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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	
−10	−20
°F	°C
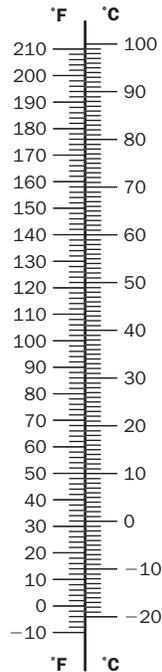
100°C = water boils
0°C = water freezes

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
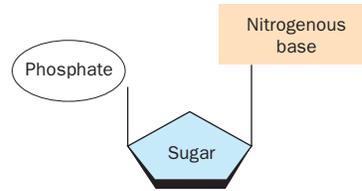
Purine-containing nucleotides

Adenine
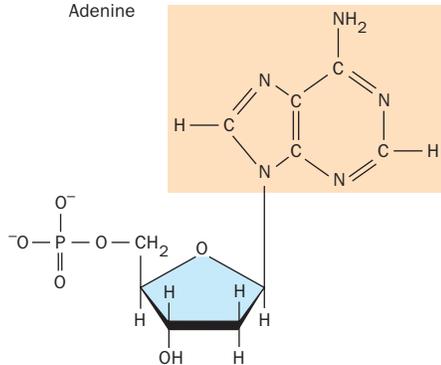
Pyrimidine-containing nucleotides

Thymine
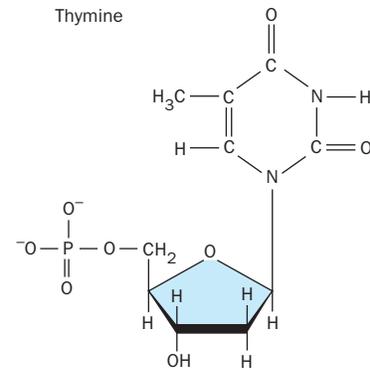
Guanine
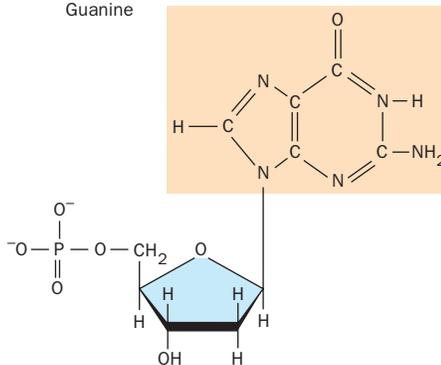
Cytosine
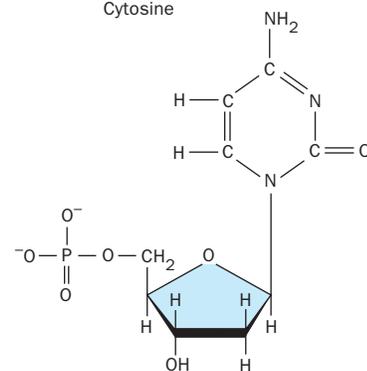
DNA NUCLEOTIDES PAIR UP ACROSS THE DOUBLE HELIX

5' to 3' direction

5' to 3' direction

5' end

Thymine (T)

Adenine (A)

3' end

Cytosine (C)

Guanine (G)

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
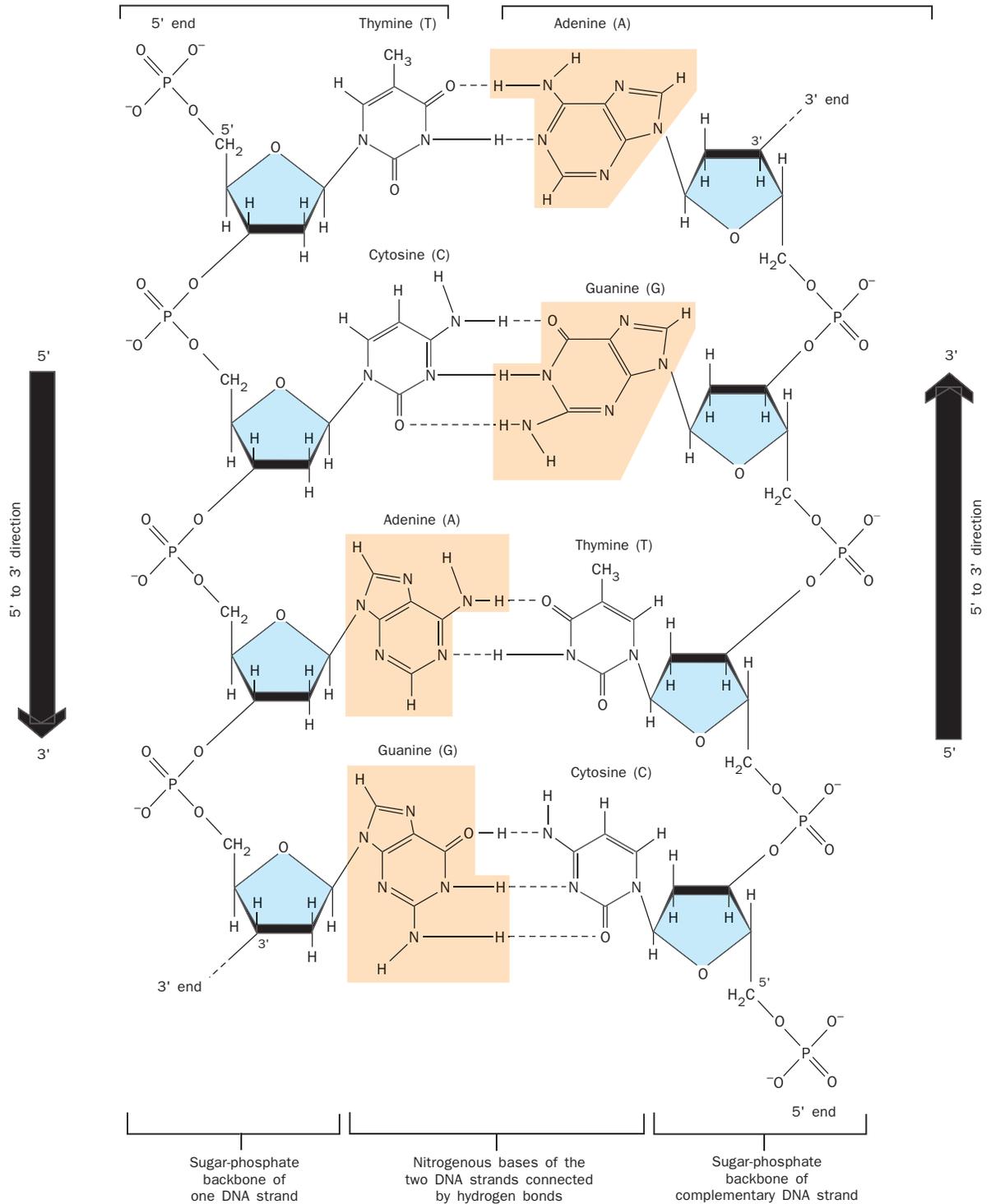
COMPARISON OF DNA AND RNA

HOCH$_2$ O   OH

Deoxyribose

HOCH$_2$ O   OH

Ribose

DNA

RNA

A   T

C   G

G   C

T   A

A

C

G

U

Thymine

Uracil
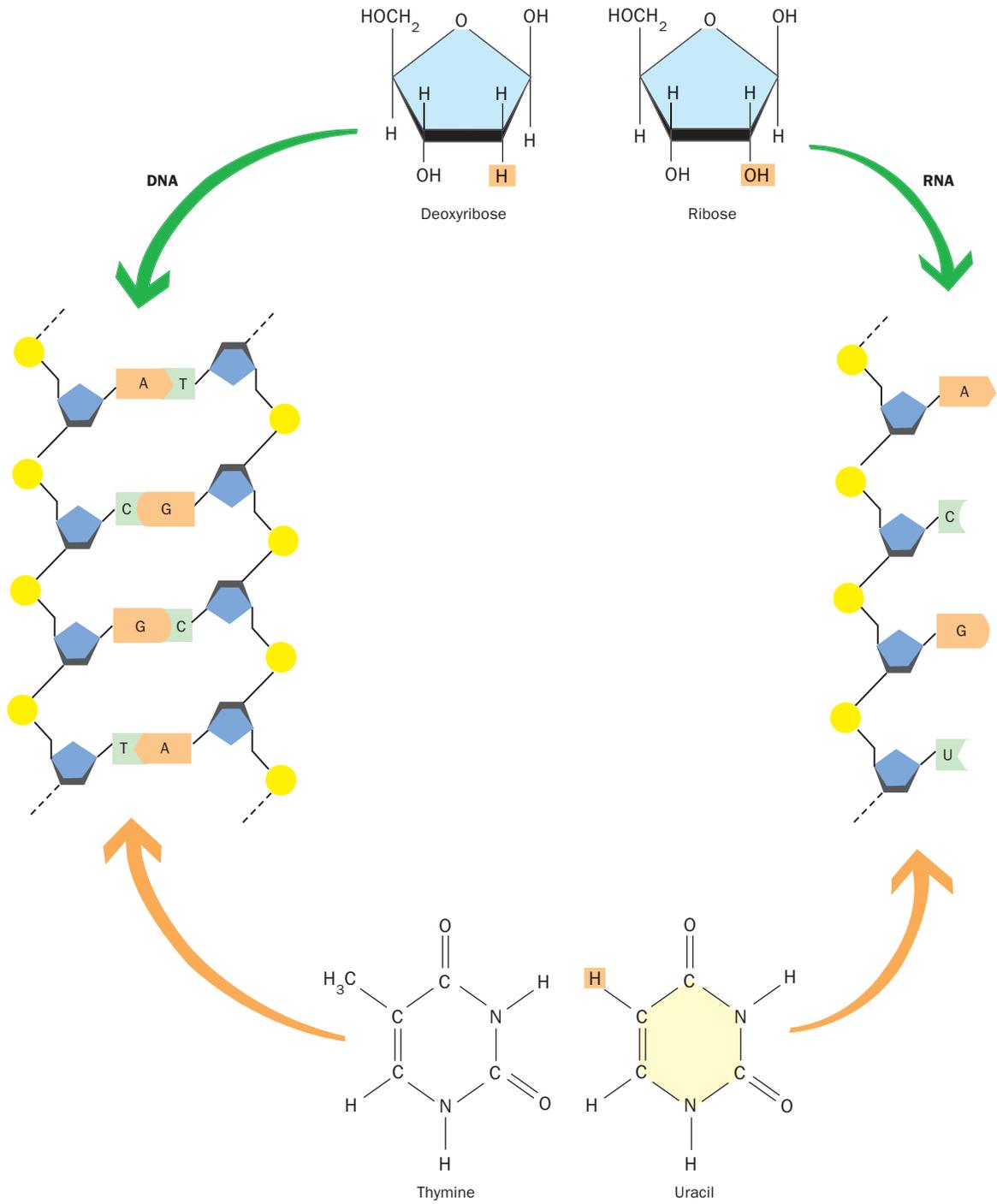
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Imaging in Medicine

As recently as in the 1970s, the diagnosis of some diseases often required exploratory surgery, opening a body cavity to "have a look around" for visible disorders. The risks of infection, anesthesia, and imperfect healing weigh against exploratory surgery, but the diagnostic benefit may make the risk worth taking. In the last few decades, however, a variety of medical imaging techniques has made most exploratory surgery unnecessary and has greatly accelerated progress in medicine. Although the basic principles of some of these techniques have been known for much longer, they did not become clinically useful until computer technology had advanced enough to process data into clear images of the body, mostly since the 1970s.

Radiography

Radiography, use of X rays, is the oldest imaging technique. The term "X ray" can refer either to the type of radiation used or to the photographic image produced (the radiogram). X rays were discovered in 1885, and Marie Curie (1867–1934) trained military doctors in the use of X-ray machines in World War I. X rays are relatively simple and inexpensive to make, and they are commonly used in dentistry, mammography, chest examinations, and diagnosis of fractures. They are best used for dense structures such as bone, but hollow organs can be visualized by filling them with a radiopaque substance such as barium, given by swallow or enema to X ray the stomach or colon. Angiography is the X-ray visualization of blood vessels after injection with a radiopaque dye.

Sonography

Sonography, or ultrasound imaging, is the second oldest imaging method, and the second most widely used. An outgrowth of the sonar technology developed in World War II, it uses a handheld probe to "bombard" the body with ultrasound waves and a computer to analyze the reflected signal into an image. Sonography avoids the harmful effects of X rays and is commonly used to examine fetuses.

Computed Tomography (CT)

Formerly called a CAT scan, computed tomography (CT) is a more sophisticated use of X rays to produce more finely detailed images. The
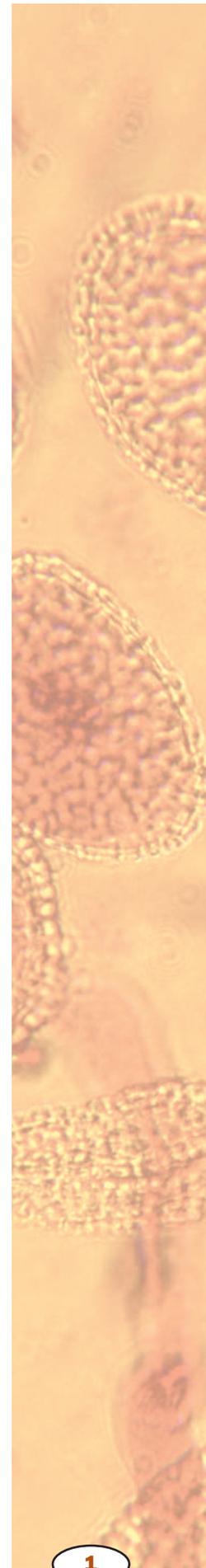
A magnetic resonance imaging (MRI) scan of a human brain, cervical spine, and spinal marrow.
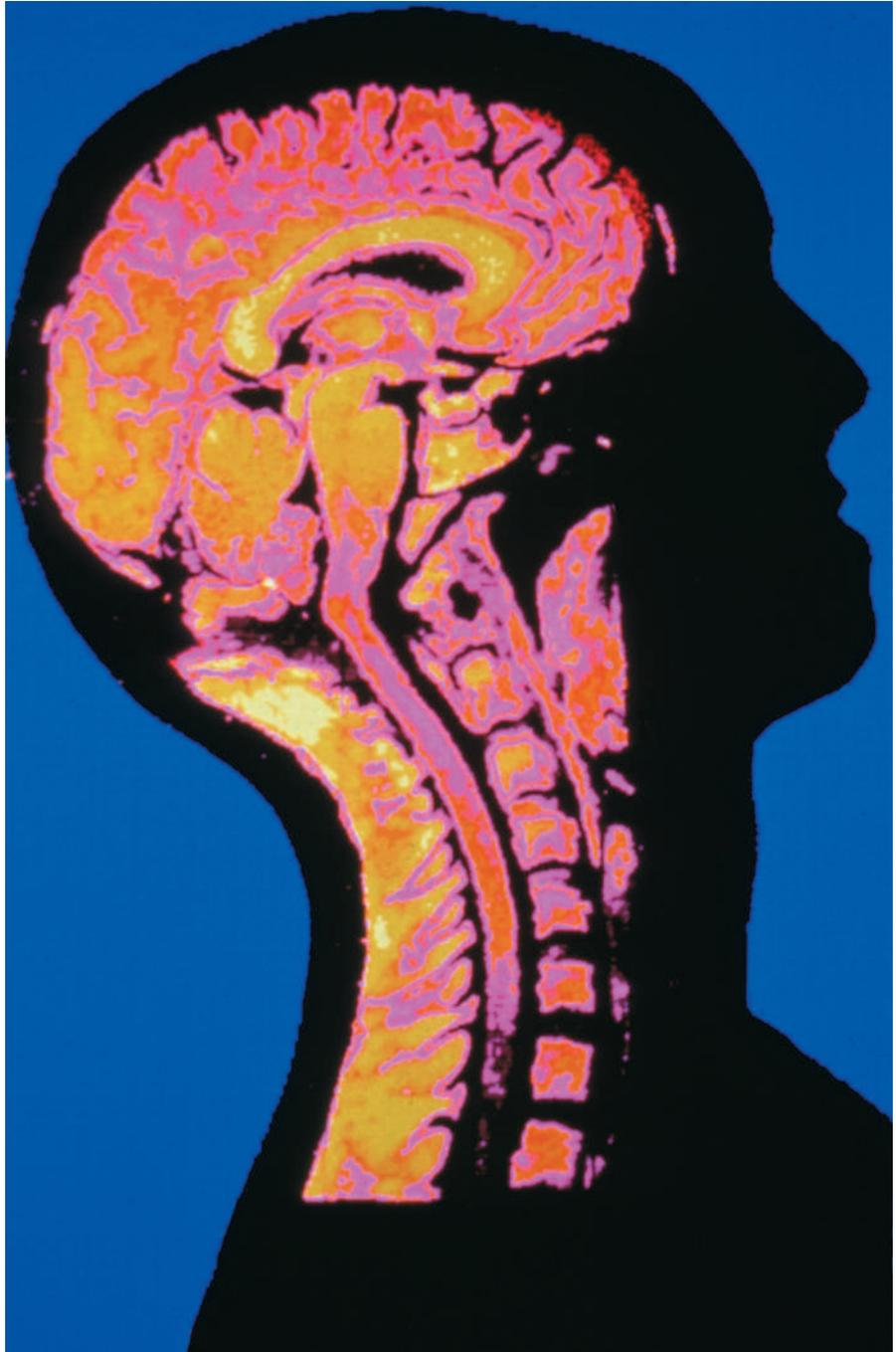
aneurysm bulging of the wall of a blood vessel

patient is moved through a machine that emits low-intensity X rays on one side and receives them with a detector on the other side. By imaging body slices as thin as a coin, CT scans show less overlap of organs than conventional X rays and thus produce sharper images. CT scans are useful for identifying tumors, **aneurysms**, cerebral hemorrhages, kidney stones, and other disorders.

Magnetic Resonance Imaging (MRI)

With magnetic resonance imaging (MRI), a cylindrical device surrounds the body with a magnetic field three thousand to sixty thousand times as

strong as Earth's. Hydrogen atoms align themselves with this field. The patient is then irradiated with radio waves. Hydrogen **ions** absorb this energy and align in a new direction. When the radio waves are turned off, they realign to the magnetic field and emit energy at rates that vary with the type of tissue. This emitted energy is received by a detector and analyzed by a computer into an image of the body's interior. MRI can see through **cranial** and vertebral bone to visualize brain and spinal cord tissue in finer detail than CT.

ion an electrically charged particle

cranial related to the cranium, or brain cavity

Positron Emission Tomography (PET)

Positron emission tomography (PET) is used to visualize the metabolic state of a tissue. The patient receives an injection of radioactively labeled **glucose**, which emits charged particles called positrons. When a positron and electron meet, they annihilate each other and give off gamma rays that are picked up by a detector and analyzed by computer. The result is a color-coded image that shows which tissues were using the most glucose (that is, were most metabolically active) at the time. In cardiology, a PET scan can show the location and extent of dead heart tissue. In neuroscience, it can show which parts of the brain are active from moment to moment as a person engages in various sensory, motor, or intellectual tasks.

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

Functional MRI (fMRI)

A new variation of MRI, functional MRI (fMRI) detects the **anaerobic** activity of active **neurons** of the brain. It can pinpoint brain activity to within 1 or 2 millimeters, and is even more precise and useful than PET scans for studies of brain function. It also has the advantage of requiring no injections or radioactive **isotopes**, and it is much quicker than a PET scan. The PET and fMRI techniques not only have been valuable for clinical diagnosis but have added enormously to our knowledge of brain function, pinpointing abnormalities correlated with depression, schizophrenia, and attention deficit disorder. They have also provided images of the mind at work, so to speak, identifying areas involved in consciousness, memory, thought, musical perception, reading, motor control, and speech.

anaerobic without oxygen, or not requiring oxygen

neuron nerve cell

isotopes forms of an atom that differ by the number of neutrons in the nucleus

Radiology is the medical specialty that embraces all of these imaging techniques. Nuclear medicine is a branch of medicine that uses radioisotopes in the making of medical images, as in PET scans, and in the treatment of diseases such as cancer. Noninvasive techniques are those that require no break in the body surface whatsoever: conventional X rays; sonography; and CT, MRI, and fMRI scans. If a technique involves even such a slight invasion of the body as an injection or a barium swallow, it is considered an invasive procedure (angiography and PET scans, for example). SEE ALSO BRAIN; DOCTOR, SPECIALIST.

Kenneth S. Saladin

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Immune Response

Among the many threats organisms face are invasion and infection by bacteria, viruses, fungi, and other foreign or disease-causing agents. All organisms have nonspecific defenses (or innate defenses) that provide them with some of the protection they need. This type of defense exists throughout the animal kingdom, from sponges to mammals. Vertebrate animals, however, have an additional line of defense called specific immunity. Specific immunity is also called acquired immunity, adaptive immunity, or, most simply, an immune response.

Overview

One characteristic of specific immunity is recognition. Immune responses begin when the body recognizes the invader as foreign. This occurs because there are molecules on foreign cells that are different from molecules on the body's cells. Molecules that start immune responses are called **antigens**. The body does not usually start an immune response against its own antigens because cells that recognize self-antigens are deleted or inactivated. This concept is called self-tolerance and is a key characteristic that defines immune responses.

antigen foreign substance that provokes an immune response

A second characteristic is specificity. Although all immune responses are similar, each time the body is invaded by a different antigen, the exact response is specific to that antigen. For example, infection with a virus that causes the common cold triggers a response by a different set of cells than infection with bacteria that causes strep throat.

A third characteristic is memory. After an antigen is cleared from the body, immunological memory allows an antigen to be recognized and removed more quickly if encountered again.

Antigen Presentation

Three groups of white blood cells are involved in starting an immune response. Although immune responses can occur anywhere in the body these cells are found, they primarily occur in the **lymph** nodes and spleen. These organs contain large numbers of antigen-presenting cells (APCs), T lymphocytes (or **T cells**), and **B lymphocytes** (or B cells).

lymph pale fluid that circulates in the lymphatic system, principally composed of blood plasm and cell fluid

T cell white blood cell that controls the immune response

B lymphocyte white blood cell that makes antibodies

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

APCs include macrophages, dendritic cells, and B cells. These cells encounter the foreign invader and present the invader's antigens to a group of T cells called helper T cells (T_H cells). APCs do this by first engulfing an invader and bringing it inside the cell. The APC then breaks the invader apart into its antigens and moves these antigens to its cell surface.

Receptors are cell surface **proteins** that can attach to antigens. Each T_H cell has a different receptor, allowing each cell to recognize a different antigen. The APC "shows" the antigen to the T_H cells until there is a match between a T_H cell receptor and the antigen. The contact between the two cells stimulates the T_H cell to divide rapidly. This process is called clonal selection because only the T_H cells that recognize the foreign invader are selected to reproduce. Stimulated T_H cells also produce chemical messengers called cytokines. Cytokines are made by all immune cells and control the immune response.

Antigen Presentation

displayed antigen

antigen presenting cell

invader with antigens

T$_H$ cells with different receptors

Antigen Clearance

The large numbers of T$_H$ cells activate two other populations of white blood cells: cytotoxic T cells (T$_C$ cells) and B cells. Like T$_H$ cells, each T$_C$ cell and B cell has receptors that match one antigen. This is why the immune system can recognize millions of antigens with specificity. The cells with the appropriate receptor encounter the antigen, preparing them for activation. They receive the final signal necessary for clonal selection from T$_H$ cells and cytokines.

Cloned T$_C$ cells attach to invaders they recognize and release a variety of chemicals that destroy the foreign cell. Because this must happen through cell-to-cell contact, it is called cell-mediated immunity (or cellular immunity). It is especially effective at destroying abnormal body cells, such as cancerous cells or virus-infected cells.

