensation compaction of chromosome strands into a tight structure

conformation three-dimensional shape

congenital present at birth; inherited

conjunctiva eye membrane that helps seal the eye socket

connective tissue one of four types of body tissue, characterized by few cells and extensive extracellular material

consanguineous descended from the same ancestor

constitutive at a constant rate or continually

contiguous adjacent to or touching

continental shelf submerged offshore area demarcated by land on one side and deep sea on the other

coralloid resembling coral

coronary artery artery supplying blood to the heart

cortical related to the cortex, or outer portion

cotyledon seed leaf, which stores food and performs photosynthesis after germination

cranial related to the cranium, or brain cavity

cryptobiosis when a plant or animal becomes so inactive that its life processes nearly come to a stop

cutaneous related to the skin

cutaneous respiration gas exchange through the skin

cytology study of cells

cytoplasm material in a cell, excluding the nucleus

cytoskeleton internal scaffolding in a cell, composed of protein

cytosol fluid portion of a cell, not including the organelles

Darwinian fitness capacity to survive and reproduce

deciduous trees that shed their leaves in the fall

deciliter one-tenth of a liter; a unit of volume

dementia neurological illness characterized by impaired thought or awareness

desiccation drying out

desynchronized not happening at the same time

deuterostome "mouth second"; referring to the early development of the anal pore during gut tube formation

dialysis cleansing by partial filtration

dicot plant having two cotyledons, or seed leaves

dikaryotic cell cell with a pair of nuclei

dilation expansion or swelling

dimer polymer formed from two molecules of a simple compound
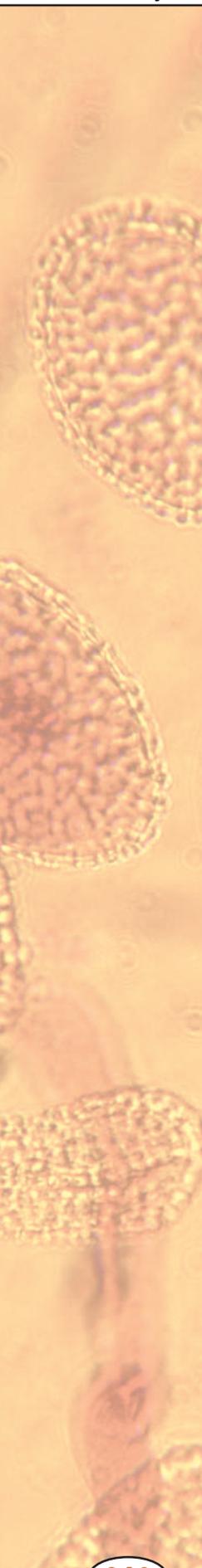
dimerizes forms a pair

diploid having pairs of chromosomes in the nucleus

dissociate break apart

distal away from

diurnal active during the daytime

dorsal to the back of

ecosystem an ecological community and its environment

effector organ at the end of a nerve, such as a muscle or gland

efferent conducting outward or directing away from

electrolytes ions in body fluids

electromagnetic radiation light, X rays, and other forms of radiant energy

electron transport system membrane-bound system of proteins that extracts energy from high-energy electrons, found in mitochondria and chloroplasts

electrophoresis technique that uses electricity to separate molecules based on size and electric charge

electrophoresis gel porous medium through which molecules can be separated using an electric current

embalming treating a dead body to protect it from decay

embryology development of the embryo

emulsify suspend in solution through interaction with soap or similar molecules

endocrine related to the system of hormones and glands that regulate body function

endogenous caused by factors inside the organism

endometriosis disorder of the endometrium, the lining of the uterus

endoplasmic reticulum network of membranes within the cell

endosperm nutritive tissue within a seed

endosymbiosis symbiosis in which one partner lives within the other

endothermic characterized by regulation of body temperature through metabolic activity