Cloned B cells destroy foreign invaders differently. After activation by T$_H$ cells, B cells release proteins called antibodies. Antibodies travel through the body's fluids and attach to antigens, targeting them for destruction by nonspecific defenses. This type of immune response is called **antibody**-mediated immunity (or humoral immunity). It is especially effective at destroying bacteria, extracellular viruses, and other antigens found in body fluids.

antibody immune system protein that binds to foreign molecules

Immunologic Memory

A primary immune response happens the first time that the body encounters a specific antigen. It takes several days to begin and one or two
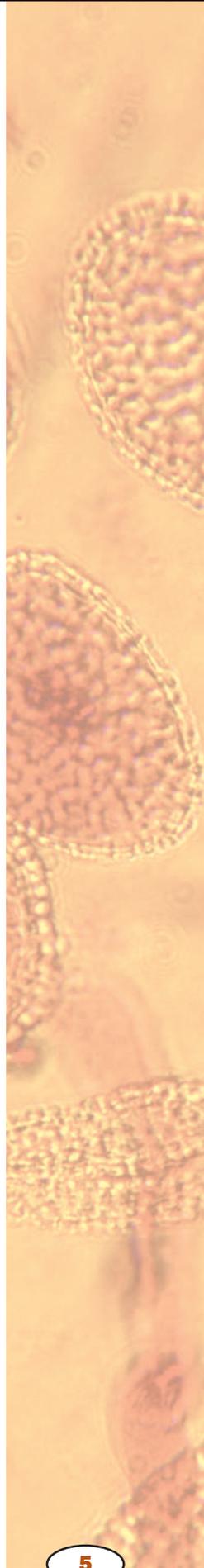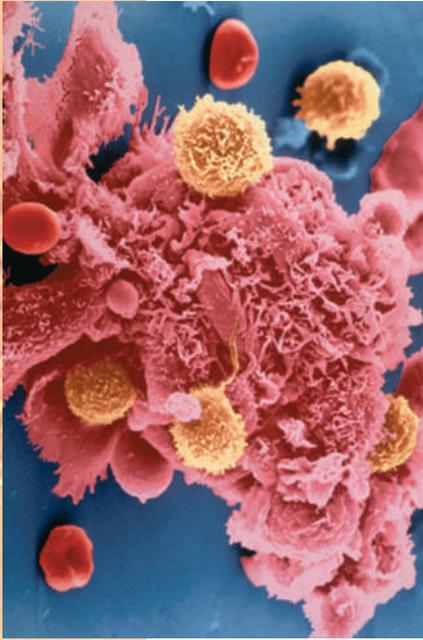
weeks to reach maximum activity. A secondary immune response occurs if the body encounters the same antigen at a later time. It takes only hours to begin and may peak within a few days. The invader is usually removed before it has a chance to cause disease. This is because some of the cloned T_C cells and B cells produced during a primary immune response develop into memory cells. These cells immediately become activated if the antigen appears again. The complex interactions among cells described above are not necessary.

In fact, this is what happens when an individual is immunized against a disease. The vaccination (using weakened or killed **pathogens**) causes a primary immune response (but not the disease) and the production of memory cells that will provide protection if exposed to the disease-causing agent.

Immune System Disorders

Studying immune responses also allows scientists to understand immune system diseases. For example, hypersensitivity disorders occur when the immune system overreacts to an antigen, causing damage to healthy tissues. The result of this excessive antibody and T_C cell activity can be relatively harmless (as with allergies to pollen, poison ivy, or molds) or deadly (as with **autoimmune diseases** or allergies to bee venom and antibiotics).

At the opposite end of the spectrum are immunodeficiency diseases, conditions in which the body does not respond effectively against foreign invaders. HIV (human immunodeficiency virus) infection causes AIDS (acquired immunodeficiency syndrome) by attacking T_H cells. Occasionally an individual is born with a deficient immune system, but these disorders are usually acquired (for example, from radiation treatment, chemotherapy, or infection with HIV). Whatever the cause, the individual has a more difficult time fighting infections.

Because immune responses exhibit the characteristics of self-tolerance, specificity, and memory, a healthy body is well equipped to remove foreign invaders and prevent recurrent infections. Age, nutrition, exercise, and stress all affect the ability of the body to fight disease. SEE ALSO AIDS; ANTIBODY; AUTOIMMUNE DISEASE; NONSPECIFIC DEFENSE

John M. Ripper

A scanning electron micrograph of a cancer cell (red in image) being attacked by tumor-infiltrating lymphocytes.

pathogen disease-causing organism

autoimmune disease disease in which the immune system attacks the body's own tissues

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Ingenhousz, Jan

Dutch physician and plant physiologist
1730–1799

Jan Ingenhousz was a pioneer in plant physiology and demonstrated that oxygen is produced during photosynthesis. Born in the Netherlands, Ingenhousz practiced medicine in several European countries and served as a court physician to Empress Maria Theresa of Austria for twenty years. Ingenhousz promoted vaccination against smallpox and helped develop a new vaccination procedure.

Ingenhousz used the gas-measuring techniques of his friend Joseph Priestley to study how plants alter the air. Priestley had shown that animals or burning candles "spoil" air, making it unfit for breathing. He had also reported that plants restore the air, but other experimenters could not replicate his results.

Ingenhousz attacked this problem systematically and meticulously. By placing different plant parts in sealed containers either exposed to or hidden from sunlight, Ingenhousz showed that plants do restore the air by the production of oxygen (a gas that Priestley had recently discovered) and that the green leaves must be exposed to sunlight for this to occur. In this way, Ingenhousz began the scientific understanding of photosynthesis, a process elucidated further by Swiss agriculturist Nicolas de Saussure and others. Ingenhousz contemplated using oxygen to treat patients but did not develop the equipment to do so. SEE ALSO DE SAUSSURE, NICOLAS; PHOTOSYNTHESIS; VAN HELMONT, J. B.

Richard Robinson

Insect

Insects are a class of **arthropods**. Like other arthropods, they have **exoskeletons** made from the carbohydrate **chitin**, segmented bodies, and jointed **appendages**. Insects are distinguished by having three major body segments (head, thorax, and abdomen), with three pairs of legs attached to the thorax. Ancestral head appendages have been modified to form antennae and mouth parts, while abdominal appendages are either absent or modified to aid in reproduction. Most insects possess wings as adults, also attached to the thorax.

Sensory Systems

The insect head bears a single pair of compound eyes, composed of many individual units, called ommatidia, each of which senses a small portion of the visual field. Hunting insects such as the dragonfly may have thousands of ommatidia per eye, while others, such as ants, have many fewer. A single pair of antennae serves as chemical sensors to help find food or mates. In many species, including the tobacco hornworm moth, the female releases airborne chemicals called **pheromones** that attract the male. The highly branched antennae of the male moth can detect the molecules of the female pheromone, and can track the scent to find the female over very long

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

exoskeleton external skeleton

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

appendage attached organ or structure

pheromone molecule released by one organism to influence another organism's behavior
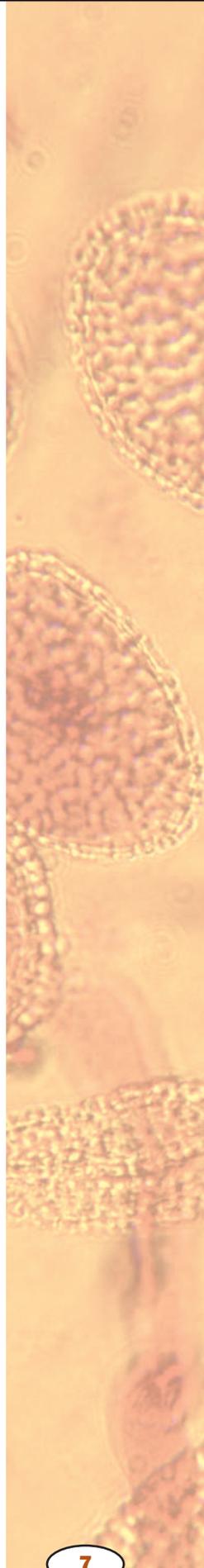
A katydid. Insects are distinguished by having three major body segments (head, thorax, and abdomen), with three pairs of legs attached to the thorax.

distances. Chemoreceptors are also located on the feet, allowing an insect to taste its food as it walks across a leaf or a table. The numerous hairs covering the insect body are linked to mechanoreceptors, which aid its sense of touch. Some mechanoreceptors can sense changes in air pressure, useful for flying or evading a swooping predator. Receptors for carbon dioxide, water, and temperature also exist.

Ingestion, Digestion, and Excretion

Insect mouth parts vary tremendously in their shapes, reflecting adaptations to a wide variety of feeding habits. Mosquitoes, for instance, have a long hypodermic needlelike stylet, perfect for piercing skin to suck blood. Butterflies and moths, among others, have a very long, flexible strawlike mouth part, the proboscis, which they unfold to sip nectar from the base of flowers. Houseflies have a spongy tonguelike labrum for sopping up a variety of foods. Grasshoppers and beetles have small, sharp mouth parts adapted for chewing. The insect gut is divided into three regions, with most digestion occurring in the midgut. Suspended into the midgut are the Malpighian tubules, which filter nitrogenous waste from the blood and deposit it as crys-

tals within the gut, avoiding the water loss that urine formation would entail. In termites, the hindgut houses a complex group of protists and bacteria that digest wood.

Legs and Wings

Insect legs are used for walking and climbing. In some predatory species such as the praying mantis, the front pair of legs has been modified for capturing prey, with barbed surfaces that hold other insects tightly. Almost all insects have wings, although a few primitive forms do not. In the ants, only the reproductive members of the colony have wings, which they shed after their "nuptial flight," in which they mate with members of the opposite sex.

Respiration and Circulation

Insects do not have lungs, but instead employ a highly branched network of internal tubes, called tracheae, to deliver oxygen to the tissues. Tracheae connect with the atmosphere through openings in the exoskeleton called spiracles. Insect circulatory systems transport nutrients and wastes in a fluid called hemolymph, which is pumped into and out of internal chambers surrounding the organs, an arrangement called an open circulatory system.

Reproduction and Development

Most insects reproduce sexually, although the aphids are a notable exception. Aphids reproduce by parthenogenesis, in which the egg develops into a new organism without **fertilization**. In honey bees and some other social insects, only one female per colony reproduces, and males are **haploid**, whereas females are **diploid**, a system called haplodiploidy. The queen produces new (diploid) females (workers, soldiers, and future queens) from fertilized eggs. Males are produced from eggs that are not fertilized, and thus males are haploid.

Insects vary in their degree of **metamorphosis** during development. Butterflies, beetles, and flies, for example, undergo complete metamorphosis, in which the egg hatches into a feeding larva, which then pupates. Within the pupa, the larval tissues dissolve and rearrange into the adult form. In contrast, grasshoppers, cockroaches, and cicadas undergo incomplete metamorphosis, emerging from the egg as a miniature adult, but minus the wings and genitals. To grow, all insects must molt, or shed their exoskeleton, which then reforms around the larger individual.

Metamorphosis often allows juvenile and adult individuals of the same species to avoid competition for food. Larval moths feed voraciously and can be significant agricultural pests, while adult moths either don't feed or consume only nectar.

Diversity

Insects are the most diverse of all groups of organisms, with over 800,000 species named and many thousands, probably millions, yet to be discovered. Insect diversity may be linked to their close association with the angiosperms (flowering plants). The Coleoptera (beetles) are the most diverse of all insect orders, with at least 350,000 species, representing one fourth of all known animal species. (Asked what could be inferred about the work of the

fertilization union of sperm and egg

haploid having single, nonpaired chromosomes in the nucleus

diploid having pairs of chromosomes in the nucleus

metamorphosis development process that includes a larval stage with a different form from the adult
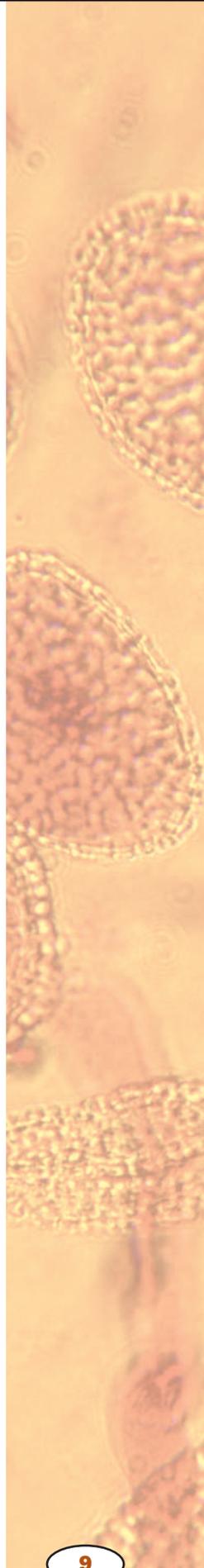
Creator from a study of His works, British scientist J. B. S. Haldane is reported to have quipped, "an inordinate fondness for beetles.") The evolutionary reasons for the mind-boggling diversity of this single order are not clear. Other major orders of insects include the Diptera (flies), Hymenoptera (bees and wasps), Hemiptera (true bugs), and Lepidoptera (moths and butterflies). Note that each name describes the wing (*ptera* means "wing"). For instance, Diptera means "two wings," referring to the presence of only one wing pair in this order. In the Coleoptera ("sheath wings"), the first pair of wings is modified into a hard covering for the rear pair, which is easily observed in a lady beetle, for instance. SEE ALSO ANGIOSPERMS; ARACHNID; ARTHROPOD; BIODIVERSITY; OSMOREGULATION; PHYSIOLOGICAL ECOLOGY; PLANT PATHOGENS AND PESTS; SYMBIOSIS

Richard Robinson

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Invasive Species

Animals, plants, and other organisms that are newly introduced into an area from another part of the world are sometimes referred to as "alien" or "exotic" species. These words are used to distinguish newly arrived species from the native species that have lived in the environment for very long periods of time. Although some people refer to all exotic species as invaders, some scientists believe it makes more sense to use the term "invasive species" only when referring to new species that are spreading rapidly and having a large negative impact on the environment, economic activities, or human health.

Many of these invasive species have been introduced into new environments by human activities. Sometimes they are introduced intentionally, such as European starlings, kudzu, and purple loosestrife, three species that spread very rapidly across the United States beyond their initial range of introduction and are believed to have reduced the abundance of native bird and plant species in many areas. However, most species introductions probably occur inadvertently by humans, a byproduct of frequent movements around the globe. For example, small ocean organisms are commonly picked up in the ballast water of ocean ships. When the ships release their ballast water at a port in another part of the world, these organisms are introduced into a new environment. Logs and other wood and fiber products imported into the United States sometimes contain insects from their country of origin, which accounts for the introduction of Chestnut Blight fungus in the United States.

In many cases, the new species do not spread very much nor do they have a large impact. However, many of these new species have created huge problems. Zebra mussels are reducing populations of native mussels in many

Kudzu overgrowing a house in Tennessee. Kudzu was intentionally introduced in the United States, but it spread very rapidly beyond its initial range of introduction.
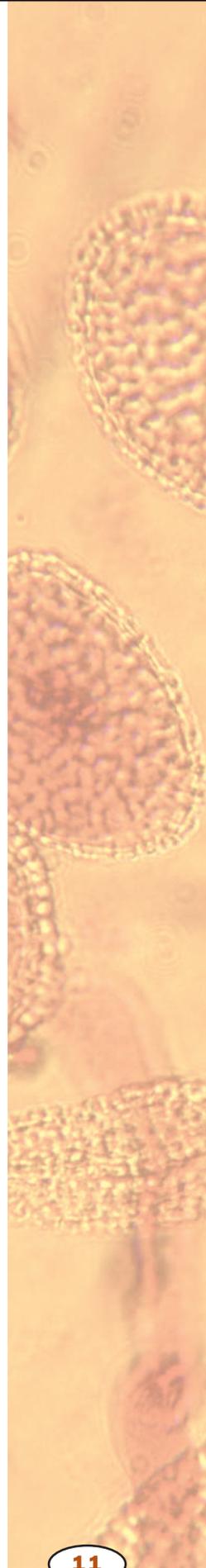
areas of the United States, and they are so numerous in places that they are clogging up water intake pipes of power plants and municipal water supplies. Leafy spurge, an introduced poisonous plant of grassland, has covered large regions of the northern Great Plains and threatens many of the livestock operations in these areas.

One of the most famous ecological disasters associated with invasive species is the brown tree snake that was accidentally introduced on to the Pacific island of Guam. In just a few decades, through its hunting habits, the snake was responsible for the extinction of several of the island's bird species that were found nowhere else on Earth. Problems produced by invasive species are believed to cost billions of dollars every year.

Scientists are working very hard to find out what factors facilitate these biological invasions in hopes of providing some help to those trying to control their negative effects. It is clear that trying to prevent the introduction of new species into an area in the first place is the primary step to take. Some scientists are also trying to determine why some environments seem to be invaded more easily than others, or why some environments are

invaded only at certain times. Some think that environments that have a high diversity of native species may be more resistant to invasions by new species, while others believe that disturbances and other factors that free up new resources are more important to opening an environment to invaders. There is still much work that needs to be done to increase scientists' understanding of the causes and effects of invasive species. SEE ALSO BIODIVERSITY; CONSERVATION; EXTINCTION; GLOBAL CLIMATE CHANGE

Mark A. Davis

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Ion Channels

Ions are charged particles such as Na^+, H^+, K^+, Ca^{2+}, and Cl^-. Ions have a significant effect on many cell processes and also influence the amount of water in the cell. Cells use **inorganic** ions for transmitting signals across the cell membrane or along the surface of the cell. Other cellular functions as diverse as **secretion** of **hormones** to **fertilization** of egg cells require ion transport across the cell membrane. However, ions have great difficulty passing through the membrane by simple diffusion because cell membranes are composed of **hydrophobic** phospholipids that oppose the passage of **hydrophilic** ions. Furthermore, the negatively charged phosphate head groups of the phospholipids tend to repel negatively charged anions and trap positively charged cations. Therefore, an ion as small as a hydrogen ion (H^+) requires a specific portal **protein** to facilitate its transport through the membrane. Such a protein molecule is called an ion channel.

Molecular Structure of Potassium and Sodium Channels

An ion channel is usually equipped with four basic parts: a central conduction pathway (opening) for ions to pass through, an ion recognition site to allow passage of specific ions (selectivity filter), one or more gates that may open or close, and a sensor that senses the triggering signal and transmits it to the gate.

The Shaker-type voltage-gated potassium channel of nerve and muscle provides a good example of the four parts of the ion channel. The name *Shaker* arises from the **gene** coding for this channel in the fruitfly (*Drosophila melanogaster*), whose mutation causes the fly to shake. Humans have many potassium channels belonging to the Shaker family. This channel is composed of four identical subunits arranged like a four-leaf clover, with the center serving as the ion conduction pathway. Each subunit has six segments that cross the membrane and are termed S1 through S6. The region between S5 and S6 segments from each subunit contributes to form the ion conduction pathway; hence, it is called the "pore" or "P-region."

inorganic not bonded to carbon

secretion material released from the cell

hormone molecule released by one cell to influence another

fertilization union of sperm and egg

hydrophobic "water hating," such as oils

hydrophilic "water loving"

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

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

Shaker Voltage-gated K$^+$ Ion Channel

pore

chain

ball
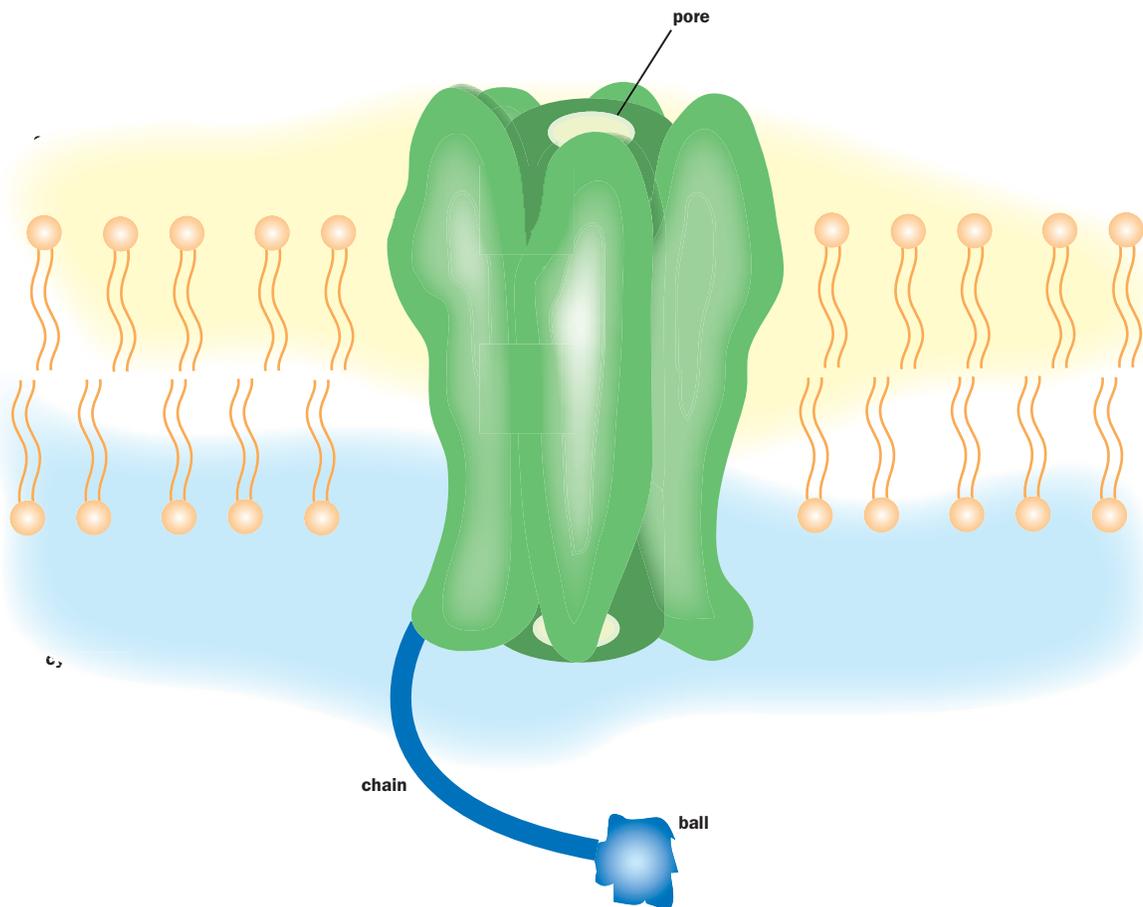
In the P-region, a few critical **amino acids** from each subunit gather to form the selectivity filter that specifically recognizes only potassium ions. The S4 segment contains positively charged amino acids on every third position and serves as a voltage sensor. When the potential on the internal surface of the membrane becomes more positive, the potential drives the S4 segment toward the outside. This movement triggers a channel gate to open. The voltage-gated sodium channel has a similar architecture, except that the four subunits are strung together in a long peptide chain like a train of parading elephants linking up trunk-to-tail. This channel is highly selective for sodium ions.

The shaker-type voltage-gated potassium channel of nerve and muscle provides a good example of the parts of the ion channel.

amino acid a building block of protein

Biophysics

As the charged ions flow across the membrane, they generate an electric current. The amount of current flow is determined by three factors. First, when the gate of an ion channel opens, ions flow down the concentration **gradient** from high to low across the membrane, which is typical of the passive transport mechanism. Second, the flow of ions is controlled by the voltage difference across the membrane. For instance, if the cell interior is

gradient difference in concentration between two places
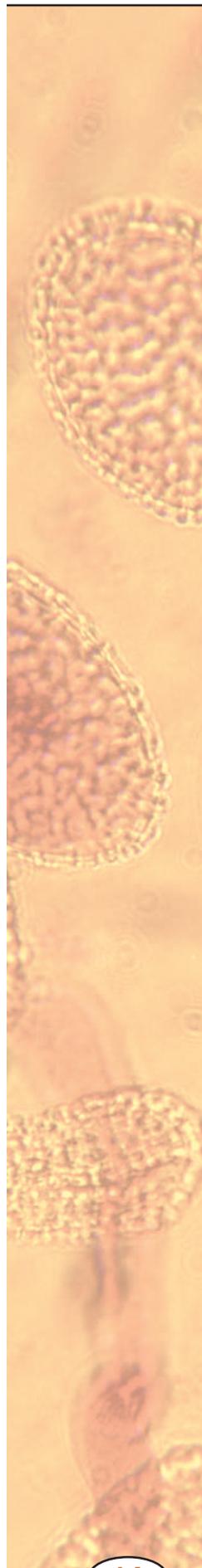
already highly positive, less K$^+$ will flow in. Third, a channel may be highly selective for a specific ion (such as the voltage-gated sodium channel) or rather nonselective (such as the mechano-sensitive channel). Thus, the total ion flow is influenced by the concentration gradient of the ions, the voltage difference across the membrane, and the permeability of the ions.