Enlightenment eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

enzymatic related to the function of an enzyme

enzyme protein that controls a reaction in a cell

epidemic rapid spread of disease through a population, or a disease that spreads in this manner

epistasis supression of a characteristic of one gene by the action of another gene

epithelium one of four tissue types found in the body, characterized by thin sheets and usually serving a protective or secretory function

esophagus tube connecting the throat to the stomach

eudicot "true dicot"; plants with two seed leaves that originated from the earliest of flowering plants

eukaryotic cell a cell with a nucleus

eutrophication process by which waters become enriched in dissolved nutrients that promote plant growth which results in depletion of dissolved oxygen

evapotranspiration loss of water from a plant by evaporation within the leaf

evidentiary DNA profile analyzed DNA from a sample used as evidence

excrete deposit outside of

exocrine gland gland that secretes substances to an external or internal surface rather than into the bloodstream

exoskeleton external skeleton

extensibility ability to expand or grow larger

fallopian tubes tubes through which eggs pass to the uterus

fecundity ability to reproduce

feedback process in which the output or result influences the rate of the process

fertilization union of sperm and egg

fibroblast undifferentiated cell normally giving rise to connective tissue cells

filtrate material passing through a filter

focal at a point

follicle a vesicle that contains a developing egg surrounded by a covering of cells

food web set of feeding relations in an ecosystem

forb broad-leaved herbaceous plant

forensic related to legal proceedings

fulcrum pivot point of a lever

fungi major group of parasitic, lower plants that obtain their food from the products of organic decay (e.g. molds, smuts, etc.)

gamete reproductive cell, such as sperm or egg

gametophyte a haploid plant that makes gametes by mitosis

ganglia cluster of nerve cell bodies

gastroenteritis inflammation of the gastrointestinal tract, often from infection

gene portion of DNA that codes for a protein or RNA molecule

gene expression use of a gene to create the corresponding protein

genetic code relationship between triples of RNA nucleotides and the amino acids they code for during protein synthesis

genitalia reproductive organs

genome total genetic material in a cell or organism

germ line cells creating eggs or sperm

gestation period of fetal development within the mother

glial supporting tissue of the elements of nervous tissue, including the brain, spinal cord, and ganglia

glucose simple sugar that provides energy to animal cells; it is the building block of cellulose in plants

glycogen complex carbohydrate used as storage in animals and some other organisms

glycolysis initial stages of sugar breakdown in a cell

gradient difference in concentration between two places

grafting attachment and fusing of parts from different plants

guard cells paired cells on leaves that control gas exchange and water loss

gymnosperms "naked seed" plants, including conifers

hallucination altered sensory experience resulting in the perception of objects that are not real

haploid having single, nonpaired chromosomes in the nucleus

hectare 10,000 square meters (2.47 acres)

heme the deep red, iron containing, nonprotein portion of hemoglobin and myglobin

hemicellulose complex carbohydrate related to cellulose and found in cell walls of plants and some other organisms

hemoglobin oxygen-carrying protein complex in red blood cells

herbarium a collection of dried plant specimens systematically arranged for reference

hermaphrodite organism possessing both male and female reproductive structures

heterodimer complex molecule composed of two different parts

heterogeneous composed of, or containing, different parts or types

heterozygous characterized by possession of two different forms (alleles) of a particular gene

hexamer a structure composed of six parts

histogenesis origin or production of tissues

histology study of tissues

histone protein around which DNA wraps to form chromosomes

homologous similar in structure

homologous chromosomes chromosomes carrying similar genetic information

homologous recombination exchange of DNA segments between chromosomes

homozygous containing two identical copies of a particular gene

hormone molecule released by one cell to influence another

hybrid combination of two different types

hydrocarbon molecule or group composed only of C and H

hydrogen bond weak bond between the H of one molecule or group and a nitrogen or oxygen of another

hydrolyze to split apart using water

hydrophilic "water loving"

hydrophobic "water hating," such as oils

hydroponics growing of plants without soil

hydroxyl chemical group consisting of -OH

hypersalinity very high level of salt

hypersecretion excess secretion

hypersensitivity reaction immune reaction characterized by rapid and severe response, often with swelling of airways

hyphae threadlike part of the vegetative portion of the fungus

hyposecretion lack of secretion

hypothermia subnormal temperature of the body

ice-out a thawing of ice covering a lake or other body of water

immunoglobulin an immune protein, also called an antibody

immunosuppressant inhibition of the immune response

in utero inside the uterus

in vitro "in glass"; in lab apparatus, rather than within a living organism

inbred repeatedly bred with close relatives, creating organisms with very little genetic variation

inducible able to be switched on

inflorescence characteristic arrangement of flowers on a stalk

infrastructure roads, phone lines, and other utilities that allow commerce

inorganic not bonded to carbon

insectivorous insect-eating

integrins a family of transmembrane linking proteins

interferons signaling molecules of the immune system

intermediate filament protein one type of cytoskeleton protein

interspecific between different species

interstitial space space between cells in a tissue

intracellular within a cell

intraocular within the eyeball

intrinsic to intimate part of; within

intron untranslated portion of a gene that interrupts coding regions

ion an electrically charged particle

ionic based on or functioning by means of ions

ionizing radiation high-energy radiation that destroys chemical bonds

isometric relating to contraction without movement

isotopes forms of an atom that differ by the number of neutrons in the nucleus

keratin a major structural protein

kilobase one thousand DNA bases; a measure of size of a piece of DNA

kilobasepair one thousand DNA base pairs; a measure of size of a piece of DNA

kinase enzyme that adds a phosphate group to another molecule, usually a protein

Krebs cycle central metabolic pathway in mitochondria

lactation production of milk by the mammary glands

laparoscopic surgery surgery in which an instrument is inserted through a very small incision, usually guided by some type of imaging technique

larynx "voice box"; muscles at the top of the trachea that control pitch and loudness

lateral side-to-side

lethargy lack of excitability; torpor

lignified hardened by impregnation with lignin, a compound formed in plants

lignin organic molecule used in plant cell walls to add stiffness to cellulose

lineage ancestral line

lipid fat or waxlike molecule, insoluble in water

lipoprotein combination of protein and lipid, or fatlike molecule

locus site on a chromosome (plural, loci)

lotic of, relating to, or living in actively moving water

lymph pale fluid that circulates in the lymphatic system, principally composed of blood plasma and cell fluid

lymphatic system network of tubes that permeates the body for transport of lymph and combat of infection

lymphocyte white blood cell found in lymph nodes

lyse break apart

lysine an amino acid

lysing disintegration or dissolution of cells

macromolecules large molecules such as proteins, carbohydrates, and nucleic acids

marsupials kangaroos and other mammals that gestate young in an external pouch

materialism the belief that life is due entirely to biochemical interactions, without the intervention of supernatural forces

matrix a network, usually of threadlike fibers

medium nutrient source

meiosis cell division that forms eggs or sperm

membrane potential electrical and chemical differences across a membrane leading to storage of energy and excitability

metabolism chemical reactions within a cell

metabolite molecule involved in a metabolic pathway

metamorphosis development process that includes a larval stage with a different form from the adult

metaphase intermediate stage in cell division, in which chromosomes line up before separating

metastasis breaking away of cancer cells from a solid tumor to travel elsewhere in the body

metazoans animals other than sponges

methylation addition of the methyl group CH_3

micron one-millionth of a meter; also called a micrometer

mid-dorsal middle of the back

middle lamella layer of material between two plant cells that holds them together

minerals iron, calcium, sodium, and other elements needed by living organisms

missense mutation nucleotide change that causes a change in the amino acid normally added to the protein

mitochondria subcellular organelle that creates ATP used for energy-requiring processes in a cell