The patch clamp technique developed in 1980 has enabled scientists to record current flow through a single ion channel. This technique uses extremely fine glass electrodes attached to membranes to measure electrical activity in a very small part of the membrane. One of the most exciting results from the development of the patch clamp technique is direct observation of the opening and closing of a single channel, like observing the twinkle of a little star in the night sky. The opening of a channel represents a **conformational** change of the channel molecule from a closed state to an open state. If the rate for such a conformational change is dependent on voltage, then the channel is said to be voltage-gated. A channel may stay in the open state for less than a millisecond to tens of seconds. The current flow through a single channel may range from less than a picoampere to hundreds of picoamperes (a picoampere is 10^{-12} ampere).

conformation three-dimensional shape

Drugs and Toxins Acting on Ion Channels

Nature produces a wide variety of highly potent toxins that target specific ion channels. The toxins are usually packaged in venom and delivered by stings or fangs. A large number of toxins have been isolated from scorpions, sea anemones, cone snails, and snakes. They have been used for studying various ion channels. One of the most famous toxins is tetrodotoxin, which selectively blocks the sodium channel. It is contained in the poisonous puffer fish, which ironically is the most expensive delicacy served in Japanese restaurants. Only chefs who have passed rigorous licensing examinations are allowed to prepare the fish. Tetrodotoxin is also commonly portrayed in fictions and movies; it almost killed the fictitious Agent 007 James Bond in *From Russia with Love.* Drugs have been developed to target ion channels and to prevent the channels from conducting ions. They are widely used as local anesthetics, antiarrhythmic drugs to prevent irregular heartbeats, antihypertensive drugs to lower blood pressure, and anti-epileptic drugs to prevent seizures.

Genetic Defects of Ion Channels

Several genetic diseases exhibiting defects in the physiological functions of ion channels have now been shown to be caused by mutations in the genes coding for specific ion channels. For example, a cardiac potassium channel named HERG (human ether-a-go-go-related gene) acts to protect the heart against inappropriate rhythmicity. People lacking a functional HERG gene exhibit an abnormality on their electrocardiogram called "long Q-T syndrome," which predisposes them to sudden cardiac arrest when they are under stress. Cystic fibrosis results from mutations of a particular chloride channel called the cystic fibrosis transmembrane conductance regulator. SEE ALSO MEMBRANE PROTEINS; MEMBRANE TRANSPORT; NEURON; SYNAPTIC TRANSMISSION

Chau H. Wu

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Kidney

The kidneys of vertebrates have the vital function of removing metabolic wastes from the blood and otherwise maintaining its normal composition. The two kidneys of a normal human adult produce 1 to 2 liters (about 30 to 70 fluid ounces) of urine each day that contain wastes, excess water, and other unneeded molecules. Production of less than 0.4 liter (13.5 fluid ounces) of urine per day is insufficient to eliminate wastes and regulate the composition of blood. Such a condition is always fatal within a few weeks unless the underlying cause is corrected, a new kidney is transplanted, or the blood is artificially cleared by **dialysis**.

The human kidney belongs to one of three kinds of kidneys that occur among different vertebrates at various developmental stages. The first type, called the pronephros, lies toward the front of some fishes and the embryos of many vertebrates. The mesonephros lies more posteriorly and occurs in most adult fishes and amphibians and in the embryo of humans and other mammals. The metanephros occurs still farther posteriorly and is the type of kidney in adult reptiles, birds, and mammals, including humans.

Each human kidney is about the size of a fist, shaped like a kidney bean, and located on one side of the lower abdomen toward the back. At any given

dialysis cleansing by partial filtration
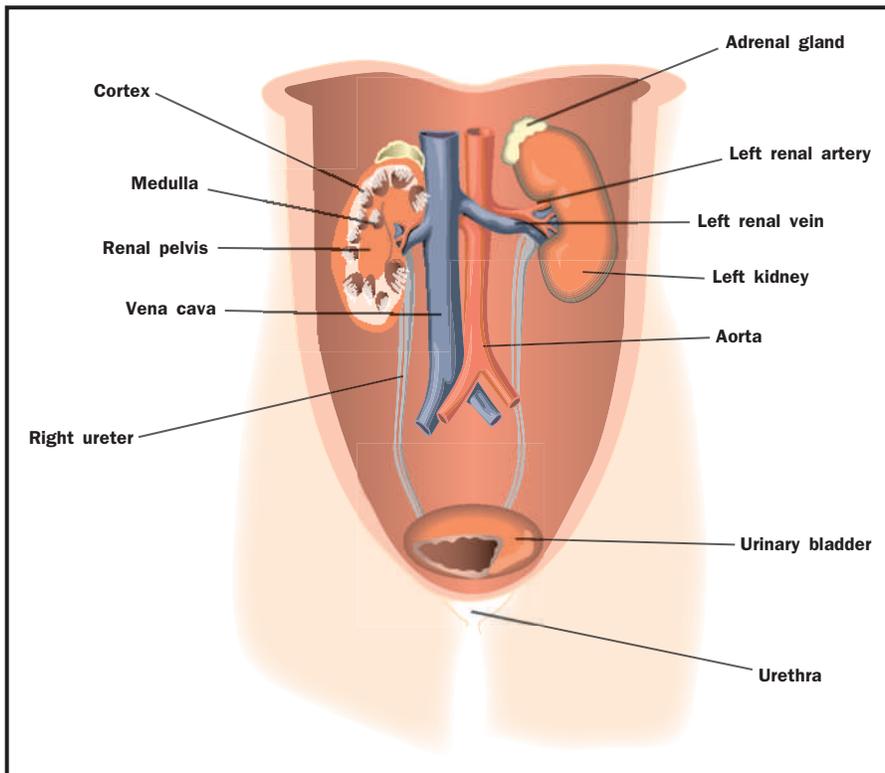
Location and gross anatomy of the human kidneys. Blood enters the kidney via the renal artery, and almost all of it leaves the kidney through the renal vein. The kidney removes excess ions, water, and other molecules, which are excreted through the ureters as urine.

time about one-fifth of the body's blood is flowing through the kidneys. The blood enters each kidney from the body's major artery, the aorta, by means of the renal artery. (The word "renal" refers to kidney.) Blood leaving the kidney enters the major vein, the vena cava, via the renal vein. Also connecting to the kidney is a third tube, the ureter, which conducts urine to the urinary bladder for temporary storage.

From this "plumbing diagram" one can get an overview of renal function: blood enters the kidney, wastes and excess molecules are removed with the urine, and the blood is returned to the circulatory system. To appreciate how the kidneys function, however, one must take a microscopic view of one of the million or so structures called **nephrons** within each kidney. Each nephron begins its work by producing a **filtrate** of blood. Filtration occurs in a tuft of capillaries called the glomerulus. The lining of the glomerulus is leaky enough to allow blood pressure to force water, **ions**, and small molecules out while retaining cells and very large molecules in the blood. The filtrate, which is very much like the fluid portion of blood (plasma), enters Bowman's capsule, which encloses the glomerulus like a helmet. Bowman's capsule conducts the filtrate into the first part of the nephron tubule, called the proximal convoluted tubule. In humans approximately 180 liters of filtrate (almost enough to fill a 50-gallon drum) make it this far each day. Fortunately, not all of it goes into urine. In the proximal tubule, many of the **inorganic** ions and almost all of the **glucose** and **amino acids** get pumped out of the filtrate and go back into the blood. Most of the water in the filtrate is also drawn back into the blood.

The tubular fluid next passes through a hairpin turn called the loop of Henle, which helps the nephron return more water to the bloodstream rather than allowing it to be lost in the urine. How this works will be explained later. Tubular fluid then enters the **distal** convoluted tubule of the nephron. Here further transport of particular ions may occur, depending on whether the concentration of that ion in the blood is too high or too low. For example, if the **pH** of the blood is too low, hydrogen ions (H^+) are transported out of the blood and into the tubular fluid. If the pH is too high, H^+ ions are transported from the fluid into the blood.

By the time the fluid has completed its journey through the distal convoluted tubule, it is essentially dilute urine, called preurine. Preurine from several nephrons enters a tube called the collecting duct. As preurine passes through the collecting duct, more water can be removed and returned to the blood.

Water is drawn out of the collecting duct by **osmosis** due to an increasing concentration of ions surrounding the collecting duct. The loops of Henle produce this concentration **gradient** by a combination of transport and diffusion of ions and urea. Urea is a molecule that temporarily stores the nitrogen produced by the **metabolism** of **proteins**. After helping to create the concentration gradient, urea is eventually eliminated with the urine. SEE ALSO BLOOD; DRUG TESTING; EXCRETORY SYSTEMS; HEART AND CIRCULATION; OSMOREGULATION; PITUITARY GLAND

C. Leon Harris

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Alcohol suppresses antidiuretic hormone (ADH), which normally reabsorbs water in the kidneys, and so increases urine volume.

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

filtrate material passing through a filter

ion an electrically charged particle

inorganic not bonded to carbon

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

amino acid a building block of protein

distal away from

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

osmosis passage of water through a membrane in response to concentration differences

gradient difference in concentration between two places

metabolism chemical reactions within a cell

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

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Kingdom

Kingdom is the highest category in the hierarchical classification of organisms created by Carolus Linnaeus around 1750. Linnaeus recognized two kingdoms, plants and animals, a scheme that worked reasonably well for large multicellular organisms but failed as microscopes revealed diverse unicellular organisms. In 1959 Robert Whittaker devised a five-kingdom system that maintained kingdoms Plantae and Animalia but added kingdoms Monera, Protista, and Fungi (see Table).

A COMPARISON OF THE FIVE KINGDOMS

Characteristic	Monera	Protista	Plantae	Fungi	Animalia
Internal cell membranes	Absent (Prokaryotes)	Present (Eukaryotes)	Present (Eukaryotes)	Present (Eukaryotes)	Present (Eukaryotes)
Cell wall	Present	Present or Absent	Present	Present	Absent
Organization	Unicellular	Unicellular or Multicellular	Multicellular	Mainly multicellular	Multicellular
Mode of nutrition	Autotrophs or Heterotrophs	Autotrophs or Heterotrophs	Autotrophs	Heterotrophs	Heterotrophs
Representative groups	Archaea, eubacteria	Protozoa, algae, slime molds	Mosses, ferns, seed plants	Molds, yeasts, mushrooms	Animals with and without backbones

Note: An autotroph is an organism that uses solar energy or energy from inorganic chemicals to make organic molecules. A heterotroph obtains organic molecules by consuming other organisms or their products.

Whittaker placed bacteria in their own kingdom, Monera, because of fundamental organizational differences between **prokaryotic** bacterial cells, which lack membrane-enclosed nuclei and **organelles**, and the **eukaryotic cells** of other organisms that possess internal membranes. Plantae, Fungi, and Animalia consist of complex, multicellular eukaryotic organisms that differ from each other in details of cell structure and in how they secure and process energy. Protista is a collection of single-celled eukaryotic organisms and simple multicellular forms, some animal-like, some plantlike.

Molecular evidence, particularly from ribosomal ribonucleic acid (RNA), suggests that the five-kingdom scheme is also too simple. Some biologists believe that Protista should be partitioned into three or more kingdoms. Similarly, kingdom Monera contains two very biochemically distinct groups of prokaryotes: archaebacteria, and eubacteria. A proposed system acknowledges this ancient evolutionary split by creating a higher level of classification, domain, above kingdom. This system distinguishes three domains: Archaea, Eubacteria, and Eukarya (containing protists, plants, fungi,

prokaryotic without a nucleus

organelle membrane-bound cell compartment

eukaryotic cell a cell with a nucleus
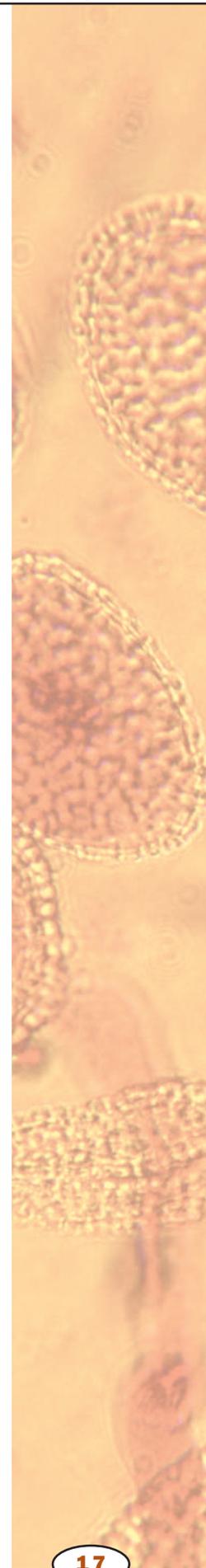
and animals). SEE ALSO ANIMALIA; ARCHAEA; EUBACTERIA; FUNGI; LINNAEUS, CAROLUS; PLANT; PROTISA

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Krebs Cycle

When **glucose** is converted to **pyruvate** during **glycolysis**, two adenosine triphosphates (**ATPs**) are formed, but most of the energy in the original glucose remains in pyruvate. In most **aerobic** cells, the pyruvate formed by glycolysis is further degraded in a pathway called the Krebs cycle (also called the tricarboxylic acid cycle or citric acid cycle). In the Krebs cycle, the carbon of pyruvate is fully oxidized to carbon dioxide in a series of **oxidation-reduction** reactions. During these reactions, much of the energy in the original pyruvate is carried as high-energy electrons by the electron shuttles NADH and $FADH_2$. These electrons will ultimately be passed to the electron transport chain, where their energy will be used to synthesize ATP by **oxidative phosphorylation**. Much more ATP is made by the Krebs cycle and oxidative phosphorylation than by glycolysis alone.

In **eukaryotic cells**, pyruvate is transported to the **mitochondrial matrix**, where the Krebs cycle takes place. Before entering the Krebs cycle, the three-carbon pyruvate is oxidized to a two-carbon acetate molecule and carbon dioxide, producing one molecule of NADH. The acetate joins to a molecule of coenzyme A to form acetyl coenzyme A, which carries the acetyl group to the Krebs cycle. The acetate enters the cycle by combining with OAA (oxaloacetic acid) to form citric acid. At this point, two of the original three carbon atoms in pyruvate have been incorporated into citric acid and one has been oxidized to carbon dioxide, and one molecule of NADH has been produced.

As the reactions of the Krebs cycle continue, the two acetyl carbons are successively oxidized to carbon dioxide, forming two molecules of NADH and one of $FADH_2$, which will provide electrons to the electron transport chain to form ATP. In addition, one guanosine triphosphate (GTP) is formed directly by substrate-level **phosphorylation**, or transfer of a phosphate directly from the reacting molecules. (The GTP eventually transfers its phosphate to form ATP.) The final unoxidized product of the entire cycle is OAA, which can accept another acetyl group to start the cycle again.

The Krebs cycle occupies a central position in cellular **metabolism**. It can break down the pyruvate produced in glycolysis, but these two pathways do not form an isolated system in cells. Both are linked to other processes in many ways. Acetyl coenzyme A is produced by other means, notably by fatty-acid oxidation, and the Krebs cycle will oxidize this acetyl coenzyme A as readily as that produced from pyruvate.

Similarly, other substances are fed into the Krebs cycle at this and other points, either to be consumed as fuel or to be transformed for other cellu-

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

pyruvate the ionized form of pyruvic acid, a key intermediate in cell metabolism

glycolysis initial stages of sugar breakdown in a cell

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

aerobic with oxygen, or requiring it

oxidation-reduction oxidation is loss of electrons, and reduction is gain of electrons

oxidative phosphorylation use of oxygen to make ATP

eukaryotic cell a cell with a nucleus

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

matrix innermost space within a mitochondrion

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

metabolism chemical reactions within a cell
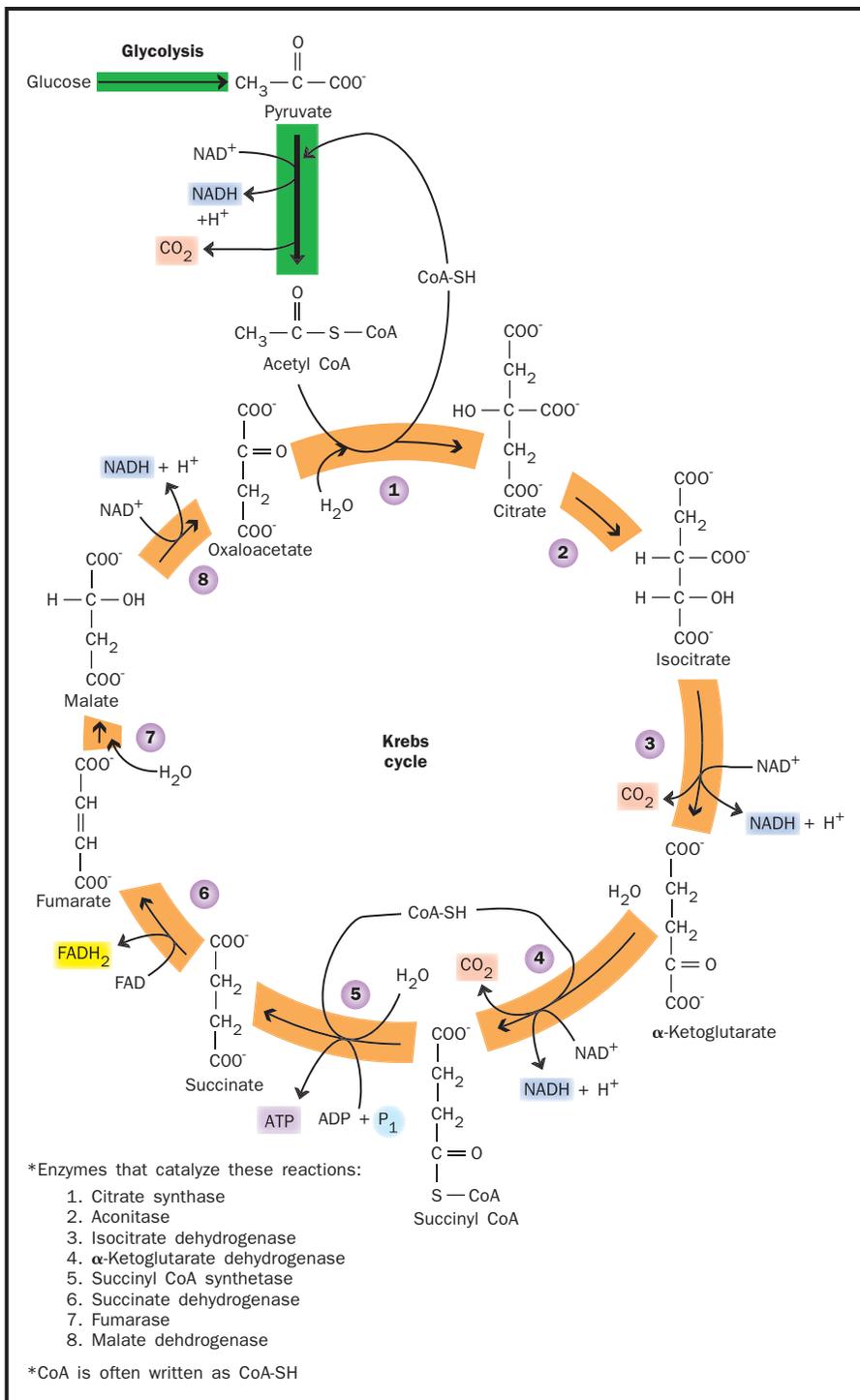
The series of reactions that make up the Krebs cycle.
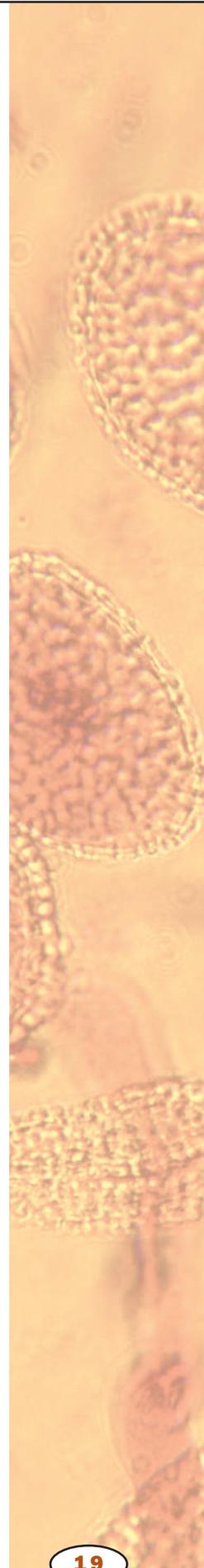
lar needs. For example, **amino acids** can be consumed by entering the Krebs cycle at several points. Conversely, several amino acids can be synthesized from intermediates of the Krebs cycle. Thus the Krebs cycle can serve either to degrade amino acids, releasing energy in the process, or to supply precursor molecules for amino acid synthesis. Which of these activities prevails depends on the needs of the cell at any particular time. SEE ALSO

amino acid a building block of protein

Glycolysis and Fermentation; Metabolism, Cellular; Mitochondrion; Oxidative Phosphorylation

David W. Tapley

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Laboratory Technician

Laboratory technicians do almost all of the hands-on work in scientific research, development, and analysis. One of the benefits of being a laboratory technician is being the first to see experimental outcomes, whether they are prize-winning projects or more routine medical exams.

The different types of jobs that laboratory technicians have and the skills and training required for those jobs can vary tremendously. For example, a laboratory technician working on a research project might operate an electron microscope, isolate DNA (deoxyribonucleic acid), make behavioral observations of animals, monitor pharmaceutical effects in test subjects, or monitor environmental quality. In a clinical laboratory, a laboratory technician may examine blood samples for cell counts, examine tissue samples for **parasites**, or test fluids for chemical contaminants or drugs. In industrial production environments, laboratory technicians may conduct product quality tests and monitor product quality control. In all settings, laboratory technicians work with the most modern and sophisticated laboratory and computer equipment available. Potential employers include government and private research laboratories, universities, hospitals, and private industries. These employers may have research, development, clinical, **forensic**, or production-oriented objectives. With growth in technology, the job market for laboratory technicians is expected to expand.

Education and training for a laboratory technician is based in science and technology. Preparation in high school should include college preparatory courses that will support extensive college requirements for mathematics and science. Entry-level positions for laboratory technicians almost always require a two-year associate's or a four-year bachelor's degree in a scientific area (commonly biology, chemistry, physics, biotechnology, or natural resources). In some cases, a master's of science degree or professional certification program and exam must be completed. Almost all beginning laboratory technicians receive additional on-the-job training, and laboratory technicians should expect to continue updating their education and training as technology advances. SEE ALSO MEDICAL ASSISTANT; MICROSCOPIST

Michael G. Scott

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

forensic related to legal proceedings

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Lakes and Ponds

Lakes and ponds are inland bodies of standing or slowly moving water. Although lakes and ponds cover only 2 percent of the world's land surface, they contain most of the world's fresh water. Individual lakes and ponds range in area from a few square meters to thousands of square kilometers. In general, ponds are smaller than lakes, though regional idiosyncrasies of naming abound—Henry David Thoreau's famous Walden Pond in Massachusetts has a surface area of 64 acres. Lakes and ponds are an important source of fresh water for human consumption and are inhabited by a diverse suite of organisms.

Formation

Lakes and ponds are formed through a variety of events, including glacial, tectonic, and volcanic activity. Most lakes and ponds form as a result of glacial processes. As a glacier retreats, it may leave behind an uneven surface containing hollows that fill with water. Glacial activity at the end of the Pleistocene epoch (ten thousand to twenty thousand years ago) resulted in the formation of most of the lakes and ponds in the Northern Hemisphere, including the Great Lakes of North America. Some of the oldest lakes and ponds (more than three hundred thousand years old) were formed by tectonic activity related to movement of Earth's crust. For example, Lake Baikal in Siberia formed from the movement of **tectonic plates** and is the largest freshwater lake by volume in the world. Volcanic activity can also lead to lake and pond formation. For example, the collapse of a volcanic cone of Mount Mazama in Oregon led to the formation of Crater Lake, the seventh deepest lake in the world.