mitogen substance that stimulates mitosis

mitosis separation of replicated chromosomes

molecular hybridization base-pairing among DNAs or RNAs of different origins

monocot any of various flowering plants, such as grasses and orchids, that have a single cotyledon in the seed

monoculture cultivation of a single type of crop in a large area

monomer "single part"; monomers are joined to form a polymer

monophyletic a group that includes an ancestral species and all its descendants

montane mountainous region

morphology related to shape and form

motile able to move

motor neuron nerve cell that controls a muscle or gland

mucous membrane outer covering designed to secrete mucus, often found lining cavities and internal surfaces

multimer composed of many similar parts

multinucleate having many nuclei within a single cell membrane

muscle tone low level, constant muscle contraction

mutualism symbiosis between two organisms in which both benefit

mycorrhizae symbiosis between soil fungus and plant root to maximize absorption

myxedema thyroid disorder characterized by dry skin, swelling in the face, and mental deterioration

nanometer 10^{-9} meters; one-billionth of a meter

natural selection process by which organisms best suited to their environments achieve greater reproductive success thus creating more "fit" future generations

nematode worm of the Nematoda phylum, many of which are parasitic

nephron functional unit of the kidney that performs filtration, reabsorption, and excretion

neritic zone near the shore

neural related to nerve cells or the nervous system

neurologist doctor who treats brain disorders

neuron nerve cell

neurotransmitters molecules released by one neuron to stimulate or inhibit another neuron or cell

niche the habitat supplying the right environment for a particular species

nm nanometer; one-billionth of a meter

nocturnal characterized by activity at night, or related to the night

nondisjunction failure of separation of homologous chromosomes during meiosis

nuclear envelope double membrane surrounding the cell nucleus

nucleated having a nucleus

nucleotide the building block of RNA or DNA

nucleus membrane-bound portion of cell containing the chromosomes

obligate required or necessary, especially referring to a metabolic process or mode of nutrition

octomer composed of eight parts

oligosaccharide chain of several sugar molecules

oncogene gene that causes cancer

oocyte unfertilized egg

opportunistic caused by a microorganism that is usually harmless but which causes infection in an immunosuppressed person

organelle membrane-bound cell compartment

organic composed of carbon, or derived from living organisms; also, a type of agriculture stressing soil fertility and avoidance of synthetic pesticides and fertilizers

osmosis passage of water through a membrane in response to concentration differences

osseous related to bone

outcross fertilization between two different plants

ovipary production of eggs that hatch outside the body

ovovivipary production of eggs that hatch within the female's body

ovule multicellular structure that develops into a seed after fertilization

oxidation reaction characterized by loss of electrons, or reaction with oxygen

oxidation-reduction oxidation is loss of electrons, and reduction is gain of electrons

oxidative characterized by oxidation, or loss of electrons

oxidative phosphorylation use of oxygen to make ATP

oxidize to react or make react with oxygen

palatine bone bone of the hard palate at the roof of the mouth

paleoanthropology study of ancient humans

palindromic reading the same forward and backward

pandemic disease spread throughout an entire population

papillate small, nipplelike projection

parasite organism living in close association with another from which it derives most of its nutrition

parasitology study of parasites

parasympathetic nervous system branch of the nervous system promoting nutrient absorption and other maintenance activities

pathogen disease-causing organism

pathogenesis pathway leading to disease

pathologic related to disease

pectin carbohydrate in plants that forms crosslinks to stabilize cell walls

peptide bond bond between two amino acids

peptidoglycans polymer that is composed of polysaccharides and peptic chains

perianth combined sepals and petals

peripheral outside the central nervous system (brain and spinal cord)

pH measure of acidity or alkalinity; numbers below 7 are acid, above are basic

phage short for bacteriophage

phagocytosis engulfing of cells or large fragments by another cell, including immune system cells

pharynx throat

phase-contrast microscopy technique that manipulates passage of light through transparent specimens to reveal internal features

phenotype observable characteristics of an organism

pheromone molecule released by one organism to influence another organism's behavior