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

Physical and Chemical Features

Light and temperature are two key physical features of lakes and ponds. Light from the sun is absorbed, scattered, and reflected as it passes through Earth's atmosphere, the water's surface, and the water. The quantity and quality of light reaching the surface of a lake or pond depends on a variety of factors, including time of day, season, latitude, and weather. The quality and quantity of light passing through lake or pond water is affected by properties of the water, including the amount of particulates (such as algae) and the concentration of dissolved compounds. (For example, dissolved **organic** carbon controls how far ultraviolet wavelengths of light penetrate into the water.)

organic composed of carbon, or derived from living organisms

Light and wind combine to affect water temperature in lakes and ponds. Most lakes undergo a process called thermal stratification, which creates three distinct zones of water temperature. In summer, the water in the shallowest layer (called the epilimnion) is warm, whereas the water in the deepest layer (called the hypolimnion) is cold. The middle layer, the metalimnion, is a region of rapid temperature change. In winter, the pattern of thermal stratification is reversed such that the epilimnion is colder than the hypolimnion. In many lakes, thermal stratification breaks down each fall and spring when rapidly changing air temperatures and wind cause mixing. However, not all lakes follow this general pattern. Some lakes mix only once a year and others mix continuously.
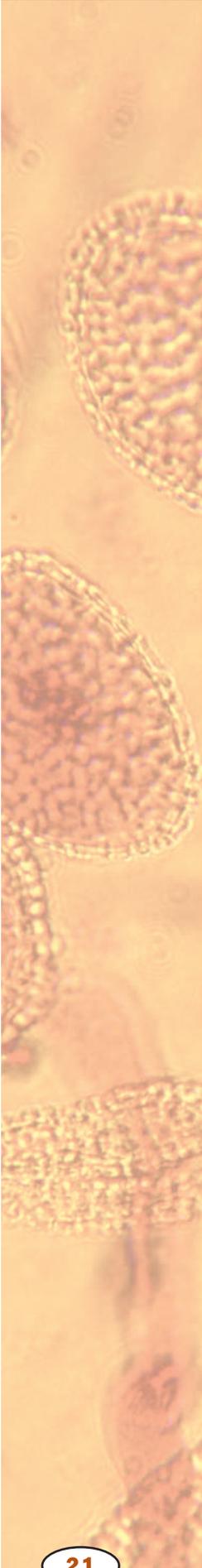
A mountain lake in the Canadian Rockies. Although lakes and ponds cover only 2 percent of the world's land surface, they contain most of the world's fresh water.

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

ion an electrically charged particle

The chemistry of lakes and ponds is controlled by a combination of physical, geological, and biological processes. The key chemical characteristics of lakes and ponds are dissolved oxygen concentration, nutrient concentration, and **pH**. In lakes and ponds, sources of oxygen include diffusion at the water surface, mixing of oxygen-rich surface waters to deeper depths, and photosynthesis. Oxygen is lost from lakes and ponds during respiration by living organisms and because of chemical processes that bind oxygen. The two most important nutrients in lakes and ponds are nitrogen and phosphorus. The abundance of algae in most lakes and ponds is limited by phosphorus availability, whereas nitrogen and iron are the limiting nutrients in the ocean. The acidity of water, measured as pH, reflects the concentration of hydrogen **ions**. The pH value of most lakes and ponds falls between 4 and 9 (the pH value of distilled water is 7). Some aquatic organisms are adversely affected by low pH conditions caused by volcanic action, acid-releasing vegetation surrounding bog lakes, and acid rain.

Habitats and Diversity

Lakes and ponds are characterized by three main habitats: the pelagic zone, the littoral zone, and the benthic zone. The pelagic zone is the open water

area of lakes and ponds. In large lakes, the pelagic zone makes up most of the lake's volume. The littoral zone is the inshore area where light penetrates to the bottom. This zone often contains large, rooted plants called macrophytes. The areas of the lake or pond bottom that are not part of the littoral zone are referred to as the benthic zone. This zone contains fine sediment that is free of plant life because light levels are too low to support plant growth.

Lakes and ponds typically contain a diversity of organisms that perform different ecological functions. Many of the organisms in lakes and ponds are quite small and can only be seen with a microscope. Plankton are microscopic aquatic organisms, including bacteria, algae, and zooplankton, that have little or no means of locomotion. In addition, there are many larger vertebrate animals that inhabit lakes and ponds, including fish and amphibians. Other organisms that use lakes and ponds for some activities include birds such as ducks, mammals such as beavers, and reptiles such as snakes.

Larger lakes can support as many as four or five different **trophic** levels, or groups of organisms that get energy in the same way. For instance, the major trophic levels in the pelagic zone, or open water areas, are **phytoplankton**, zooplankton, planktivorous (plankton-eating) fish, and piscivorous (fish-eating) fish. Microbes such as bacteria and protists are also important in lakes and ponds due to their role in decomposition and nutrient recycling. The **food web** in the pelagic zone is connected to the inshore food web because many mobile organisms from the pelagic zone (especially fish) use the inshore areas for shelter and food. SEE ALSO ALGAE; ECOSYSTEM; ESTUARIES; LIMNOLOGIST; RIVERS AND STREAMS; WETLANDS

Janet M. Fischer and Katharine E. Yoder

trophic related to feeding

phytoplankton microscopic floating creatures that photosynthesize

food web set of feeding relations in an ecosystem

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Lamarck, Jean-Baptiste

French naturalist
1744–1829

Jean-Baptiste Lamarck is best remembered for the incorrect hypothesis that evolutionary change occurs due to the inheritance of acquired characteristics. However, Lamarck's contributions to biological thought are much more important than being the champion of a failed idea. He was the first really important thinker about evolution, and he established the central role of the environment in determining the adaptations of all types of organisms.

Born into a military family, Lamarck had a brief career as a soldier before turning his attention to medicine and science. His *Flore Française* (1778) on the plants of France brought him to the attention of French naturalist Comte de Buffon (Count Buffon), who became his sponsor in scientific circles. He was appointed professor at the National Museum of

Natural History, in charge of insects and "worms," meaning all invertebrates. Lamarck was the first to propose separating the arachnids (spiders), mollusks, and crustaceans from the insects, placing them in separate classes.

Lamarck's appreciation of the enormous diversity of the invertebrates (a term he invented) strengthened his belief that species evolve over time. Lamarck proposed that environmental changes cause a change in an organism's needs, which leads to a change in behavior. For instance, scarce prey might lead to the need for a hawk to search the ground more carefully from a greater height. The increased use of its eyes would, according to Lamarck, improve the hawk's eyesight. Furthermore, this acquired improvement would be inherited by the hawk's offspring over time. Alternatively, the disuse of an organ would cause it to shrink or weaken. Lamarck published his hypothesis in his book *Philosophie Zoologique* (1809).

Lamarck also believed that all animals were becoming progressively more complex and "perfect" over time, leading him to propose that **spontaneous generation** accounted for the appearance of the simplest of organisms.

spontaneous generation the theory that life began from nonliving matter

We now know that heritable change cannot be induced by use or disuse, but can only arise through changes in an organism's deoxyribonucleic acid (DNA); nor does spontaneous generation occur. Despite his incorrect mechanism for evolution, Lamarck focused evolutionary thought on the idea of adaptation to the environment, an idea that was to be central to English naturalist Charles Darwin's concept of **natural selection** fifty years later. SEE ALSO ADAPTATION; BUFFON, COUNT (GEORGES-LOUIS LECLERC); DARWIN, CHARLES; EVOLUTION; NATURAL SELECTION

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

Richard Robinson

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Landscape Ecology

Landscape ecology is the study of the causes and ecological consequences of spatial pattern in landscapes. While there is no specific spatial extent that defines a landscape, most landscape ecologists are interested in large areas ranging from a few square kilometers to entire continents. Within landscapes it is usually possible to define a series of different **ecosystem** types occurring as patches within the greater landscape. For example, in an agricultural landscape the patches might be different fields, woodlots, hedgerows, buildings, and ponds. The goal of a landscape ecologist is to understand and describe landscape structure; how this structure influences the movement of organisms, material, or energy across the landscape; and how and why landscape structure changes over time.

ecosystem an ecological community and its environment

A landscape's structure can be quantified by describing characteristics of patches, such as their number, size, shape, position, and composition. Landscape ecologists have defined measures to quantify each of these at-

tributes. For example, a shape index has been defined as the ratio of the patch's perimeter to the perimeter of a circle the same area as the patch. A circular patch would have the value of 1, and as the patch became more convoluted in shape, its shape index would increase in value.

A landscape's structure has an important influence on various ecological processes occurring in the landscape. For example, consider two landscapes having equal areas of forest and agricultural land. In one landscape the forest is divided into many small patches, whereas in the other landscape the forested area occurs as one large patch. The more fragmented landscape will provide more habitat to those organisms that thrive at boundaries between two ecosystem types, whereas the less fragmented landscape will be better for those species that require larger areas of undisturbed forest. So, just knowing what percentage of the landscape is forest versus cropland is not sufficient to predict what species may occur; it is also important to know how the patches are distributed across the landscape.

Another example of how landscape structure can be important comes from studies of lakes within a forested landscape. The position of a lake within the landscape can be an important determinant of the lake's physical, chemical, and biological characteristics. Because water flows downhill, lakes that are lower in the landscape receive more water from streams and groundwater than lakes higher in the flow system, which receive most of their water from precipitation. Lakes higher in the landscape tend to be smaller, more dilute chemically, and have fewer species of fish than lakes lower in the landscape, even though all of the lakes in the landscape experience the same weather and are situated in the same geological **substrate**.

substrate underlying surface

Landscape structure can change through natural geological or biological processes. Earthquakes, volcanoes, and landslides are examples of geological processes. The work of beavers building a dam to flood an area is an example of a biological activity that can change landscape structure. Human activity, such as the clearing of forest land for agriculture or the expansion of urban areas, has also caused significant changes in landscape structure. These changes in structure, whether caused by natural forces or by humans, can have significant impacts on the ecology of landscapes.

Although landscape ecology is a relatively new scientific discipline, since the 1980s landscape ecologists have begun to understand how to characterize landscape structure, how landscape structure influences ecological processes, and how landscape structure changes. SEE ALSO COMMUNITY; ECOSYSTEM; FOREST, TEMPERATE; LAKES AND PONDS

Timothy K. Kratz

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Leakey Family

The Leakey family has been the most famous and one of the world's most productive groups of paleoanthropologists, scientists who study human origins. Over the span of more than seventy years, they have made major discoveries proving that humans originated in Africa, and that human ancestors were much older than previously believed.

Louis Leakey (1903–1972) was born and raised in Kenya, Africa, as the son of missionaries. He began research there in 1924, convinced that humans originated in Africa rather than Asia, as many scholars thought at the time. In 1931, he began work at Olduvai Gorge in Tanzania, which became the site of many of the most important discoveries of human fossils. In 1936, Leakey married Mary Nicol (1913–1996), who joined him in his work and eventually became the principal scientist after Louis Leakey began to devote more time to fundraising and lecturing to support their research. They were later joined by their sons Jonathan and Richard, Richard's wife Maeve, and Richard and Maeve's daughter Louise.

The Leakeys continue to research human origins throughout East Africa. For many years, they have been assisted by Kamoya Kimeu, a Tanzanian who has actually made many of the greatest fossil discoveries under the direction of the Leakeys. Among the major discoveries by the Leakeys are the prehuman *Zinjanthropus* (now called *Australopithecus boisei*) and *Homo habilis*, or "handy man," which, at approximately two million years old, is the oldest known primate with human characteristics.

In addition to their paleoanthropological work, the Leakeys have been central figures in promotion of conservation of Africa's biodiversity. Louis Leakey was also the mentor for three great field primatologists: Jane Goodall, who continues to study chimpanzees in Africa; Dian Fossey, who died studying gorillas; and Birute Galdikas, who studies orangutans in Borneo. SEE ALSO HUMAN EVOLUTION; PALEONTOLOGY; PRIMATE

Richard Robinson

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Mary and Louis Leakey.

FOSSEY, DIAN (1932–1985)

American zoologist and authority on the behavior of mountain gorillas. Fossey established the Karisoke Research Center in the mountains of Rwanda. The wild gorillas accepted her presence, and she was able to record every detail of their behavior. In 1985, however, her efforts to protect the gorillas from poachers resulted in her own murder.

Learning

Learning produces a relatively long-lasting change in behavior as a result of experience. The ability to learn, to gain from experience, allows animals to adapt to and cope with variable environments and therefore contributes to reproductive fitness.

Habituation and Sensitization

Habituation, the most rudimentary learning process, can occur in single-celled animals as well as all higher animals. Habituation is the reduction of a response to a stimulus as a result of repeated low-level stimulation. For example, protozoans contract when touched. However, repeated touching causes a gradual decrease in this response and is not the result of fatigue or

sensory adaptation but rather true learning. In fact, habituation in planaria survives regeneration; when a planarian is split in two, both new planaria exhibit the response learned by the original one. Increased response magnitude, or sensitization, can also occur to a repeated stimulus if it is of high intensity or aversive (unpleasant). Sensitization has only been observed in multicellular organisms with at least a rudimentary nerve network.

Animals with **central nervous systems** can learn through more complex processes that allow them to adapt to a larger variety of environmental circumstances. The main types are classical conditioning, operant conditioning, imitation, and imprinting.

Classical Conditioning

Classical conditioning (also called Pavlovian conditioning after its discoverer Ivan Pavlov) involves the creation of a conditioned reflex. In a classic experiment, a bell (neutral stimulus) is rung just before meat powder (unconditioned stimulus) is squirted into a dog's mouth. The meat powder produces the reflexive response of salivation (unconditioned response). If the bell is rung and followed by a squirt of meat powder into the mouth many times in succession (with a rest period between presentations), eventually salivation will occur to the sound of the bell *before* the meat powder is squirted into the mouth. The bell is now a conditioned stimulus, and the salivation to the bell is now called a conditioned response; they comprise a new conditioned reflex. The conditioned response will be sustained as long as the ringing of the bell continues to be correlated with the presentation of the meat powder. As in this example, conditioned responses are probably adaptive because they prepare the organism for the forthcoming unconditioned stimulus.

Operant Conditioning

A second type of conditioning, operant conditioning, does not involve reflexes at all. Rather, certain kinds of voluntary behavior, usually skilled motor behavior, are affected by the consequences that follow. Stimuli associated with particular contingencies do not force a response as in the case of reflexes. Rather, such stimuli alter the likelihood that a behavior will occur. For example, the "open" sign on the door of a restaurant makes it likely someone who is ready for a meal will open the door because of past experience.

In general, pleasant events increase the likelihood of, or reinforce, voluntary (operant) behavior, and unpleasant events weaken or punish operant behavior. New behavior can be created through operant conditioning using a procedure called shaping, or the reinforcement of successive approximations of a target behavior. For example, a dog can learn to roll over if a skillful trainer provides it with food and praise (the reinforcement) for closer and closer approximations of rolling over during a training session.

Imitation

Many species also learn through imitation. In general, it is a fast and efficient way of learning functional new behaviors. For example, in England some birds had learned to get milk by piercing the caps of milk bottles on doorsteps. Over a period of years, this behavior spread to several species of birds and other parts of the British Isles. There is disagreement about

The ability to learn, to gain from experience, allows one to adapt to and cope with variable environments.

central nervous system
brain and spinal cord

whether imitation is a special case of operant conditioning or an additional type of learning.

Imprinting

Imprinting is the development of an attachment to the mother or, if the mother is absent, any moving object close by during a certain brief period in the life of a young animal. For example, a newly hatched goose or duck will become attached to a shoe box, a human being, or any object if the goose or duck is removed from its nest shortly after hatching. Comparable behavior can be observed in many mammal species such as sheep, deer, and dogs. The adaptive value of following a mother is obvious. Again, there is disagreement over whether imprinting is a special case of operant conditioning or a unique type of learning. SEE ALSO BEHAVIOR, GENETIC BASIS OF; NATURAL SELECTION; NERVOUS SYSTEMS

Lynda Paulson LaBounty

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Leaves

Leaves are plant organs primarily adapted for photosynthesis, although many species have modified leaves that serve a variety of functions besides photosynthesis. Imagine walking through a forest on a summer day surrounded by the green leaves attached to the branches of trees, shrubs, and herbs. The grain in a nearby farmer's field is a sea of narrow green grass leaves, and the pond behind his barn has green water lily leaves floating on the surface and the green leaves of cattails protruding from the water.

At first glance one might come to the erroneous conclusions that all leaves are green, and that which is green in nature is a leaf. While often this is the case, there are numerous exceptions. Plant organs are green because of the presence of chloroplasts in the cells near the surface, which reflect green light and absorb other wavelengths as a source of energy for photosynthesis. Certain cells in many leaves contain these **organelles**, but chloroplasts are also found elsewhere in other organs, such as the stems of cacti of the desert and twigs of sassafras trees in the deciduous forest. In addition, flowers such as the head of broccoli, and fruits such as watermelons also contain chloroplasts.

Conversely, many leaves are not green. The winter holiday season brings potted poinsettia plants into many homes. The bright red or pink organs on these plants are not the flowers; they are specialized leaves called bracts, with cells that contain so much pigment that the limited amount of chlorophyll in the chloroplasts is obscured from view. Some poinsettias are white; usually a close look reveals that they have a green tinge due to the presence of a few chloroplasts. Poinsettias do, however, produce flowers. They are

organelle membrane-bound cell compartment

less conspicuous small, round yellow and green organs nestled at the apex of the stem, surrounded by the colorful modified leaves.

Similarly colored pigments are present in virtually all leaves, but there is often an abundance of chlorophyll, which predominates during the summer months. However, the green chlorophyll pigment often degenerates as summer transitions to fall, yielding leaves with vibrant red, yellow, brown, and orange pigments that were hidden during much of the growing season.

Leaf Anatomy

What defines a leaf? An organ is a leaf, and not some other organ, if there is a **lateral** bud in the angle above where the leaf stalk attaches to the stem (called the axil of the leaf). Under the proper circumstances, lateral buds can grow into a branch, a shoot with flowers, or a modified branch such as a thorn. Most true leaves in vascular plants are attached by petioles (leaf stalks) to stems at specific locations, called nodes. In many plants, near the base of the petiole there is a layer called the **abscission** zone, which has cells that degenerate during senescence, the aging of the leaf, and ultimately form the weakest point. This allows the leaf to drop from the tree in autumn in deciduous forests. If only one leaf is attached at each node, the plant has an alternate leaf arrangement; if the leaves occur in pairs at the node, the arrangement is opposite; and more than two leaves can even be attached in a whorl similar to the ribs of an umbrella.

Typical leaves are flat, multicellular organs with a single layer of cells on both the upper and lower surface forming the epidermis, a sheet of cells without chloroplasts. Scattered throughout the epidermis (primarily the lower epidermis) are pairs of specialized cells with chloroplasts called **guard cells**. A pore, the stoma, lies between these cells, and allows gases to pass into and out of the leaf. This includes the carbon dioxide needed for photosynthesis, the oxygen it produces in the light-dependent reactions, and escaping water vapor resulting from transpiration. The outermost side of the epidermis is generally coated with the cuticle, a waxy layer produced by the underlying cells. This layer is impervious to water and restricts or prevents evaporation from tissues within the leaf except through the **stomata**, the structure formed by the guard cells. When the guard cells swell, the stomate closes, and this prevents the leaf from drying out.

Between these protective epidermal layers, the leaf is filled with thin-walled parenchyma cells containing chloroplasts. Photosynthesis occurs within these cells, and evolution has produced modifications to aid this process. For instance, the cells in the layer just beneath the upper epidermis (closest to the incoming sunlight) are lined up like the logs driven into the ground to construct the stockade of a frontier fort. The cells in this palisade parenchyma are extremely efficient in capturing light, thereby enhancing photosynthesis.

Parenchyma cells below the palisade layer form the spongy mesophyll, so called because they are often loosely packed allowing for air circulation between them. A network of veins is found within this layer, composed of both **xylem** to conduct water in the transpiration stream, and **phloem** to transport water containing sugar produced by photosynthesis in the leaves to other parts of the plant (translocation). Larger veins can be seen in thin leaves when they are held in front of a light, with many small veins nested
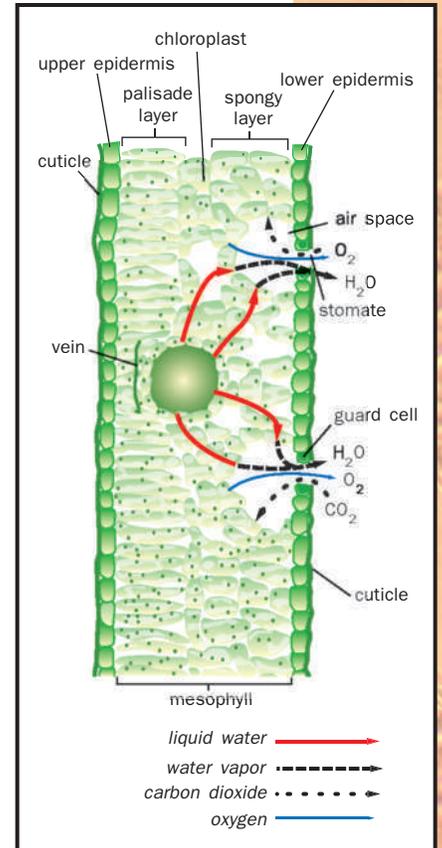
lateral side-to-side

abscission shedding of leaves; falling off

guard cells paired cells on leaves that control gas exchange and water loss

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

xylem water-transporting system in plants

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

29

Many leaves, like the spines of this cactus, take different shapes and may have special functions.

between them. Finally, a major vein, the midrib, often runs from the tip of the blade to where it joins the petiole. However, some species have more than one major vein, resulting in a fan-shaped (palmate) pattern of venation.

Modifications

The shapes, sizes, and fine details of leaves are highly variable, and many leaves do not fit this typical pattern. Evolutionary selection pressures favor modifications that result in the leaves being adapted to many different environments. Leaves of plants living in dry habitats have a number of adaptations to reduce water loss. Stomates may be sunken into the leaf tissue within a moist depression or chamber, causing a reduction in the rate of evaporation; fine hairs may protrude from the epidermal cells, giving the leaf a "white" appearance that reflects sunlight and helps cool the leaf; or the cuticle may be very thick to prevent virtually all water loss. Leaves on aquatic plants have big intercellular air spaces that facilitate flotation, and the stomates are generally on the upper surface of the leaves allowing gas exchange with the air. Even leaves on the same plant can differ, with those exposed to bright sunlight being thicker and smaller while those in the shade being larger and thinner. Finally, many leaves take different shapes and may have special functions, such as the flasklike structure that captures insects on a pitcher plant; the tendrils of climbing pea plants; the spines on a cactus; the needles on a pine; or the expanded leaf petiole forming a stalk of celery. SEE ALSO ANATOMY OF PLANTS; CHLOROPLAST; PLANT; PLANT DEVELOPMENT; PHOTOSYNTHESIS; SENESCENCE; TRANSLOCATION; WATER MOVEMENT IN PLANTS

Dean Cocking

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Leeuwenhoek, Antony van

Dutch naturalist
1632–1723

Antony van Leeuwenhoek is often credited with inventing the microscope. In actuality, Galileo, Robert Hooke, and Jan Swammerdam had built microscopes before him; compound (double-lens) microscopes were invented nearly forty years before Leeuwenhoek was born. Those early microscopes, however, were relatively crude and could magnify only twenty to thirty times. This was enough for Galileo to recoil at how ugly he thought a flea was at such a scale, but it was Leeuwenhoek who first produced microscopes capable of seeing single cells, achieving useful magnifications up to two hundred times.

This important step forward was due to Leeuwenhoek's extreme patience and skill in grinding lenses, and to his insatiable curiosity, acute eyesight, and keen observational skills. These personal qualities were more

important than higher education or scientific expertise, for Leeuwenhoek was not a scientist and, indeed, had no university education. He nevertheless became one of the most important figures in the history of biology.

Leeuwenhoek was a textile merchant and minor city official in his native city of Delft, Holland. His original motive for designing a microscope was to examine the weave of fabrics more closely so he could judge their quality and set a fair price. His simple (single-lens) microscope consisted of a ground glass bead mounted over a hole in a rectangular brass plate, with a tiny clip for holding a specimen near the lens. The plate had to be held close to the eye, with good backlighting and great patience.

Intent on studying more than fabric, Leeuwenhoek examined pond water, tooth scrapings, animal tissues, and almost anything else he could lay hands on. He was the first to see protozoans, bacteria, sperm and blood cells, muscle striations, and blood capillaries. Leeuwenhoek was hesitant at first to communicate with scientists, who were more highly educated and somewhat intimidating to him, but in 1673 he began corresponding with the Royal Society of London, describing his observations in such vivid prose that even twenty-first-century biologists can instantly recognize the organisms he had seen. To Leeuwenhoek, they were an esthetic delight; "little animals, very prettily a-swimming" was how he described bacteria from the mouths of men who had gone all their lives without cleaning their teeth.

Leeuwenhoek became famous for his reports and was elected to the Royal Academy in 1680. The cell theory—the idea, among other principles, that all living things are composed of cells—is probably the single most important principle in biology and medicine, and it all began with a modest Dutch cloth-seller. SEE ALSO CELL; HISTORY OF BIOLOGY: CELL THEORY AND CELL STRUCTURE; LIGHT MICROSCOPY

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Lichen

A lichen is a compound organism built of a fungus intimately entwined about cyanobacteria or cells of an alga. From a distance, a lichen is a brightly colored coat on a tree, a low, bushlike structure, or greenish growths hanging from branches. Lichens are found in diverse places, from tropical rain forests to dry grasslands, shrinking where water is scarce and growing lushly where water is plentiful. They are particularly plentiful in the tundra, where they feed reindeer and are known as "reindeer moss." Some lichens even grow in association with a third organism, such as on the cuticle of an insect.

Each partner of a lichen contributes different synthetic capabilities. The cyanobacterium or algal cell, which comprises less than 10 percent of the mass of the dual organism, is vital to its survival because it can photosynthesize, capturing solar energy. The fungus secretes acids that release **minerals** and water from rocks. The fungus seems to benefit more from this

minerals iron, calcium, sodium, and other elements needed by living organisms
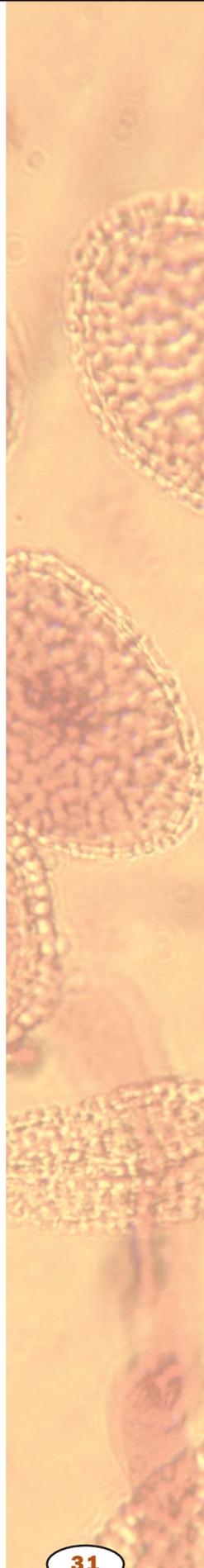
living partnership, for it grows more slowly alone than when part of a lichen, but the situation is the opposite for the alga or cyanobacterium. Lichens may reproduce with knoblike structures that house sex cells from both components. These reach new sites carried by rain, wind, or animals.

Lichens play key roles in **ecosystems**. They can survive extremes of altitude and temperature that either component alone cannot. By growing within rock crevices, they contribute to soil formation, the first event as life comes to an area. Despite their hardiness, lichens are exquisitely sensitive to pollution because they cannot detoxify and **excrete** harmful chemicals.

Humans have used lichens in various ways. As a food, it might have been the biblical "manna from heaven." Various cultures have used lichens to create and dye fabrics, to tan leather, to poison arrows, and to treat infections. About 13,500 types of lichen are recognized. SEE ALSO ALGAE; FOREST, BOREAL; FUNGI; PLANT

Ricki Lewis

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Life Cycle, Human

The human life cycle begins at fertilization, when an egg cell inside a woman and a sperm cell from a man fuse to form a one-celled **zygote**. Over the next few days, the single, large cell divides many times to form a hollow ball of smaller cells. On the sixth day after fertilization, this hollow ball burrows into the wall of the mother's uterus, or womb. The cells then form three layers that fold and bend into the more complex shape of an early embryo. Gradually, the cells begin to become different from one another, forming, for example, the nervous system and the circulatory system.

On the twenty-second day after fertilization, a simple tubelike heart begins to beat. The embryo has no other working organs: the first brain activity will not begin for five more months. But in just one more month, all the major organs will have formed in miniature, including tiny eyes and ears, liver, and kidneys. These organs do not work, but they are there. Once all the organs have formed, the individual is called a fetus. During the fetal period, all the organs begin to mature. Cells from the embryo and its mother also combine to form a placenta, an organ in the uterus that connects the embryo to the mother's blood supply.

Biologists count the days of development starting from fertilization, but medical doctors count from the first day from the last menstrual period, which is about two weeks before fertilization. So, where a biologist would say the embryo's heart begins beating at three weeks, a medical doctor would say the heart begins beating at five weeks. The total time from fertilization to birth is about thirty-eight weeks. At the end of the embryonic period (eight weeks), the embryo is about 30 millimeters (just over 1 inch) long. Between three months and nine months the fetus grows until it is about twenty times as long.

Lichens take the appearance of a brightly colored coat on a tree, greenish growths hanging from branches, or a low, bushlike structure, such as this golden-hair lichen (*Teloschistes flavicans*).

ecosystem an ecological community and its environment

excrete deposit outside of

zygote fertilized egg

At birth, the muscles of the mother's uterus begin to contract and push the baby out through the vagina. This process is called "labor," because it is hard work and can take a long time. In the first stage, called **dilation**, the lower end of the uterus, called the cervix, opens to about the same diameter as the baby's head. Dilation takes from eight to twenty-four hours in a woman who has never given birth before. In the second stage, called expulsion, the baby is pushed out of the uterus, into the vagina, and out of the body. Expulsion takes about half an hour the first time a woman gives birth. In the third stage, the mother expels the placenta. A few hours later, her uterus begins to contract to a smaller size, and her breasts begin to synthesize milk.

Within a few minutes after the baby is born, it may begin to nurse. The mother and baby can nurse as many months as they like. Women in traditional cultures may nurse for several years, but most American women nurse for about six months. Human milk is better for babies than bottled formula or other alternatives. For example, human milk contains antibodies and immune cells that protect the infant from infections. Babies who eat solid foods too early seem to be more subject to allergies later in life.

During infancy, between birth and one year, the brain continues to develop and grow. In this respect, human infants differ from other primate infants, whose brains stop growing at birth. Indeed, the human brain continues to grow new **neurons** until the child is two years old.

Infants' bodies also grow and develop rapidly, though not as fast as the brain. A one-year-old human typically weighs three times what he or she did at birth, has several teeth, and has begun to walk. At about two years, most humans begin to speak in sentences. During childhood (one to thirteen years), humans develop their first set of teeth, lose them, and begin to develop a second, or adult, set of teeth.

Between eleven and thirteen, children enter puberty. After puberty, adolescent humans can produce viable eggs and sperm, and many girls can carry a baby to term. Girls and boys develop secondary sexual characteristics, including body hair, deeper voices (especially in boys), breasts (in girls), and larger external **genitalia** (in both girls and boys). Boys begin to produce fertile sperm for the first time. Girls begin a monthly cycle of ovulation (releasing eggs) and menstruation (shedding the uterine lining) that will continue until they are in their fifties.

The changes that adolescents go through are so dramatic that many biologists compare puberty to the **metamorphosis** that tadpoles go through when they become frogs. For example, before puberty, boys and girls have the same amount of muscle mass, bone mass, and body fat. After puberty, men have 1.5 times as much bone and muscle mass as women, and women have twice as much body fat as men. Changes in the brain and in behavior also occur. By their early to mid-twenties, humans have reached their adult size. The bones stop growing and the brain is fully mature.

Humans in their twenties are in their peak reproductive years. Women who reproduce at this time have the least-complicated pregnancies. For males, the late teens and twenties are a time of peak death rates from accidents and other misfortunes, most likely due to the behavioral effects of high testosterone levels.

Infants' bodies grow and develop rapidly, though not as fast as the brain. After age thirty, human beings begin to age noticeably.

dilation expansion or swelling

neuron nerve cell

genitalia reproductive organs

metamorphosis development process that includes a larval stage with a different form from the adult

hormone molecule released by one cell to influence another

After age thirty, human beings begin to age noticeably. **Hormone** levels decline, skin becomes thinner and less flexible, gray hair and wrinkles appear, muscle mass decreases, bones lose calcium, blood vessels stiffen, and brain cells begin to die. Starting around age thirty-five, humans may lose one hundred thousand brain cells per day. The ears, the eyes, and other sensory organs also become less sensitive. Women gradually stop ovulating and menstruating in their fifties, and men experience a slow decline in testosterone levels that is most often noticed in the fifties.

Why people age is not completely understood. But some aspects of aging result when cells can no longer divide and replace themselves as they die. Some cells also begin to lose their ability to repair mistakes in the DNA (deoxyribonucleic acid), which leads to abnormalities, including, sometimes, cancer. Another cause of aging may be destructive molecular fragments known as free radicals, which damage DNA, **proteins**, and **lipids**. The average American woman lives seventy-nine years, and the average man lives seventy-two years. But despite advances in health care and healthier lifestyles, few people live beyond age one hundred. SEE ALSO AGING, BIOLOGY OF; DEVELOPMENT; FETAL DEVELOPMENT, HUMAN; SEXUAL REPRODUCTION

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

lipid fat or waxlike molecule, insoluble in water

Jennie Dusheck

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Life Cycles

A life cycle describes the series of stages that an individual organism passes through between the time it is conceived until the time it produces offspring of its own. This series of stages is referred to as a life cycle because offspring pass through the same series before they produce their own offspring. Hence, the life cycle is repeated each generation. The basic stages of a life cycle for all organisms include a prereproductive (or juvenile) stage in which individuals grow and mature and a reproductive (or adult) stage in which individuals produce offspring. However, species vary tremendously in the particular aspects of their own unique life cycles.

Differences among species in the basic life cycle often reflect adaptations for surviving and producing offspring under different ecological conditions. For example, some plant species live in habitats in which they are able to grow, mature, and reproduce in a single growing season. In less fertile habitats, however, plants may not grow enough to successfully complete their life cycle in one year. Consequently, plant species in these habitats may have life cycles with longer prereproductive stages. In addition to being affected by environmental conditions, life cycles are also influenced by patterns of energy allocation. Energy that is used for growth or **metabolism** cannot also be used to produce offspring. Therefore, adaptations that increase survival or reproductive success in one life cycle stage may reduce

metabolism chemical reactions within a cell

survival or reproductive success in other stages. This situation is referred to as a trade-off.

One example of such a trade-off is related to the length of the reproductive stage. Some organisms, including humans and perennial plants, have long reproductive stages and may reproduce many times during that stage. These types of organisms are said to have iteroparous (repeated births) life cycles. In contrast, salmon and annual plants are examples of species with semelparous (single-birth) life cycles. In this type of life cycle, individuals reproduce only once and then die. Intuitively, iteroparous organisms might be expected to produce more offspring than semelparous species. Due to the tradeoff in energy allocation, however, semelparous species can, in some cases, be more successful in producing offspring than iteroparous species despite the fact that they only reproduce once. Because semelparous species do not survive after reproducing, they can allocate all available energy to producing offspring. Under certain environmental conditions, this extra energy allocation can result in a larger number of offspring than an iteroparous species that must reserve enough energy to survive.

Asexual versus Sexual Reproduction

The life cycles of different species may also vary in the type of reproduction used. Many species are capable of reproducing asexually. In this type of reproduction, a single parent produces offspring that are genetically identical to themselves (and to each other). In some cases, offspring are produced by budding, where an individual grows directly out of the parent and is eventually separated to become an independent organism. This form of reproduction is common in plants and cnidarians (for example, sea anemones). Other species reproduce asexually with eggs or seeds that do not require **fertilization**. Several species of crustaceans and some lizards can reproduce asexually by producing these types of eggs.

fertilization union of sperm and egg

Organisms that reproduce through the fusion of **gametes** (eggs and sperm) from two parents are said to reproduce sexually. In this mode of reproduction, offspring differ genetically from their parents because they represent the combination of genes from each parents. Offspring also vary from one another because of differences in the particular genes inherited from each parent. Sexual reproduction is the only form of reproduction for most vertebrates and many plant species as well.

gamete reproductive cell, such as sperm or egg

Although asexual and sexual reproduction are presented as contrasting modes of reproduction, many organisms are capable of reproducing both ways. These organisms often reproduce asexually when environmental conditions are favorable for growth and reproduction. As conditions deteriorate, however, these species can switch to sexual reproduction and produce more genetically variable offspring. In many plant species, a single individual is capable of producing both eggs and sperm. Furthermore, these plant species can often fertilize their eggs with their own sperm, a process known as self-fertilization. This form of reproduction is still classified as sexual, but does not produce as much genetic variation among offspring as when eggs and sperm come from different parents.
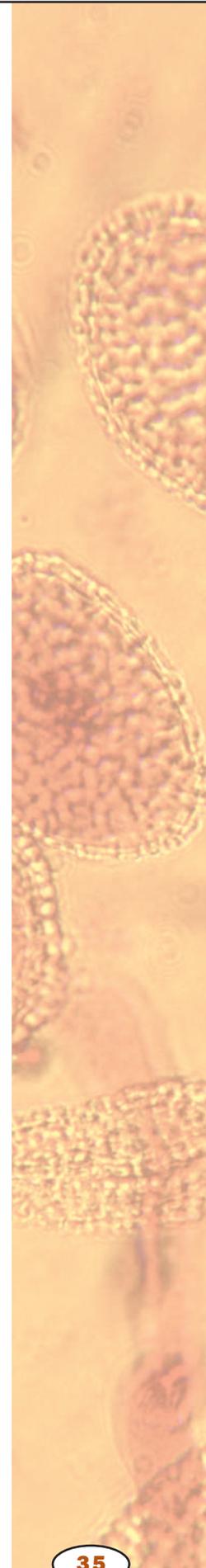
Spawning sockeye salmon run the Fraser River in British Columbia. When salmon mature, they migrate back up the same river in which they were born to reproduce and complete their life cycle.

Simple versus Complex Life Cycles

For some organisms, including humans, individuals in prereproductive and reproductive stages are morphologically very similar to one another. Although they may differ in body size, the two stages have similar appearances, live in similar habitats, and consume similar types of food. This type of life cycle is referred to as a simple life cycle to emphasize the similarity of individuals in different stages. In clear contrast to organisms with simple life cycles are organisms that change **morphology**, habitat, and diet as they move from one stage to the next. These organisms have a complex life cycle.

One example of a complex life cycle is that of the monarch butterfly (*Danaus plexippus*). Like all butterflies, prereproductive monarchs are worm-like caterpillars. After growing and molting four times, monarch caterpillars build a cocoon and enter a new stage of their life cycle, the pupae. In the pupal stage, monarchs undergo tremendous morphological change (metamorphosis) and eventually emerge as adults. Adults are morphologically distinct from caterpillars, with long legs, antennae, and wings. As adults, monarchs are capable of traveling long distances in search of food or mates.

Complex life cycles occur in a wide range of plant and animal species. Aquatic insects found in lakes, streams, and ponds have juvenile and adult stages that are both morphologically distinct and occupy different habitats. Whereas juveniles are typically found in the water, adults are often terrestrial flying insects. As these adults mate, they deposit fertilized eggs at the surface of water bodies, where juveniles will hatch and grow.

Some organisms are considered to have complex life cycles, not because of morphological changes, but because of changes in habitat. For example, many birds migrate long distances between their summer breeding grounds and their more southern wintering grounds. **Anadromous** fish, such as salmon, also migrate between rivers and streams where they are born downstream to the ocean. Once in the ocean, salmon will continue to grow and eventually reach reproductive maturity. When salmon mature, they migrate

morphology related to shape and form

anadromous returning to the rivers where they were born in order to breed

back up the same river in which they were born to reproduce, thus completing their life cycle. SEE ALSO ADAPTATION; ALTERNATION OF GENERATIONS; BONY FISH; INSECT

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Life, What Is

"Is it alive?" Children ask that question when they see a bug or perhaps a mouse that is very quiet. Then they poke it, and if it moves they say, "It's alive!" But single-celled organisms such as yeast cannot move. How does one know if yeast is alive? If one puts a few yeast cells into a clear solution of sugar and comes back the next day, the solution is cloudy and full of yeast cells. Maybe a better definition of life is that living things reproduce themselves. But what about an old pet cat? She is too old to reproduce, yet there is no doubt that she is alive. There is more to a definition of life than just reproduction.

Instead of starting with a complex organism like a bug or a cat, or even a yeast cell, think about an even simpler system. Scientists know that all living things are composed of molecules such as **proteins**, nucleic acids, **carbohydrates**, and **lipids**. Could a scientist (or a student in his high-school biology class) put together a mixture of molecules in the laboratory that is alive?

Using this approach, a definition of life can be created. A "thought experiment" with the yeast cells might garner such a definition. First, use a soapy detergent to dissolve the yeast cell membranes so that all the cell components fall out into the detergent solution. No matter how one recombines the parts, one cannot regenerate the living yeast cell even though all the components that were in the yeast are present in the mixture. Why not? Because the components became disorganized when they were dumped out of the original yeast cells. To prove this, add a single yeast cell that has all the same components but organized within its cell membrane. When one returns the next day, that single yeast has used the nutrients and energy available in the growth **medium** to produce millions of new yeast cells. It is definitely alive.

Living things are complex, and the definition of life must also be complicated. In fact, the definition used here has three parts. The first is that something is alive if it is an organized system of molecules that can use energy and nutrients (a process called **metabolism**) to grow by linking smaller molecules to make larger molecules. This energy-dependent process is called polymerization, and all life grows by making polymers from smaller molecules.

The second part of the definition is that a living organism also has the potential to reproduce itself at some point in its life cycle. The reason that

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

lipid fat or waxlike molecule, insoluble in water

medium nutrient source

metabolism chemical reactions within a cell
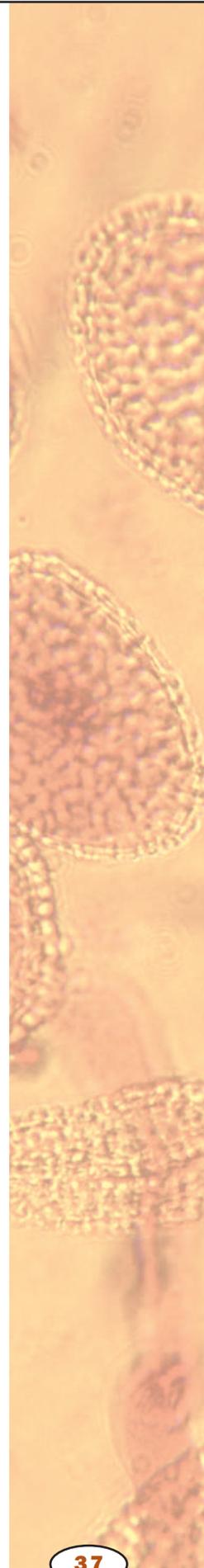
A chicken embryo. Something is considered alive if it is an organized system of molecules that captures energy and nutrients to grow, has the ability to reproduce at some point, and has the potential to evolve.

an old cat is considered to be alive is that she can use energy and nutrients (cat food) to grow. And, of course, when she was younger she could reproduce by giving birth to kittens, so during her life cycle the cat had the potential to reproduce, even though it may no longer be possible.

The third part of the definition of life takes into account the fact that populations of living organisms can change over time from generation to generation and thereby respond to changes in their environment. This process is called evolution. Living organisms do not need to evolve to be alive, but as populations they must have the potential to evolve, and this potential is part of the definition of life.

In summary, life can be defined as an organized system of molecules that captures energy and nutrients to grow by polymerization reactions, has the ability to reproduce at some point in its life cycle, and has the potential to evolve in response to changes in the environment. SEE ALSO EVOLUTION; FUNGI; ORIGIN OF LIFE

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Light Microscopy

A light microscope (LM) is an instrument that uses visible light and magnifying lenses to examine small objects not visible to the naked eye, or in finer detail than the naked eye allows. Magnification, however, is not the

most important issue in microscopy. Mere magnification without added detail is scientifically useless, just as endlessly enlarging a small photograph may not reveal any more detail, but only larger blurs. The usefulness of any microscope is that it produces better resolution than the eye. Resolution is the ability to distinguish two objects as separate entities, rather than seeing them blurred together as a single smudge. The history of microscopy has revolved largely around technological advances that have produced better resolution.

History of the Light Microscope

Light microscopes date at least to 1595, when Zacharias Jansen (1580–1638) of Holland invented a compound light microscope, one that used two lenses, with the second lens further magnifying the image produced by the first. His microscopes were collapsing tubes used like a telescope in reverse, and produced magnifications up to nine times (9x).

Antony van Leeuwenhoek (1632–1723) invented a simple (one-lens) microscope around 1670 that magnified up to 200x and achieved twice the resolution of the best compound microscopes of his day, mainly because he crafted better lenses. While others were making lenses by such methods as squashing molten glass between pieces of wood, Leeuwenhoek made them by carefully grinding and polishing solid glass. He thus became the first to see individual cells, including bacteria, protozoans, muscle cells, and sperm.

Englishman Robert Hooke (1635–1703) further refined the compound microscope, adding such features as a stage to hold the specimen, an illuminator, and coarse and fine focus controls. Until 1800, compound microscopes designed by Hooke and others were limited to magnifications of 30x to 50x, and their images exhibited blurry edges (spherical aberration) and rainbowlike distortions (chromatic aberration). The most significant improvement in microscope optics was achieved in the nineteenth century, when business partners Carl Zeiss (1816–1888) and Ernst Abbe (1840–1905) added the substage condenser and developed superior lenses that greatly reduced chromatic and spherical aberration, while permitting vastly improved resolution and higher magnification.

Tissue Preparation

The advancement of light microscopy also required methods for preserving plant and animal tissues and making their cellular details more visible, methods collectively called histotechnique (from *histo*, meaning "tissue"). In brief, classical histotechnique involves preserving a specimen in a fixative, such as formalin, to prevent decay; embedding it in a block of paraffin and slicing it very thinly with an instrument called a microtome; removing the paraffin with a solvent; and then staining the tissue, usually with two or more dyes. The slices of tissue, called histological sections, are typically thinner than a single cell. The colors of a prepared tissue are not natural colors, but they make the tissue's structural details more visible. A widely used stain combination called hematoxylin and eosin, for example, typically colors cell nuclei violet and the **cytoplasm** pink.