phloem plant tissue that conducts sugars from leaves to roots and other tissues

phosphodiester the link between two nucleotides in DNA or RNA

phosphorylate add a phosphate group to

phosphorylation addition of the phosphate group $PO_4{}^{3-}$

phyletic gradualism the belief that evolutionary change is slow and steady

phylogenetic related to phylogeny, the evolutionary development of a species

phylum taxonomic level below kingdom, e.g., arthropod or chordate

physiology branch of biology that deals with the functions and activities of living matter

phytoplankton microscopic floating creatures that photosynthesize

pinnate featherlike

pinocytosis introduction of fluids into a cell by enclosing it and pinching off the plasma membrane

pipette lab instrument for precise measurement and transfer of small volumes of liquids

pistil female reproductive organ of a flower

placental related to mammals that nourish the fetus with a placenta, an exchange organ in the uterus

plankton microscopic floating organisms

plant hybridization creation of offspring by union of two different types of plants, such as wheat and rye

plasmid small ring of DNA found in many bacteria

plasticity change form

plate tectonics the movement of large plates of Earth's crust

polar partially charged, and usually soluble in water

polar covalent bond in which electrons are unevenly shared

polymer molecule composed of many similar parts

polymerase enzyme complex that synthesizes DNA or RNA from individual nucleotides

polymerization linking together of similar parts to form a polymer

polypeptide chain of amino acids

polysaccharide carbohydrate composed of many individual units of sugar

posterior toward the back

postmortem after death

prebiotic before the origin of life

Precambrian before the Cambrian era; before 600 million years ago

primer short nucleotide sequence that helps begin DNA replication

progeny offspring

prokaryote single-celled organism without a nucleus

promoter DNA sequence to which RNA polymerase binds to begin transcription

prostaglandins hormonelike molecules released by one cell that affect nearby cells, including smooth muscle

prostrate face downward

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

proteolysis breakdown of proteins

protoecology early ecology

protoplasm fluid portion of a plant cell within the cell wall

protostome "mouth first"; referring to the early development of the oral pore during gut tube formation

protozoa any of a phylum of minute protoplasmic animals present in almost every kind of habitat, some of which pose serious threats to humans and animals

pseudopod "false foot"; an extension of the plasma membrane during locomotion by an amoeba or similar crawling cell

psychosis severe mental disorder characterized by diminished connection with reality

psychotropic affecting consciousness, thought, or emotion

punctuated equilibrium pattern of evolution in which long periods of relatively little change are punctuated by rapid change

pyruvate the ionized form of pyruvic acid, a key intermediate in cell metabolism

quarternary fourth level

radially symmetric symmetric, or similar, about a central point (a wheel is radially symmetric)

reproductive isolation isolation of a population from other populations of the same species due to inability to successfully reproduce; an early stage in species formation

respire use oxygen to burn cellular fuel

restriction enzyme enzyme that cuts DNA at a particular sequence

restriction fragments fragments of DNA created by restriction enzymes

reticular netlike

retrograde backward

reverse transcriptase enzyme that copies RNA into DNA

reverse transcription creation of DNA from an RNA template

ribonucleoprotein combination of RNA and protein

ribosome protein-RNA complex in cells that synthesizes protein

rickettsia (pl. -sias or siae) any of a family of polymorphic microorganisms that cause various diseases