Other methods of histotechnique have been developed for special purposes. One variation is to embed the tissue in special plastics (resins),
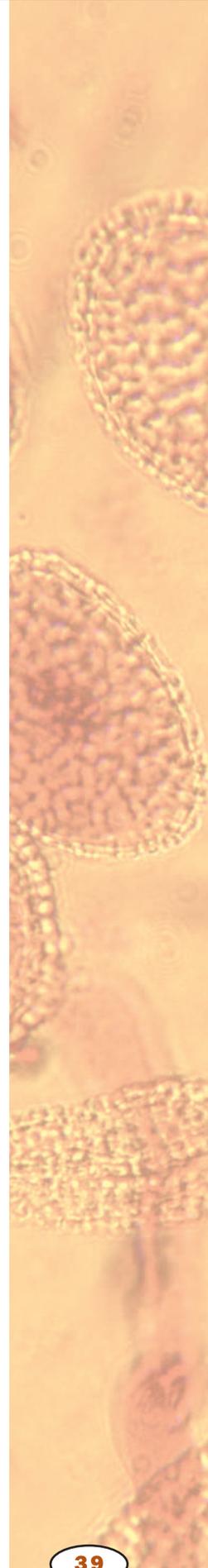
cytoplasm material in a cell, excluding the nucleus

A compound light microscope.
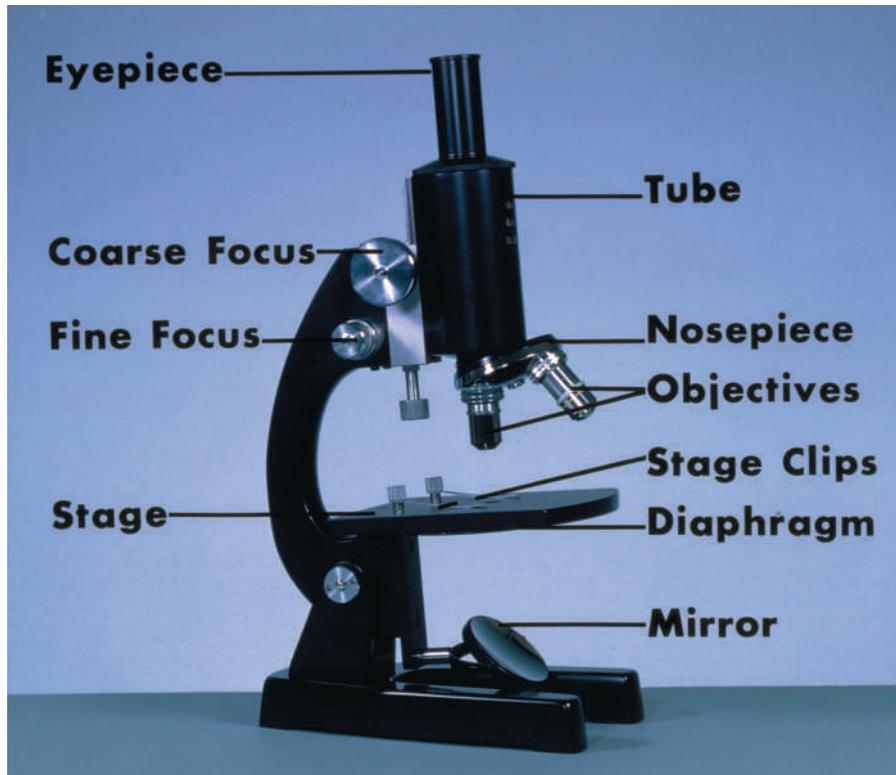
allowing for thinner sectioning. Another is the frozen section method, in which a tissue is frozen with compressed carbon dioxide and sectioned with a special cold microtome, eliminating the time-consuming process of paraffin embedding. Some prefer this method for its relative simplicity, and its speed is an asset in hospitals, where a biopsied tissue may need to be examined rapidly and the diagnosis reported to the surgeon while the patient is in the operating room.

Varieties of Light Microscopes

Most compound microscopes today have an illuminator built into the base. A condenser located below the stage has lenses that focus the light on the specimen and a diaphragm that regulates contrast. After passing through the specimen on the stage, the light enters an objective lens. Most light microscopes have three or four objective lenses on a rotating turret. These lenses magnify the image by 4x to 100x. The light then passes up the body tube to an ocular lens that magnifies the image another 10x to 15x. Research-grade microscopes and the better student microscopes have a pair of ocular lenses so that one can view the specimen with both eyes at once.

There are many varieties of compound light microscopes for special purposes. For viewing tissue cultures covered with liquid media, biologists can use an inverted light microscope in which the culture is illuminated from above and the objective lenses are positioned below the specimen. The phase contrast microscope can be used to enhance contrast in living specimens,

thus avoiding the use of lethal fixatives and stains. The polarizing light microscope is used for analyzing crystals and **minerals**, among other things. The fluorescence microscope is used to examine structures that bind special fluorescent dyes. It can be used, for example, to identify where a dye-tagged **hormone** binds to its target cell.

Compound light microscopes achieve useful magnifications up to 1200x and resolutions down to about 0.25 micrometers. That is, two objects in a cell can be as close as 0.25 micrometers and still detected as separate entities. Such resolution is good enough to see most bacteria and some **mitochondria** and microvilli.

These microscopes generally require thin, transparent, relatively small specimens. They also require that the user adjust to the phenomenon of optical inversion; if a specimen is moved to the left, it appears under the microscope to move right; when moved up, it appears to move down; and vice versa. The stereomicroscope works at much lower magnification and resolution, but has several advantages: (1) it has two lens systems that view the specimen from slightly different angles, thus giving the specimen a stereoscopic (three-dimensional) appearance; (2) it can use either transmitted or reflected light; and with reflected light, it can be used to view opaque specimens such as rocks, fossils, insects, electronic circuit boards, and so forth; (3) it has a much greater working distance between the specimen and objective lens, allowing for the examination of relatively large objects and for easier manipulation of objects under the microscope; (4) the working distance enables relatively easy dissection of specimens such as insects, allowing hands and instruments to reach the working space while one looks through the microscope; and (5) it does not produce optical inversion; that is, movements to the right appear to go to the right, making dissection and other manipulations much easier.

The utility of light microscopy is governed by its use of visible light, which limits resolution. The shorter the wavelength of the illumination, the better the resolution. Electron beams have shorter wavelengths than photons. The invention of the electron microscope in the late 1930s and its refinement over the next half century permitted vastly improved visualization of cell and tissue fine structure. SEE ALSO CELL CULTURE; ELECTRON MICROSCOPY; HISTORY OF BIOLOGY: CELL THEORY AND CELL STRUCTURE; LEEUWENHOEK, ANTONY VAN; MICROSCOPIST

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

hormone molecule released by one cell to influence another

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

Limnologist

In an era when most of the world's population lacks access to clean drinking water, the science of limnology (the study of bodies of fresh water) is making a resurgence in both the scientific and political communities. Earth's water supply is limited, with no new sources in sight. This is important to public policy-making given that growing populations are placing increased demands on the water supply and that pollution is posing a greater threat to the health of that supply.

Limnologists study rivers, streams, lakes, and wetlands. The field of limnology has become an interdisciplinary one, filled with creative scientists from several disciplines. This group of scientists participates in areas that range from field studies to serving as White House fellows who assist in policy-making.

To become a limnologist, a broad education is necessary. In middle and high school, it is imperative that one master science and mathematics classes. In college, most limnologists choose a major in biology, chemistry, physics, geology, or mathematics.

Many seek additional formal training in graduate school programs. It can be equally important to gain some hands-on experience and perhaps to even participate in a research project before applying to graduate school. Classes and volunteer programs are available at aquariums, nature groups, and science museums.

A career in limnology can be challenging and exciting. There are many varied opportunities. One of the biggest challenges facing the science is protecting and improving the quality of fisheries and fresh drinking water supplies. One other benefit, as stated by Mia Tegner, a research biologist at Scripps Institute of Oceanography, is the opportunity to "do science outdoors rather than in an indoor laboratory." SEE ALSO LAKES AND PONDS; MARINE BIOLOGIST; RIVERS AND STREAMS

Leslie Carlson

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Linkage and Gene Mapping

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

Linkage refers to the presence of two different genes on the same **chromosome**. Two genes that occur on the same chromosome are said to be linked, and those that occur very close together are tightly linked. Study of linkage provides information about the relative position of genes on chromosomes, allowing the construction of chromosome maps.

Basic Concepts

Different forms of the same gene, called **alleles**, are present on matching, or homologous, chromosomes in similar positions, or loci. For instance, in Gregor Mendel's experiments with peas, green and yellow are two alleles for pod color. In a heterozygote, which has both alleles, the two alleles occupy the same loci on homologous chromosomes. Similarly, round and wrinkled are alleles for seed texture. In the pea, these two genes—pod color and seed texture—are on different pairs of homologs and are therefore not linked. When **gametes** form in double heterozygotes (for example, a green/yellow–round/wrinkled plant), these genes assort independently, because the two chromosomes that bear them assort independently. Therefore, **meiosis** will create equal numbers of green-round, green-wrinkled, yellow-round, and yellow-wrinkled gametes. Mating between double heterozygotes (called a dihybrid cross) will give a characteristic ratio of the different possible plant types.

However, if the two traits were located close to one another on the same chromosome—in other words, if they were linked—the observed ratio will be quite different from that seen for unlinked traits. Allele combinations that began together (for instance, round-green) will tend to stay together, and the offspring will show a skewed ratio reflecting the original combinations.

Despite being on the same chromosome, the round and green alleles could become separated during meiosis by crossing over, a form of genetic recombination. During crossing over, homologous chromosomes exchange segments. This could allow the yellow allele to switch places with the green allele and lead to a round-yellow gamete. If the loci for the two genes are very close, crossing over is unlikely to separate alleles, whereas if they are far apart, crossing over is much more likely to separate them. Therefore, the frequency of crossing over is related to the physical distance between the loci for the two genes.

The particular combination of alleles on the homologous chromosomes in the dihybrid parent (for example, round-green) is known as linkage phase. Separation of this combination by crossing over is said to be a change in phase. The two alleles of a particular gene are said to be markers for that site of the chromosome.

Linkage in Fruit Flies

An example of using linkage to explore gene position is provided by inheritance of eye color and body color in fruit flies, both of which are located on the X chromosome. This example begins with purebred (homozygous) parents, one yellow-bodied and red-eyed, the other grey-bodied and white-eyed. They mate to produce all **heterozygous** daughters, who carry the yellow-red combination on one **homologous** chromosome and the grey-white combination on the other. When the heterozygotes create gametes, the eye-color alleles cannot assort independently from the body-color alleles because they are linked. Some crossing over can occur, though. As in humans, male fruit flies carry only one X chromosome, and so will show exactly what alleles are present on their X. When one counts the male offspring, approximately 49.5 percent are yellow-bodied and red-eyed, 49.5

allele a particular form of a gene

gamete reproductive cell, such as sperm or egg

meiosis cell division that forms eggs or sperm

heterozygous characterized by possession of two different forms (alleles) of a particular gene

homologous similar in structure

homologous chromosomes

cross
ov

meiosis

crossing over has created new
gene combinations ABc and abC
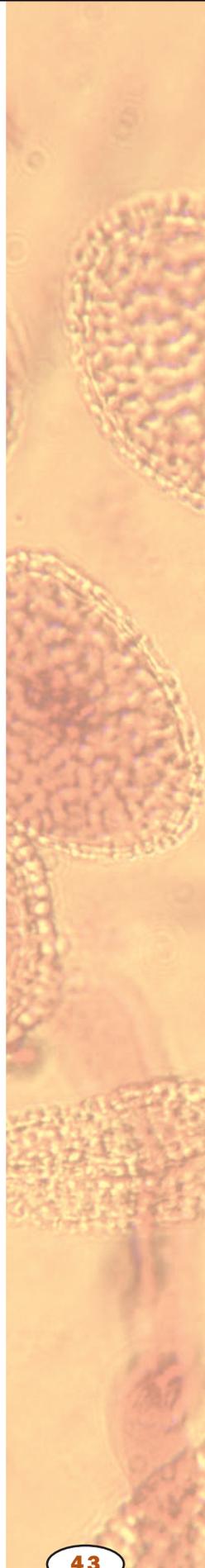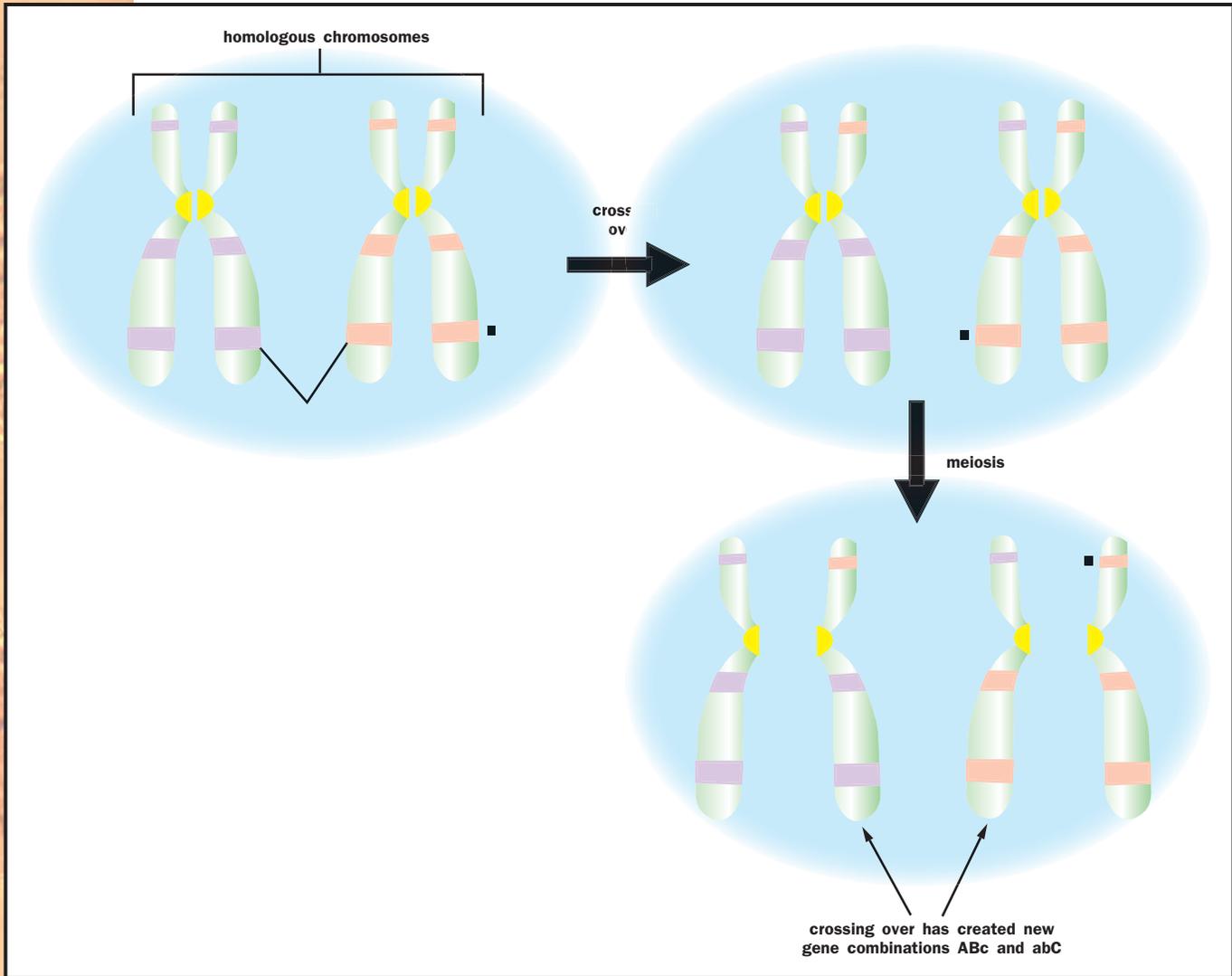
Crossing over between
homologous chromosomes
creates new combinations
of alleles.

percent are grey-bodied and white-eyed, 0.5 percent are yellow-bodied and white-eyed, and 0.5 percent are grey-bodied and red-eyed. This indicates very tight linkage—close proximity—of the two genes.

In this example, the yellow-body allele and the white-eye allele are said to be "out of phase" in the parental strains. The most frequent pair of gamete types are described as "parental types" because they retain the alleles for the two genes as transmitted by the original parent strains. The two gamete types that are less frequent are the "recombinant types," which results only from an exchange or crossover of homologous chromosomes in the interval between the genes.

Gene Mapping

As an undergraduate in 1913, A. H. Sturtevant wrote a brilliant paper that extended linkage analysis into gene mapping. Sturtevant analyzed numerous linkage experiments in the fruit fly, each using two genes. For instance, a similar experiment with body color and wing shape shows many more out-of-phase offspring, indicating the wing-shape gene is further from the body-
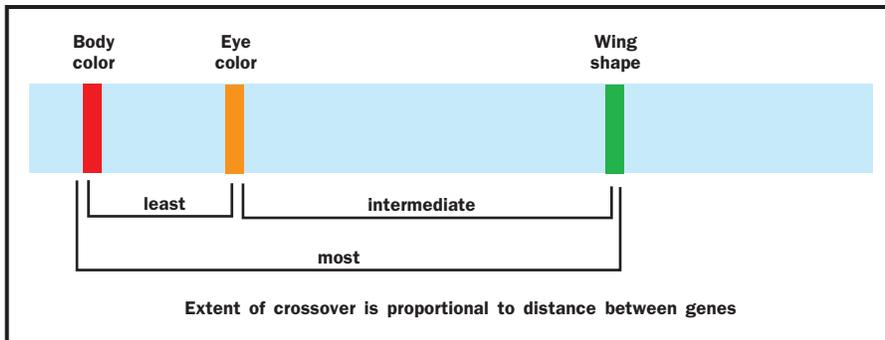
Body color   Eye color   Wing shape

least   intermediate

most

Extent of crossover is proportional to distance between genes

color gene than the eye-color gene is. Another experiment showed an intermediate number of out-of-phase offspring for eye color and wing shape. This allowed Sturtevant to reason that the body-color gene and wing shape gene are furthest apart, with eye color in between them.

Extension of this technique allowed the distance between genes to be expressed as map units. One map unit is defined as the effective distance needed to obtain a 1 percent recombination between linked alleles. The map unit is also called the centiMorgan (cM), to honor T. H. Morgan, Sturtevant's teacher and one of the founders of chromosomal genetics. Because crossing over is not equally likely between any two points, map units do not correspond directly to number of **nucleotides** along the DNA double helix.

nucleotide the building block of RNA or DNA

Sturtevant's work helped show that the chromosome is a linear sequence of genes. Gene mapping determines the position and order of genes relative to other genes along the chromosome. A well-marked linkage group extends from markers located at one end of the chromosome to those in the middle, and on to markers located at the other end. The number of linkage groups for an organism is equal to its number of homologous chromosome pairs.

Modern Applications

Sturtevant's discovery led to the golden age of chromosome transmission genetics, with an emphasis on identifying genes through alleles with visible **phenotypes**, and using them as markers for determining their position on the linkage map. Since then the emphasis in genetics has shifted to understanding the functions of genes. Linkage and gene mapping studies have progressed to being a critical tool in cloning genes and providing more description of their roles in the organism. These approaches include:

phenotype observable characteristics of an organism

- Using map locations to distinguish different genes with similar sequences, mutant phenotypes, or functions. Examples are the cell division cycle mutants of the yeast *Saccharomyces cercvisiae* or the uncoordinated mutants of the roundworm *C. elegans*. In some cases mutants with different phenotypes have been shown to be done to different mutations in the same gene, as is the case with the *Drosophila* **circadian** rhythm period mutants termed short, long, and none (per[S], per[L] and per[0]).

circadian related to a day or daylength

- Using map locations to track down genes to clone their deoxyribonucleic acid (DNA) by chromosome position. Examples are the

human cystic fibrosis transmembrane regulator gene mutated in cystic fibrosis, or the polyglutamine repeat gene that is mutated in Huntington's disease. With genome sequences available on databases, mapping mutant phenotypes points to candidate loci for the gene at the chromosome position.

New classes of markers in linkage analysis are based on naturally occurring DNA variation in the **genome**, and have many advantages. These variations are usually harmless and don't interrupt a gene, so there is no selection against them, meaning they persist over many generations. They are quite numerous and are distinguished throughout in the genome. Individuals are likely to be heterozygous from many of them and therefore the markers are informative for linkage. If the DNA variant is present heterozygously, can be detected, and shows Mendelian segregation, it is as good a linkage marker as yellow bodies or white eyes. The disadvantage is that analysis to detect the variant is sometimes more laborious and requires the techniques of molecular biology.

The common types of DNA markers and the molecular techniques used to follow their inheritance are:

- Restriction fragment length polymorphisms (RFLPs) are derived from sequence variation that results in the loss of a **restriction enzyme** digestion site. The result is a longer fragment of the DNA from that location following digestion with that enzyme. A heterozygous parent will transmit either the allele specifying the long fragment or the allele specifying the short fragment to each child. After size separation of DNA fragments by gel **electrophoresis** and transfer to a Southern blot, these DNA fragments of interest can be identified with a specific DNA or ribonucleic acid (RNA) probe that also comes from that location. If the long fragment, for example, is linked to a disease gene, the child's DNA can reveal if he or she is likely to develop the disease.

- Randomly amplified polymorphic DNAs (RAPDs) are derived from sequence variation that results in the loss of the complementary site to a primer necessary to initiate chain amplification by polymerase chain reaction (PCR). If the DNA used as template contains complementary sites for both primers, a PCR product is obtained that can be detected by gel electrophoresis. If either site is absent or changed in the template no product will be obtained from the reaction.

Human Disease Genes

Human families pose some of the greatest challenges to linkage analysis. Human families are small, and matings are not designed by the needs of genetic analysis. Mapping a mutation that causes a disease usually requires assembling enough families that transmit the mutation in hopes that some of them will be heterozygous, or informative, at some RFLP, RAPD, or other markers that are near enough to the disease gene to show linkage. Instead of determining linkage by counting crossover numbers as Sturtevant did, human genetics uses an alternative means to estimate whether linkage is present between marker and disease gene. This approach is called LOD score analysis, after Log of the Odds for or against linkage. Each child from informative parents is scored as recombinant (R) or parental (P). The total

genome total genetic material in a cell or organism

restriction enzyme enzyme that cuts DNA at a particular sequence

electrophoresis technique that uses electricity to separate molecules based on size and electric charge

number of R and P results for each family is used to calculate "scores" for the odds that the results are due to linkage at a table of recombination frequencies from 1 cM, 10 cM, 20 cM, etc., relative to the chance that the results came from independent assortment.

The logs of the odds scores for each family are added to the log scores of other families to increase the number of independent observations. A LOD score value of 3, representing no more than a 5 percent chance of mistakenly declaring linkage, is the minimum acceptable score for assumption of true linkage between marker and disease gene. The recombination value that gives the highest LOD score over all the families is the presumptive linkage distance of the disease gene mutation from the adjacent markers. The first human disease gene mapped this way was Huntington's disease, which had a LOD score of over 6 for a recombination distance from its marker of between 5 and 10 cM. Once a marker has been found, it can be used to predict whether any particular family member has inherited the marker and therefore is likely to have inherited the disease gene. SEE ALSO GENETIC ANALYSIS; GENETIC DISEASES; MENDEL, GREGOR; PATTERNS OF INHERITANCE; POLYMERASE CHAIN REACTION

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Linnaeus, Carolus

Swedish botanist and taxonomist
1707–1778

Carolus Linnaeus developed the binomial system for naming organisms. Born Carl von Linné in Sweden, Linnaeus developed an early interest in botany and classification and later developed a new classification scheme for the growing numbers of plants and animals being discovered throughout the world. Linnaeus proposed using the number and arrangement of stamens and **pistils** in flowers as a simple set of characters to classify plants. This system was used widely for a time but later was replaced by more natural systems based on larger numbers of characters.

pistil female reproductive organ of a flower

Linnaeus's most important contribution was the naming system he devised to accompany his classification system. In contrast to the complex and at times chaotic rules used by other botanists, Linnaeus proposed that each type of organism be called by a simple, two-part (binomial) name. Each plant in his system was given a genus name, which grouped the plant with other similar plants, and a species name, often a descriptive term, to make a combination unique for that organism. Each name was given in Latin. For instance, the white oak is *Quercus alba* (*alba* means white), while the red oak is *Quercus rubra* (*rubra* means red). This nomenclatural system was first

published in *Species Plantarum* in 1753 and was widely and quickly accepted. While naming systems have grown more complex since his time, Linnaeus's binomial system for the genus and species is used today by all biologists. SEE ALSO Buffon, Count (Georges-Louis Leclerc); Taxonomy, History of

Richard Robinson

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Lipids

Lipids are uniquely biological molecules, and they are synthesized and used by organisms in a variety of important ways. Unlike **proteins**, **polysaccharides**, and nucleic acids, lipids are much smaller, water-insoluble molecules. They are synthesized in association with a cellular **organelle** called the smooth **endoplasmic reticulum**. In a word, they are, as their etymology suggests, fats.

Several types of fats are made from fatty acids. Fatty acids are long, unbranched chains of **hydrocarbons** (typically made up of fourteen to twenty carbons) with a terminal **organic** acid group. In cartoon figures, fatty acids are often drawn as lollypops, consisting of long hydrocarbon "tails" and circular, polar "heads." When free in cells, the **acidic** heads give the fatty acids a negative charge, which is lost when the molecules are linked chemically with glycerol to form glycerides.

Possibly the most common fat is a glyceride, which consists of fatty acids linked to glycerol (a three-carbon alcohol). Triglycerides are the most prevalent glyceride; they each contain three fatty acids, and because they are used almost exclusively for the storage of biological energy, they are the most common component of body fat. To understand their storage function it is useful to appreciate that the fatty acids commonly found in triglycerides each contain more than twice the energy present in octane, the primary component of gasoline.

Diglycerides are also common lipids; they are especially abundant in biological membranes (unlike triglycerides, which are never found in membranes). As its name suggests, a diglyceride contains two fatty acids linked to a glycerol backbone; the third carbon of glycerol is usually linked to a much more polar substance. The most common diglycerides found in membranes are phospholipids, compounds whose polar groups consist of negatively charged phosphate groups linked to other polar compounds (such as the organic base choline, or the **amino acid** serine, or the simple sugar inositol).

Unlike triglycerides, most diglycerides are distinctly "schizophrenic" (or more technically, **amphipathic**) with respect to their solubility properties. The fatty acid residues are distinctly **hydrophobic**, whereas the polar residue is very **hydrophilic**. Thus, the polar part of a phospholipid wants to dis-

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

polysaccharide carbohydrate composed of many individual units of sugar

organelle membrane-bound cell compartment

endoplasmic reticulum network of membranes within the cell

hydrocarbon molecule or group composed only of C and H

organic composed of carbon

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

amino acid a building block of protein

amphipathic having both polar and nonpolar regions

hydrophobic "water hating," such as oils

hydrophilic "water loving"

aqueous watery or water-based

acid group

(unsaturated fatty acid)

(saturated fatty acid)

+ H₂O

fatty acids   glycerol   triglyceride   water
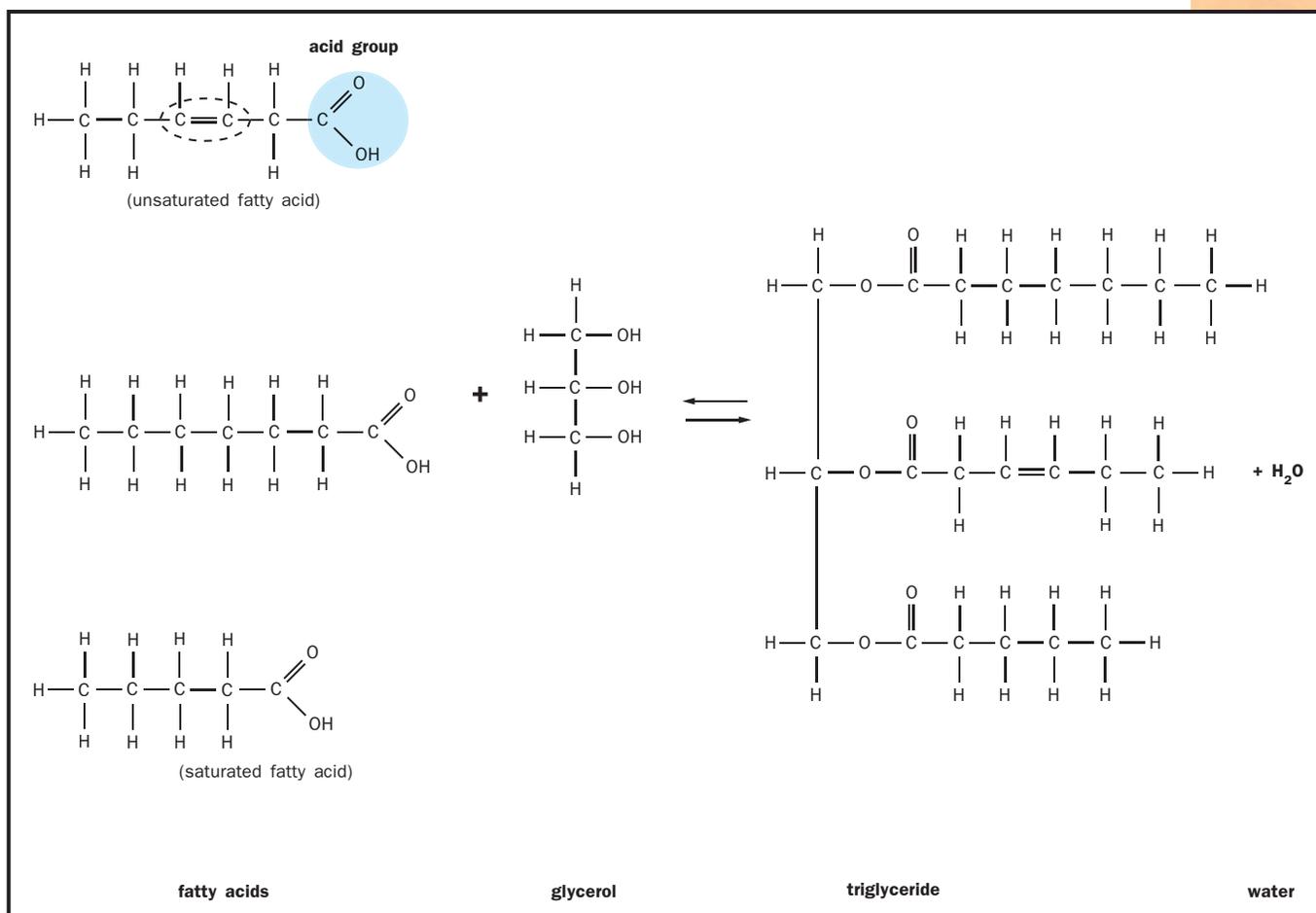
solve in **aqueous** solutions, while the nonpolar parts prefer their own company, so to speak. This amphipathic property is the basis for the spontaneous assembly of phospholipids into **bilayer** membranes and for the dynamic stability these important cellular components exhibit. For this reason phospholipid and other amphipathic membrane lipids are often called "structural lipids."

Other structural, amphipathic lipids include glycolipids with polar residues consisting of one or more **carbohydrates** and hydrophobic regions containing both hydrocarbon and fatty acid residues, and cholesterol, a complex cyclical hydrocarbon with a very small polar residue. Cholesterol is also the parent compound of a group of very important **hormones** called **steroids** (including cortisol, estrogen, progesterone, and androgen) and of bile salts that facilitate the digestion of dietary fats.

In some organisms, fatty acids may also be linked to long-chain hydrocarbon alcohols, producing compounds called waxes; the spermaceti of sperm whales and the substances used by bees to form the walls of their honeycomb are good examples. Also uncommon, but very important in some plants, are hydrocarbons called terpenes, of which turpentine and camphor are the most well-known examples, and carotenoids, a yellow plant pigment. SEE ALSO HORMONES; MEMBRANE STRUCTURE

Chris Watters

Fatty acids link to glycerol, by removal of water molecules, to make a triglyceride. If a phosphate group (PO_4^{3-}) is used instead of one of the fatty acids, a phospholipid is formed. The phosphate end dissolves in water, while the fatty acid end does not.

bilayer composed of two layers

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

hormone molecule released by one cell to influence another

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

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Liver

The liver is the largest organ in the abdominal cavity and is located under the right and central portions of the diaphragm. It performs over two hundred functions including digestive, metabolic, storage, and other functions. This reddish-brown organ consists of two major lobes, the right lobe and the left lobe, and two smaller lobes, the **caudate** lobe and the quadrate lobe.

Lying under the right lobe is the gallbladder, a muscular sac that is anatomically and physiologically associated with the liver. Emerging from the gallbladder is the cystic duct.

The lobes contain liver cells (hepatocytes), which secrete bile, an **alkaline**, yellow-green liquid that is composed of water, bile salts, and several other substances. Bile is delivered to the duodenum, the first portion of the small intestine, where the bile salts **emulsify lipids**; that is, break down large lipid globules into small droplets, in order to increase the efficiency of lipid digestion and absorption by the small intestine.

The hepatocytes secrete bile into numerous tiny ducts, which merge to form progressively wider ducts. These ducts ultimately merge to form the common hepatic duct, which descends from the liver. This duct merges with the gallbladder's cystic duct to form the bile duct, which opens into the duodenum. The opening is guarded by a **sphincter**, a circular muscle that is usually closed. Since the sphincter is usually closed, bile flowing down from the liver is prevented from entering the duodenum and, consequently, backs up via the cystic duct into the gallbladder.

Within the gallbladder, bile is stored and concentrated until it is expelled, when needed, via the cystic and bile ducts into the duodenum. Expulsion of bile occurs due to the simultaneous contraction of the gallbladder walls and relaxation of the sphincter guarding the entrance to the duodenum.

In addition to producing bile for the emulsification of dietary lipids, the liver also plays an important role in the maintenance of normal blood **glucose** concentration, inactivation of toxins, synthesis of plasma **proteins**, and the **metabolism** of **carbohydrates**, fats, and proteins. SEE ALSO BLOOD SUGAR REGULATION; DIGESTION; DIGESTIVE SYSTEM; POISONS

Izak Paul

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caudate toward the tail

alkaline chemically basic, with an excess of OH- ions

emulsify suspend in solution through interaction with soap or similar molecules

lipid fat or waxlike molecule, insoluble in water

sphincter ring of muscle regulating passage of material through a tube such as the gastrointestinal tract

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

metabolism chemical reactions within a cell

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

Locomotion

Locomotion is the active movement from one place to another. It does not include passive movements such as falling or drifting in currents of air or water. Many bacteria and protozoa are capable of locomotion, but animals move over much greater distances by a much larger variety of means, such as burrowing, running, hopping, flying, and swimming. The mode of loco-

motion used by an animal depends on the size of the animal and the medium in which it moves—whether water, air, or land.

It is convenient to divide the modes of locomotion into four categories: (1) those used by very small organisms in water; (2) those used by larger animals in water; (3) those used by larger animals in air; and (4) those used by animals in or on land.

Swimming

Very small animals, as well as protozoa, that locomote through water are commonly said to swim, but this is not actually what they do. For humans, the momentum of our bodies is very large compared with the resistance from the viscosity (stickiness) of water. For a microscopic crustacean or an **amoeba**, however, movement through water is like crawling through molasses. There are three types of locomotion commonly employed by tiny aquatic organisms. One is amoeboid motion, which is used by its namesake *Amoeba* and some other protozoans, as well as by white blood cells. Ameboid motion is performed by protruding a portion of the cell to form a **pseudopodium**, then essentially flowing into the pseudopodium.

Some protozoans, as well as the sperm of many animals, have one or a few long, hairlike structures called flagella that are responsible for locomotion in liquid. The wavelike beating of a flagellum pulls or pushes the cell through water. Many other protozoans, as well as many small animal larvae, locomote through water by means of numerous **cilia**. Cilia are identical to flagella except that they are shorter and more numerous. As each cilium beats back and forth, it extends out on the backstroke and folds on the return stroke. Ciliary locomotion can be quite fast: up to 10,000 body lengths per hour for Paramecium.

Cilia are also responsible for locomotion in some much larger organisms, such as flatworms (Platyhelminthes). These animals secrete a film of mucus, then creep through it on numerous cilia. This is called mucociliary locomotion.

Larger aquatic animals are capable of true swimming, which means that their momentum carries them forward between swimming strokes. The change in momentum that propels them forward is matched by the momentum of water that is propelled backward as a vortex. Most aquatic animals have fins that are adapted for propelling a vortex backward. In addition, fast swimmers generally have streamlined bodies that reduce the friction of water. A few aquatic animals have unusual mechanisms for swimming. Octopus and squid, for example, often escape predators by means of jet propulsion. Contraction of the body forces out a jet of water that propels the animal in the opposite direction.

Flying

Flying is more complicated than swimming since it must generate not only forward thrust but also upward lift. Wings must therefore produce vortices of air that move downward and rearward with a force equal and opposite to the gravitational force on the body. These vortices are produced by the flapping of wings during active flight or by the passive movement of air past the wings during gliding and soaring. Gliding by birds is the easiest to

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

pseudopodium "false foot"; extension of cell membrane used in amoeboid locomotion

cilia short, hairlike cell extensions of the cell membrane formed by the cytoskeleton
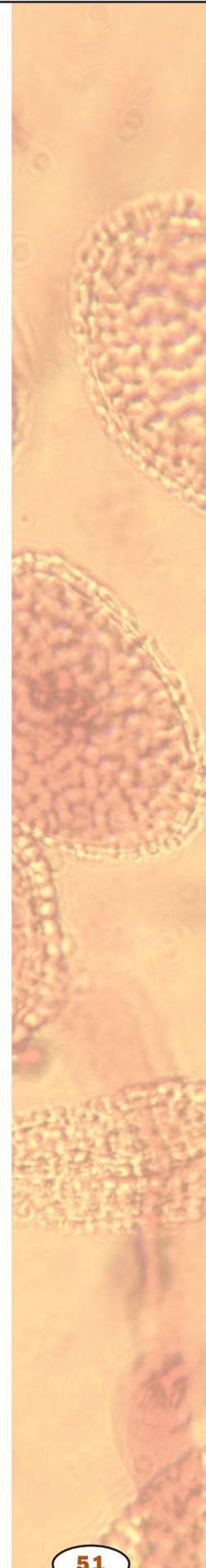
A photomicrograph of protozoans, *Ceratium tripos,* that use flagella to locomote through water.

understand. Their wings have a cross section like those of an airplane, and they work similarly. In contrast to the wings of birds and bats, those of insects are flat and rough, and they, therefore, do not generate lift and thrust from the smooth flow of air past them. Instead they have a variety of other movements that produce downward and rearward vortices.

Locomotion by terrestrial animals takes a variety of forms, such as burrowing, creeping, walking, hopping, leaping, and running. In all these modes, the propulsive force is generated as a reaction to forces applied to Earth. When people walk, for instance, they propel themselves forward by pushing the balls of the feet against the stationary Earth. SEE ALSO BONY FISH; CARTILAGINOUS FISH; INSECT; MUSCULOSKELETAL SYSTEM; PROTOZOAN DISEASES

C. Leon Harris

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Lymphatic System

The lymphatic system plays a vital role as one of the organ systems of the body. This system functions with the digestive system to absorb dietary **lipids**, which enter lymphatic vessels rather than blood vessels for transport. It also acts with the cardiovascular system to control the body's fluid balance. This is accomplished by a series of interconnected thin-walled lymphatic vessels that permeate the body's tissues that collect substances lost through the walls of capillaries. These lymphatic vessels drain into lymphatic trunks and then into veins.

If lymphatic drainage is temporarily or permanently blocked, the buildup of **interstitial** fluid creates a condition called lymphedema. In tropical areas

lipid fat or waxlike molecule, insoluble in water

interstitial space between cells in a tissue

of the world, a mosquito-borne roundworm can infect lymph nodes, blocking lymphatic drainage and thereby creating a condition called elephantiasis.

The lymphatic system also plays a vital role in immunity by providing a defensive network against **pathogens**. Multiple lymphatic organs, all with specialized functions, work together for this purpose. Lymph flowing along the lymphatic vessels passes periodically through lymph nodes, primarily in the neck, armpit, and groin regions. The nodes contain lymphocytes and macrophages that mount an immune response to any pathogen borne within this fluid. Lymphatic vessels also lead to lymph nodes near internal organs such as the heart, lungs, and alimentary canal (gut).

pathogen disease-causing organism

Cervical nodes

Thoracic nodes

Axillary nodes

Cubital nodes

Abdominal nodes

Lumbar nodes

Pelvic nodes
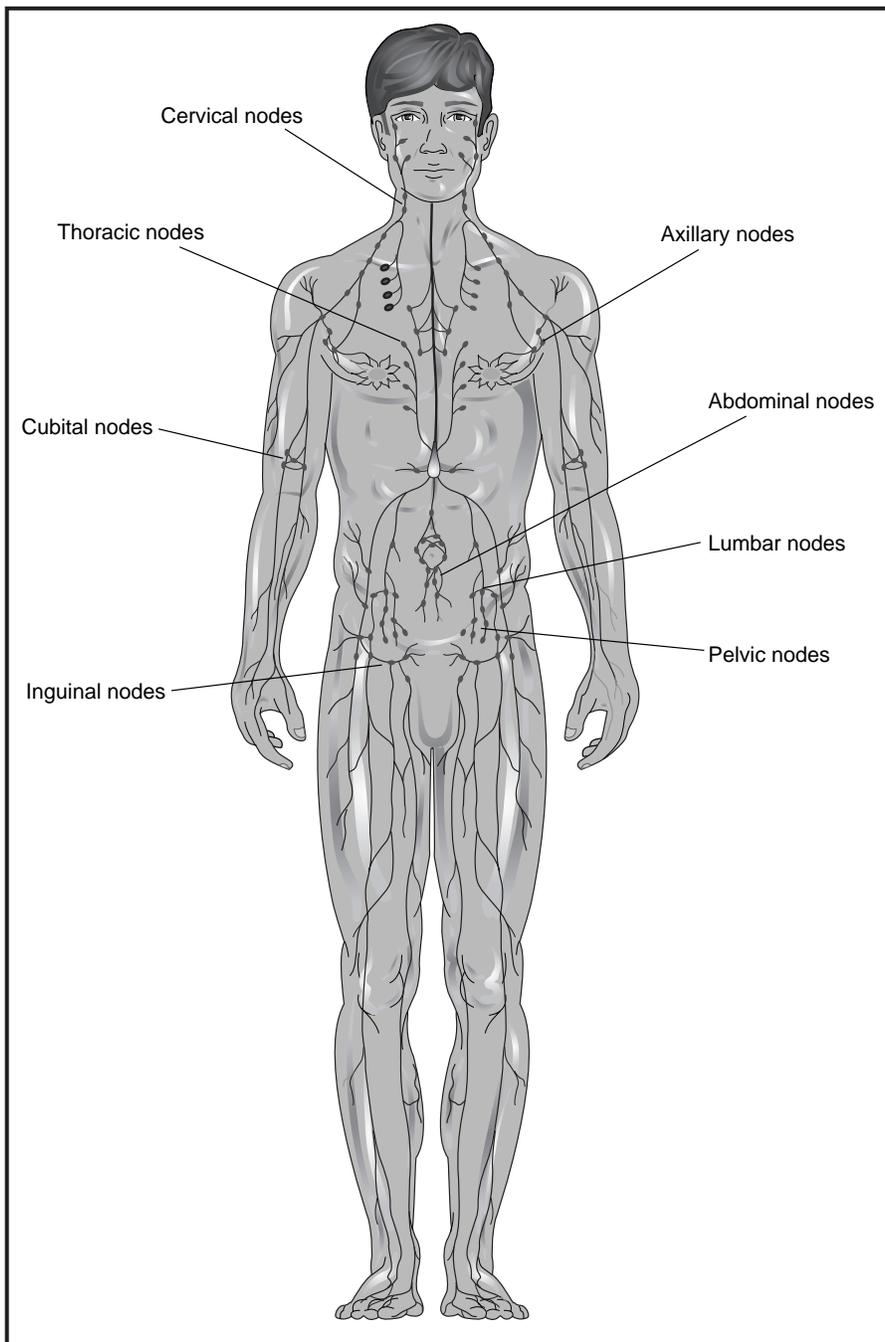
Inguinal nodes

A lymphangiograph of a man, showing cervical, thoracic, cubital, inguinal, axillary, abdominal, lumbar, and pelvic nodes of the lymphatic system.

Lining the alimentary canal are collections of mucosa-associated lymphatic tissues (MALT) that form lymphatic nodules. Clusters of lymphatic nodules are also deep to the lining of the alimentary canal. These include Peyer patches of the ileum (lower small intestine) and appendix that guard the entry of pathogens into the internal environment. When the appendix becomes inflamed, appendicitis results.

Other lymphatic organs—the tonsils, thymus, and spleen—also play a critical role in immunity. The tonsils include the pharyngeal tonsil located in the rear of the nasopharynx, the palatine tonsils to the side of the tongue, and the lingual tonsils at the base of the tongue. Together, the tonsils form patches of lymphatic tissue that encircle the back of the oral and nasal cavities as a defense mechanism to detect pathogens before they enter the alimentary canal. If the tonsils become infected, a tonsillectomy may be necessary.

The thymus is found deep to the sternum (breastbone) and **superficial** to the pericardial sac surrounding the heart. The thymus contains lymphocytes that differentiate into **T cells**. These cells are vital to the proper function of the immune system.

Finally, the spleen is located in the left upper quadrant of the abdomen. It has several functions. Its red pulp stores erythrocytes (red blood cells) for use in cases of sudden blood loss, whereas the white pulp contains macrophages and other leukocytes (white blood cells) that break down old erythrocytes as they squeeze through splenic sinuses. Additionally, these leukocytes can mount an immune response and fight infections that enter this organ. As the spleen contains many vessels, it bleeds easily when ruptured. In such cases, removal of the spleen (splenectomy) may be required to prevent fatal hemorrhage. SEE ALSO ANTIBODY; DIGESTIVE SYSTEM; IMMUNE RESPONSE; T CELLS

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Lysosomes

Lysosomes are membrane-bound **organelles** that function as the "stomachs" of **eukaryotic cells**. They contain about fifty different **enzymes** that break down all types of biological molecules including **proteins**, nucleic acids, **lipids**, and **carbohydrates**. Cells transport material into lysosomes, the material is digested by the enzymes, and the digested molecules are moved back into the **cytosol** for use by the cell. Both extracellular materials brought into the cell by endocytosis and obsolete **intracellular** materials are degraded in the lysosome.

Lysosomes vary in size and shape, but have several common features. They are surrounded by a single membrane, have an **acidic** interior pH level of about 5, and carry a high content of digestive enzymes. All of the diges-

superficial on the surface; not deep

T cell white blood cell that controls the immune response

organelle membrane-bound cell compartment

eukaryotic cell a cell with a nucleus

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

lipid fat or waxlike molecule, insoluble in water

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

cytosol fluid portion of a cell, not including the organelles

intracellular within a cell

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

Three routes to degradation in lysosomes.

tive enzymes found in the lysosome require an acidic environment to function properly and are called acid hydrolases. The low pH of the lysosome is maintained by membrane proteins that pump protons (H^+ **ions**) from the cytosol into the lysosome.

In addition to the proton pumps, the lysosomal membrane contains many other proteins that transport the digested molecules out of the lysosome and into the cytosol. Although it may seem dangerous for cells to contain enzymes that can digest most biological molecules, the contents of the cell are doubly protected from the digestive enzymes of the lysosome. First, the enzymes are enclosed in the lysosomal membrane and second, even if the enzymes were to leak out of the lysosome, they would not be active at the neutral pH of the cytosol.

Extracellular materials to be degraded in the lysosome are brought into the cell by either pinocytosis or phagocytosis. Pinocytosis, which occurs in all eukaryotic cells, is the internalization of extracellular fluid and small **macromolecules** by means of small **vesicles** that pinch off the inside of the plasma membrane. These small vesicles carrying endocytosed molecules are initially delivered to membranous organelles called endosomes. It is not precisely clear how molecules to be degraded progress from endosomes to lysosomes. Endosomes may actually mature into lysosomes when newly made acid hydrolases are delivered to the endosome.

Phagocytosis, which occurs in only specialized cell types, is the ingestion of large particles such as cell debris or whole microorganisms. Phagocytic

ion an electrically charged particle

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

vesicle membrane-bound sac

cells engulf large particles by forming a large intracellular vesicle containing the engulfed particle. The large vesicle then fuses with a lysosome, resulting in a single membranous organelle in which the digestive enzymes break down the ingested particle.

Intracellular materials, such as old organelles, are brought into a lysosome by a process called autophagy. For example, when a mitochondrion comes to the end of its ten-day life, it is engulfed by membrane derived from the **endoplasmic reticulum**. The newly enclosed mitochondrion then fuses with a lysosome, resulting in its degradation by the acid hydrolases.