RNA polymerase enzyme complex that creates RNA from DNA template

saline of, or relating to, salt

saprophyte plant that feeds on decaying parts of other plants

savanna open grassland with sparse trees

sclerophyll small, tough evergreen leaves

secretion material released from the cell

secretory pathway series of events within a cell by which molecules are brought to the plasma membrane for release from the cell

sepals whorls of flower organs outside of the petals, usually green and serving to protect the flower before it opens

serotinous developing late in the season

serotype identity of an organism or virus based on reaction to an antibody

sessile attached and remaining in one place

silviculture cultivation of forest trees

sleep apnea difficulty breathing while asleep

solenoid cylindrical coiled structure

solute dissolved substance

solvation the process of dissolving

somatic nonreproductive; not an egg or sperm

somatostatin hormone produced by the hypothalamus that influences growth

spasticity of, or relating to, spasms

spectroscopy process using light or other emitted radiation to determine properties of a sample

sphincter ring of muscle regulating passage of material through a tube such as the gastrointestinal tract

spontaneous generation the theory that life began from nonliving matter

stasis state of no change

steroid hormone group of hormones that includes estrogen, testosterone, and progesterone

steroids hormones such as testosterone or estrogens that control many aspects of physiology

stomata openings in leaves for gas exchange, surrounded and regulated by guard cells

strong bond high-energy arrangement between two atoms involving electron-sharing; strong bonds require more energy to break than weak bonds

subcutaneous below the skin

substrate the molecule acted on by an enzyme; also a surface for attachment

succession series of changes seen in some plant communities over time, in which low-growing, rapidly reproducing species are replaced by taller and more slowly reproducing ones

superficial on the surface; not deep

symbiont organism living in close association with another organism

symbiosis close relationship between two species in which at least one benefits

sympathetic nervous system branch of the nervous system that promotes heightened awareness, increased nutrient consumption, and other changes associated with "fight or flight"

synaptic transmission passage of chemicals between nerve cells to send messages or alter neuron firing

synchronously at the same time

synergism working together to create a larger product rather than a simple sum

systemic throughout the body

T cell white blood cell that controls the immune response

taxon a level of classification, such as kingdom or phylum

tectonic plate large segment of Earth's crust that moves in relation to other similar plates

template master copy

teratogens substances that cause birth defects

tertiary third level

thermoregulation temperature regulation

transcribe creation of an RNA copy of a DNA gene

transcription messenger RNA formation from a DNA sequence

transcription factor protein that increases the rate of transcription of a gene

transduction conversion of a signal of one type into another type

transgenic characterized by presence of one or more genes from a different organism

translation synthesis of protein using mRNA code

translocation movement of sugars and other nutrients throughout a plant

transverse situated or lying across

trimer a structure composed of three parts

triploid possessing three sets of chromosomes

trophic related to feeding

trophic level feeding level in an ecosystem

true breeding giving only offspring identical to the parents

turgor internal pressure

ubiquitous found everywhere

ultrasonography use of sound waves to produce an image

ungulate hoofed mammals such as cattle

uninucleate possessing one nucleus

vas deferens tube through which sperm travel from testes to urethra

vector carrier

ventral to toward the belly side

ventricle fluid-filled chamber

venule any of the minute veins connecting the capillaries with the larger systemic veins

vesicle membrane-bound sac

vestigial no longer functional

visceral related to the viscera, or internal organs

viscous thick

vivipary production of live young

volatile easily vaporized

vulva external female genitalia

weak bond low-energy arrangement between two atoms involving electron-sharing; weak bonds require less energy to break than strong bonds

X-ray crystallography use of X rays to determine the structure of a molecule

xylem water-transporting system in plants

zygote fertilized egg

Topic Outline

Lipids
Lysosomes
Membrane Proteins
Metabolism
Mitochondrion
Nitrogen Cycle
Nitrogen Fixation
Nucleotides
Origin of Life
Oxidative Phosphorylation
Pauling, Linus
Peroxisomes
Pharmacologist
Poisons
Polymerase Chain Reaction
Prion
Protein Structure
Protein Synthesis
Radionuclides
RNA
Secondary Metabolites in Plants
Separation and Purification
Structure Determination
Vitamins and Coenzymes
Water

BIOLOGY AND SOCIETY

Alcohol and Health
Anabolic Steroids
Behavior, Genetic Basis of
Biological Weapons
Biology of Race
Carson, Rachel
Creationism
Desertification
Doctor, Specialist
Dubos, René
Endangered Species
Ethnobotany
Evolution, Evidence for
Extinction, Mammals
Fire Ecology
Gene Therapy
Global Climate Change
Human Genome Project
Human Population
Invasive Species
Organic Agriculture
Pauling, Linus
Pollution and Bioremediation
Psychiatric Disorders, Biology of
Psychoactive Drugs
Recombinant DNA
Reproductive Technology
Sexually Transmitted Diseases

Smoking and Health
Sociobiology
Transgenic Techniques

BIOMES

Biogeography
Biome
Coral Reef
Desert
Field Studies in Plant Ecology
Forest, Boreal
Forest, Temperate
Forest, Tropical
Global Climate Change
Grassland
Remote Sensing
Tundra

BIOTECHNOLOGY

Antibodies in Research
Antisense Nucleotides
Bacterial Genetics
Bioinformatics
Biological Weapons
Biotechnology
Clone
Electrophoresis
Forensic DNA Analysis
Genomics
Human Genome Project
Hybridization
Polymerase Chain Reaction
Recombinant DNA
Reproductive Technology
Reverse Transcriptase
Separation and Purification
Structure Determination
Transgenic Techniques

CAREERS

Agronomist
Biochemist
Botanist
College Professor
Dentist
Doctor, Family Practice
Doctor, Specialist
Emergency Medical Technician
Entomologist
Epidemiologist
Forester
Health and Safety Officer
High School Biology Teacher
Horticulturist

Laboratory Technician
Marine Biologist
Medical Assistant
Microbiologist
Microscopist
Nurse
Nurse Practitioner
Nutritionist
Pharmaceutical Sales Representative
Pharmacologist
Physician Assistant
Plant Pathologist
Psychiatrist
Public Health Careers
Science Writer
Veterinarian
Wildlife Biologist
Zoology Researcher

CELL FUNCTION

Active Transport
Cancers
Cell Cycle
Cell Motility
Control Mechanisms
Control of Gene Expression
Cytokinesis
Endocytosis
Enzymes
Exocytosis
Glycolysis and Fermentation
History of Plant Physiology
Hormones
Ion Channels
Krebs Cycle
Lysosomes
Meiosis
Membrane Proteins
Membrane Transport
Metabolism
Mitochondrion
Model Organisms: Cell Biology and Genetics
Nuclear Transport
Oxidative Phosphorylation
Peroxisomes
Protein Synthesis
Protein Targeting
Replication
Ribosome
RNA Processing
Signaling and Signal Transduction
Synaptic Transmission
Transcription

CELL STRUCTURE

Archaea
Bacterial Cell
Cell
Cell Evolution
Cell Junctions
Cell Motility
Cell Wall
Chloroplast
Connective Tissue
Cyanobacteria
Cytoskeleton
Electron Microscopy
Endoplasmic Reticulum
Epithelium
Eubacteria
Extracellular Matrix
Golgi
History of Biology: Cell Theory and Cell
    Structure
Ion Channels
Life, What Is
Light Microscopy
Lysosomes
Membrane Proteins
Membrane Structure
Membrane Transport
Microscopist
Mitochondrion
Model Organisms: Cell Biology and Genetics
Muscle
Neuron
Nuclear Transport
Nucleolus
Nucleus
Organelle
Origin of Life
Peroxisomes
Plasma Membrane
Porter, Keith
Ribosome
T Cells
Tissue
Vacuole

CIRCULATION AND RESPIRATION

Blood
Blood Clotting
Blood Sugar Regulation
Blood Vessels
Cardiovascular Diseases
Circulatory Systems
Gas Exchange
Harvey, William
Heart and Circulation

Grassland
Habitat
Invasive Species
Lakes and Ponds
Landscape Ecology
Limnologist
Marine Biologist
Mimicry, Camouflage, and Warning Coloration
Nitrogen Cycle
Ocean Ecosystems: Hard Bottoms
Ocean Ecosystems: Open Ocean
Ocean Ecosystems: Soft Bottoms
Physiological Ecology
Pollution and Bioremediation
Population Dynamics
Predation and Defense
Remote Sensing
Rivers and Streams
Symbiosis
Theoretical Ecology
Tundra
Water Cycle
Wetlands

ENDOCRINE SYSTEM

Adrenal Gland
Anabolic Steroids
Birth Control
Blood Sugar Regulation
Endocrine System
Female Reproductive System
Hormones
Hypothalamus
Pancreas
Pituitary Gland
Sex Determination
Stress Response
Thyroid Gland

EVOLUTION AND ADAPTATION

Adaptation
Amniote Egg
Angiosperms
Biodiversity
Biogeography
Buffon, Count (Georges-Louis Leclerc)
Cambrian Explosion
Cell Evolution
C4 and CAM Plants
Convergent Evolution
Creationism
Darwin, Charles
Evolution
Evolution, Evidence for

Evolution of Plants
Extinction, Mammals
Extreme Communities
Hardy-Weinberg Equilibrium
Herbivory and Plant Defenses
History of Evolutionary Thought
Human Evolution
Lamarck, Jean-Baptiste
Leakey Family
Mimicry, Camouflage, and Warning Coloration
Natural Selection
Origin of Life
Osmoregulation
Paleontology
Physiological Ecology
Population Genetics
Predation and Defense
Scaling
Secondary Metabolites in Plants
Sociobiology
Speciation
Species

EXPERIMENTAL TECHNIQUES

Antibodies in Research
Antisense Nucleotides
Biochemist
Bioinformatics
Biotechnology
Cell Culture
Clinical Trials
Clone
Crick, Francis
DNA Sequencing
Drug Testing
Ecological Research, Long-term
Electron Microscopy
Electrophoresis
Field Studies in Animal Behavior
Field Studies in Plant Ecology
Forensic DNA Analysis
Gene Therapy
Genetic Analysis
Genomics
Hardy-Weinberg Equilibrium
History of Biology: Biochemistry
History of Plant Physiology
Human Genome Project
Hybridization
Imaging in Medicine
Ingenhousz, Jan
Laboratory Technician
Leeuwenhoek, Anton
Light Microscopy
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HISTORY OF BIOLOGY

Buffon, Count (Georges-Louis Leclerc)
Carson, Rachel
Crick, Francis
Darwin, Charles
De Saussure, Nicolas
Dubos, René
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Gray, Asa
Harvey, William
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    Structure
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Lamarck, Jean-Baptiste
Leakey Family
Leeuwenhoek, Anton
Linnaeus, Carolus
McClintock, Barbara
Mendel, Gregor
Pasteur, Louis
Pauling, Linus
Porter, Keith
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Torrey, John
Van Helmont, J. B.
Vavilov, Nikolay
Vesalius, Andreas
Von Humboldt, Alexander
Watson, James

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Antibodies in Research
Antibody
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Bacterial Genetics
Behavior, Genetic Basis of
Biology of Race
Cell Cycle
Chromosome Aberrations
Clone
DNA
Feeding Strategies
Genetic Counselor
Genetic Diseases
History of Biology: Inheritance
Hybridization-Plant
Life Cycles
Linkage and Gene Mapping
Meiosis
Mendel, Gregor
Mitosis
Model Organisms: Cell Biology and Genetics
Mutation
Patterns of Inheritance
Pedigrees and Modes of Inheritance
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Biogeography
Community
Competition
Ecological Research, Long-term
Ecology, History of
Ecosystem
Feeding Strategies
Field Studies in Animal Behavior
Field Studies in Plant Ecology
Fire Ecology
Habitat
Herbivory and Plant Defenses
Human Population
Invasive Species
Landscape Ecology
Lichen
Mimicry, Camouflage, and Warning Coloration
Mycorrhizae
Pheromone
Population Dynamics
Population Genetics
Predation and Defense