A group of genetic disorders caused by defective lysosomal enzymes demonstrates the importance of lysosomes. Called lysosomal storage diseases, these disorders are characterized by the harmful accumulation of undigested substances. The accumulated materials impair or kill the affected cells, resulting in skeletal or muscular defects, mental retardation, or even death. SEE ALSO ENDOCYTOSIS; ENDOPLASMIC RETICULUM; ENZYMES; MITOCHONDRION

Cynthia K. Damer and Scott N. Daigle

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Male Reproductive System

Reproduction is essential for any species to sustain its population. In the simplest sense, the most important function of every living organism is reproduction. Organs of the male and female reproductive systems play a central role in sexual reproduction by creating, nourishing, and housing sex cells called **gametes**.

The human male reproductive system consists of gonads called testes, a series of ducts (epididymis, **vas deferens**, ejaculatory duct, urethra) that serve to transport spermatozoa to the female reproductive tract, and accessory sex glands (seminal vesicles, prostate, and bulbourethral glands).

Testes

The testes (singular, testis) are paired structures that originally develop in the abdomen and descend into the scrotum, a sac of skin and **connective tissue** positioned outside the pelvic cavity. This scrotal location is important for maintaining a testicular temperature, approximately 1.5 to 2.5 degrees Celsius (34.7 to 36.5 degrees Fahrenheit) below body temperature, required for spermatogenesis (sperm production). Testes also serve important **endocrine** functions as the source of male sex **steroids** called androgens. The most abundant androgen is testosterone.

Inside each testis is a network of fine-diameter tubes called seminiferous tubules. Sertoli cells form the walls of a seminiferous tubule. Sertoli cells

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endoplasmic reticulum network of membranes within the cell

gamete reproductive cell, such as sperm or egg

vas deferens tube through which sperm travel from testes to urethra

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

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

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

nourish, support, and protect developing germ cells, which undergo cell division by **meiosis** to form spermatozoa (immature sperm). During spermatogenesis, germ cells begin near the wall of a seminiferous tubule, and after division they are shed into the tubule. **Proteins** produced by Sertoli cells are required for spermatogenesis, as is testosterone.

Hormonal Control

Surrounding the tubules are clusters of interstitial cells, which synthesize testosterone and secrete it into the bloodstream. Testosterone is present in infant boys, although synthesis increases dramatically at puberty around age thirteen. This increase stimulates the onset of spermatogenesis and development of accessory sex glands. All male reproductive organs require testosterone for functions such as protein synthesis, fluid **secretion**, cell growth, and cell division. Androgens also play important roles in the male sexual response and stimulate secondary sex characteristics such as skeletal development, facial hair growth, deepening of the voice, increased **metabolism**, and enlargement of the testes, scrotum, and penis.

Sperm production and androgen synthesis are controlled by a complex **feedback** loop involving the testes, hypothalamus, and pituitary gland. The pituitary controls testis function by producing follicle-stimulating **hormone** (FSH) and luteinizing hormone (LH). FSH stimulates spermatogenesis, in part by affecting Sertoli cells, while LH stimulates androgen production by interstitial cells. Pituitary production of these hormones depends on secretion of gonadotropin-releasing hormone (GnRH) by the hypothalamus. Elevated levels of GnRH initiate puberty.

How does this feedback loop prevent testosterone levels from getting too high or too low? While some may joke that the testis controls the brain in boys, there is some truth to this statement: the testis can control brain function. The production of LH is controlled by the actions of testosterone on the hypothalamus and pituitary. If testosterone concentration is elevated, testosterone inhibits production of GnRH by the hypothalamus; subsequently, LH and FSH production decreases.

Sperm Maturation

Spermatozoa leave each testis through small tubes called efferent ductules. Fluid pressure from secretions in the testis and **ciliated** cells in the efferent ductules help move spermatozoa into the epididymis. Testicular spermatozoa are immature because they cannot swim and lack the ability to penetrate an egg.

Sperm maturation occurs in the epididymis. Located adjacent to the testis, the epididymis contains a single, highly coiled tubule nearly 6 meters (19.6 feet) long. Sperm transport through the epididymis takes approximately twenty days. As sperm transit the epididymis, they are bathed in a specialized fluid rich in proteins, **ions**, and a number of other molecules. Complex interactions between spermatozoa and epididymal fluid contribute to sperm maturation. The epididymis is also a site for sperm storage and for the protection of sperm against chemical injury.
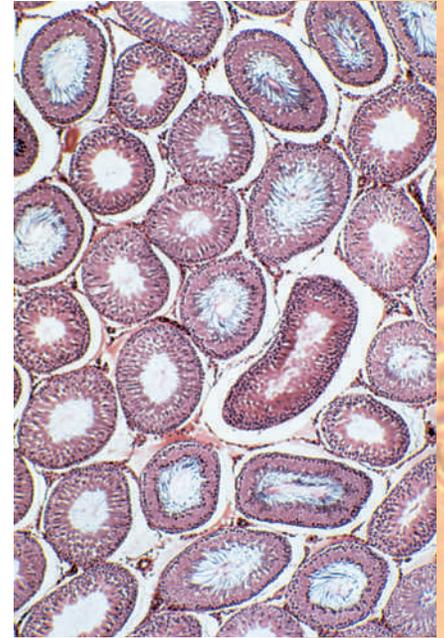
A photomicrograph of human testis showing spermatogenesis.

meiosis cell division that forms eggs or sperm

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

secretion material released from the cell

metabolism chemical reactions within a cell

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

hormone molecule released by one cell to influence another

ciliated possessing cilia, short hairlike extensions of the cell membrane

ion an electrically charged particle

The male reproductive system provides for the formation, maturation, storage, and ejaculation of sperm. Both sperm and urine exit through the urethra.

kidney

ureter

seminal vesicles

urinary bladder

prostate gland

bulbourethral gland

urethra

vas deferens

scrotum

testes

penis
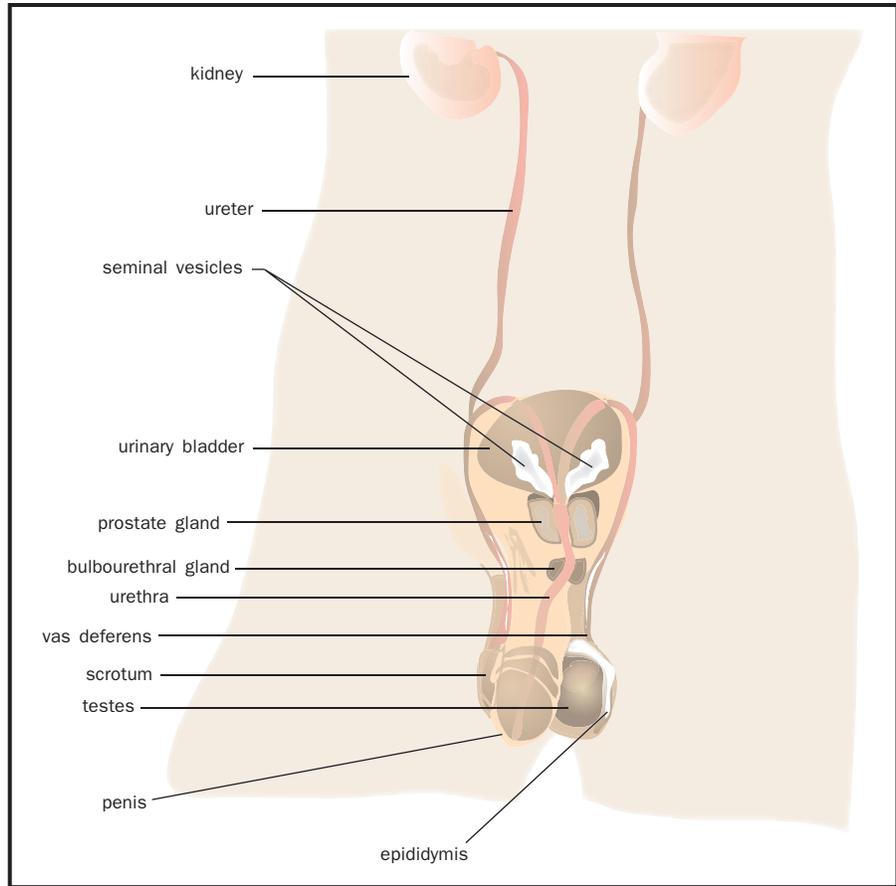
epididymis

Sperm Formation and Ejaculation

From the epididymis, spermatozoa enter a muscular tube called the vas deferens (approximately 45 centimeters [17.7 inches] long). The vas deferens contracts during the release of sperm—a process called ejaculation—to move spermatozoa out of the epididymis and into the ejaculatory duct, where sperm are mixed with secretions from the seminal vesicles. The ejaculatory duct enters the urethra as it passes through the prostate gland. In males, the urethra serves a dual purpose transporting sperm to the penis and urine from the urinary bladder.

The accessory sex glands consist of a single prostate gland and paired seminal vesicles and bulbourethral glands. The prostate and seminal vesicles secrete seminal fluid, or semen, a **viscous** mixture of spermatozoa and fluid from accessory sex glands. Spermatozoa constitute 10 percent of semen volume and number approximately 50 to 150 million sperm per milliliter. Combined secretions from the seminal vesicles and prostate account for roughly 90 percent of semen volume. The seminal vesicle secretions are rich in fructose (which serves as an energy source for spermatozoa), **prostaglandins**, and proteins that facilitate clotting of ejaculated semen in the female.

viscous thick

prostaglandins hormonelike molecules released by one cell that affect nearby cells, including smooth muscle

Prostate secretions are rich in zinc, citric acid, antibioticlike molecules, and **enzymes** important for sperm function. A protein called prostate-specific **antigen** can show elevated levels in the blood under conditions such as prostate growth. During sexual excitation, the bulbourethral glands produce a droplet of **alkaline** fluid that neutralizes residual urine in the urethra, protecting the sperm from its acidity.

The penis contains two bodies of tissue (corpora cavernosa) above the urethra and a lower cylinder of tissue (corpus spongiosum) surrounding the urethra. The enlarged tip of the penis is called the glans penis. Mechanisms responsible for penile erection are complex. During sexual arousal, penile arteries dilate and a large volume of blood fills the penis, resulting in erection. The nervous system plays an important role in controlling erection and ejaculation.

The parasympathetic division of the **autonomic** nervous system regulates erection, whereas ejaculation is triggered by sympathetic impulses. Medical and emotional conditions can cause clinical disorders of erectile dysfunction. Drugs such as Viagra increase erectile function by improving blood flow into penile tissue. Many factors result in poor fertility or infertility in males including hormone imbalances, reproductive tract blockages, decreased sperm concentration, and abnormal sperm.

The journey of spermatozoa from formation to release is complicated. Reproduction of any individual is never guaranteed, yet through combined functions of male and female reproductive organs, nature has provided a sophisticated sequence of biological events designed to maximize the likelihood that we pass our **genes** to future generations. SEE ALSO ENDOCRINE SYSTEM; FEMALE REPRODUCTIVE SYSTEM; HORMONES; HYPOTHALAMUS; PITUITARY GLAND; SEXUAL REPRODUCTION

Michael A. Palladino

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Mammal

Mammals are taxonomically separated from other animals at the class level (kingdom Animalia, **phylum** Chordata, subphylum Vertebrata, class Mammalia). Modern mammals are readily differentiated from other animals by the following characteristics: hair; a four-chambered heart with the aorta descending on the left; red blood cells that lack a **nucleus** (allowing for increased surface area for oxygen transport); a muscular diaphragm separating the abdominal and thoracic cavities that aids in breathing; descent of the testes into a scrotum to achieve a temperature environment amenable to sperm development; a variety of skin glands including sebaceous, sweat, and milk or mammary (the characteristic giving mammals
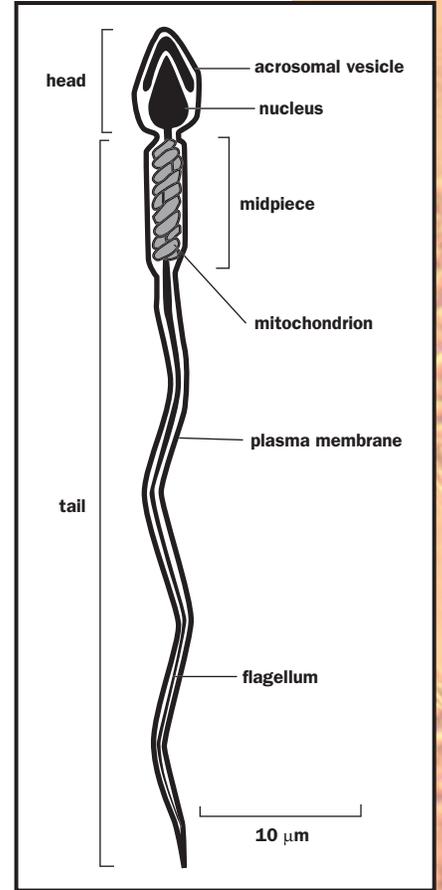
Anatomy of the human sperm.

enzyme protein that controls a reaction in a cell

antigen foreign substance that provokes an immune response

alkaline chemically basic, with an excess of OH- ions

autonomic independent; regulating involuntary actions

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

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

nucleus membrane-bound portion of cell containing the chromosomes

their name); and elaborate dermal musculature (controlling the skin), particularly in the face (associated with suckling in young). All of these characters relate to the high metabolic rate of mammals. Mammals and birds are the only vertebrates that maintain a consistent body temperature through physiological (endothermy) rather than behavioral means (ectothermy).

None of these characters are readily apparent in fossils. There are, however, a number of skeletal and dental traits that are unique to mammals. The characters most useful in tracing the origin of mammals are: a bony secondary palate in the skull; a jaw joint between the dentary (jaw bone) and the squamosal bone of the skull (other terrestrial vertebrates have a quadrate-articular jaw joint); three bony ossicles (malleus, incus, and stapes) in the middle ear for sound transport rather than just one (stapes); teeth that are specialized for a variety of functions, including stabbing, nipping, shearing, and grinding; and a limb skeleton that can passively support the body off the ground (versus the reptilian posture of legs to the side). Most of these traits also relate to the high metabolic demands of endotherms. The reptile-to-mammal transition is one of the best documented in the fossil record. The first mammals appeared over 200 million years ago, about the same time as the first dinosaurs. SEE ALSO BODY CAVITIES; EVOLUTION, EVIDENCE FOR; REPTILE; SKIN

William P. Wall

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Marine Biologist

A marine biologist is someone who studies plants, animals, and other organisms of the oceans, ranging from large marine mammals to microscopic **plankton**. Marine biologists study such subjects as animal behavior and ecology, biomedical uses of the sea, the commercial importance of the ocean's natural resources, and methods for preservation of species and habitats.

plankton microscopic floating organisms

The need for marine biologists has increased because of growing interest in conservation of the oceans, and many are employed by private and government environmental protection and resource management agencies. For example, marine biologists are needed to determine catch quotas for species of fish in order to prevent a decline in population. In addition to performing basic research, they present information to governments and in-
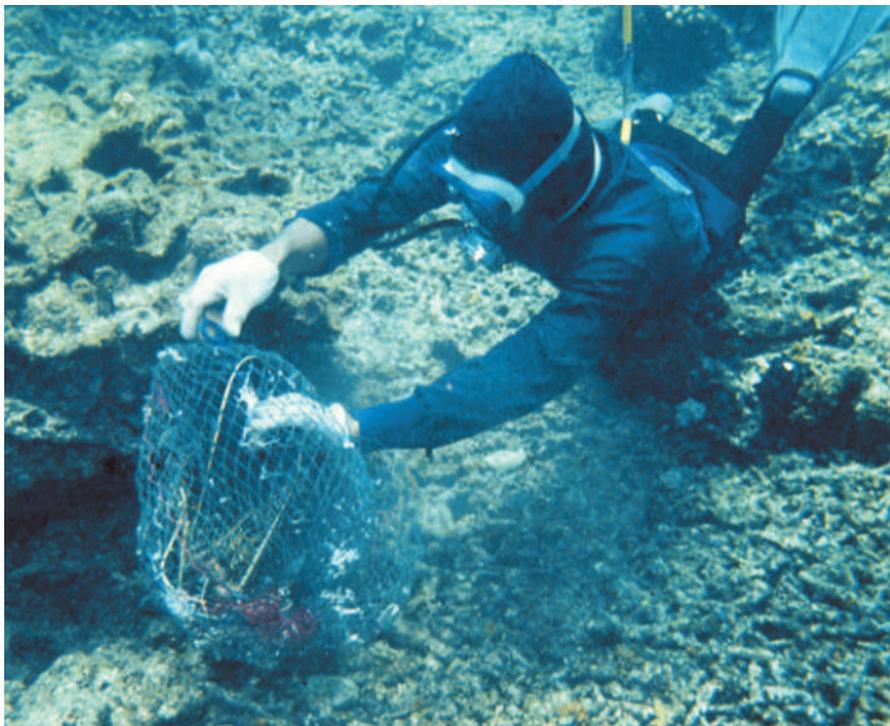
A marine biologist inspecting a coral reef in Indonesia that has been damaged by illegal fishing practices.
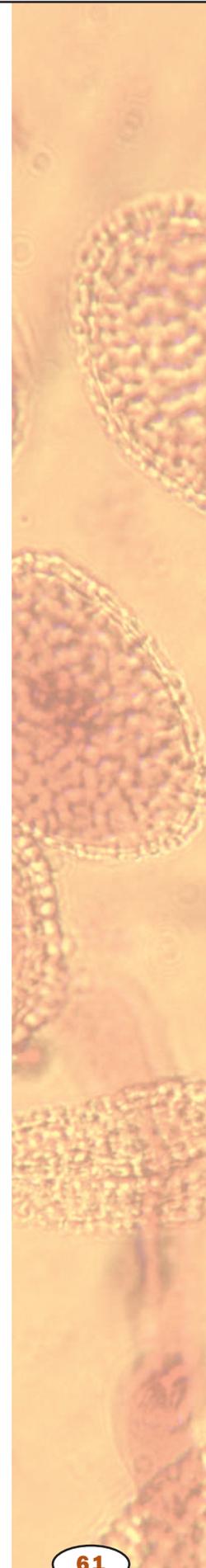
dustries to aid in resource conservation decisions. As land development increases, marine biologists are needed to determine its effects on surrounding habitats and whether an **ecosystem** can withstand human invasion. Marine biologists also find work worldwide teaching in colleges, universities, and even some high schools. Many work on oceanographic research vessels and in laboratories from polar to tropical settings.

ecosystem an ecological community and its environment

To be well prepared for a career in marine biology, a strong background in mathematics is crucial. One should also take a wide range of science courses in high school and college, such as biology, chemistry, physics, zoology, geology, marine science, oceanography, and atmospheric science. A working knowledge of computers is increasingly necessary for data collection and analysis. Satellite imaging and global information systems (GIS) are common uses of computers in the field.

Summer courses and internships are available worldwide to provide hands-on experience with marine life, the use of field and laboratory equipment, and other aspects of marine research. Employment opportunities are available from the bachelor to the doctorate level, with greater independence, decision-making responsibility, and income at the higher levels. SEE ALSO BONY FISH; CARTILAGINOUS FISH; CORAL REEF; CRUSTACEAN; ESTUARIES; OCEAN ECOSYSTEMS; PLANKTON

Lisa Nicole Saladin and Kenneth S. Saladin

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cranial related to the cranium, or brain cavity

gestation period of fetal development within the mother

lineage ancestral line

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

niche the habitat supplying the right environment for a particular species

Marsupial

Marsupials, also known as metatherian mammals, are an ancient and diverse mammal group. They are distinguished from other mammals by a number of **cranial** and skeletal characteristics, including larger numbers of teeth. Marsupials also share a unique pattern of reproduction and development of the young. Marsupial young are born at an early stage of development after a **gestation** period that can be as short as twelve days. After birth, they crawl over the mother's fur and skin and attach themselves to a nipple. Many, but not all, marsupials develop a pouch that protects the nursing young, and most development occurs within the pouch.

The marsupial **lineage** is thought to be the sister group to the lineage of **placental** mammals. The two groups are believed to have diverged 140 million years ago by the mid-Cretaceous, but are first known from the late Cretaceous fossil record. Marsupials have never evolved flying or marine forms, but they are morphologically diverse and occupy every other ecological **niche**.

Most marsupial diversity occurs in the Australasian region (about two hundred species) and in the tropical regions of Central and South America (about seventy species). Examples of marsupials are the red kangaroo (*Macropus rufus*), the koala (*Phascolarctos cinereus*), and the Virginia opossum (*Didelphis virginiana*), the only native marsupial found in the United States and Canada. SEE ALSO MAMMAL

Tanya Dewey

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Mating Systems

Mating systems are descriptions of who mates with whom in the animal world. In simplest terms, definitions of mating systems are based on how many mates an individual acquires during the breeding season. In monogamy, both males and females have only one mate at a time. This type of mating system often occurs in species in which both the male and female are required to successfully raise young or in which males have little chance of monopolizing more than one female. Monogamy is common in birds whose males can help incubate eggs and feed young.

In a polygamous mating system, individuals of one or the other sex have more than one mate during the breeding season. When males in the population mate with more than one female, it is called polygyny (*poly* means "many," and *gyne* means "female"). Males compete for females, and this leads to strong selection for traits that either attract females (for example, elaborate songs or calls, bright coloration, and courtship displays) or allow males to compete effectively with other males (for example, aggressiveness, large size, and fighting aids such as antlers). Polygyny is common in species where males are less likely to provide parental care (and thus may increase their

A male frigate bird with its throat pouch inflated to attract females.
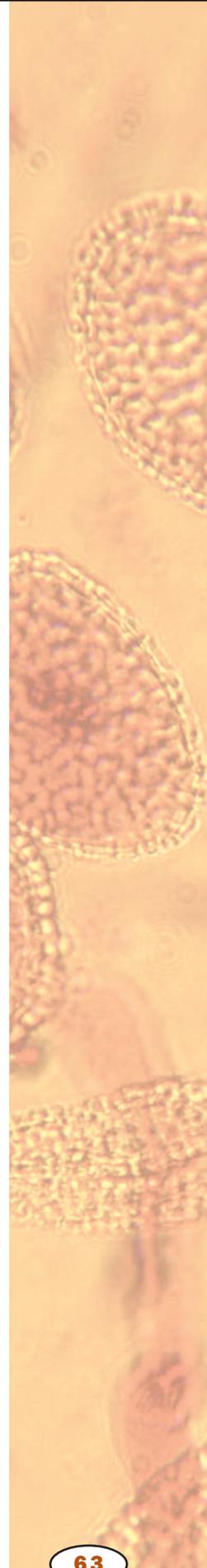
reproductive success by inseminating more females) or where males are able to monopolize more than one female (if females or the resources they require are spatially clumped). Mammalian mating systems are predominantly polygynous, in part because young develop within and are then nursed by the female.

In polyandry (*andros* means "male"), some females mate with more than one male during the breeding season. This is the rarest type of mating system. Females compete for males and may be larger and more colorful than males. In the spotted sandpiper, for example, females compete for territories in order to attract males. Once a male mates with a female, she lays a clutch of eggs that the male incubates. The female will then attempt to attract additional males for whom she will also lay eggs.

In addition to the number of mates an individual acquires during the breeding season, mating systems have also been described in terms of whether a pair bond is formed, how long the pair bond lasts, and how much each member of the pair contributes to care of the young, resulting in more complex definitions. Mating systems are also complicated by the fact that individuals of some species perform extra-pair copulations, which are copulations with individuals other than the mate. Evidence from deoxyribonucleic acid (DNA) studies of birds, mammals, and other species has shown that extra-pair copulations can result in fertilized eggs so that a presumably "monogamous" male or female may in fact have more than one mate.

Which mating system evolves is influenced by the relative parental investment of each sex and the ability of one sex to monopolize members of the opposite sex, which in turn may be driven by the abundance and distribution of resources such as food or nesting sites. Because resources vary among and within habitats, this leads to variation in mating systems, even within species. An excellent example of this is the mating system of the dunnock, a European songbird. The amount of food available affects the size of the area over which a female must forage, and this in turn affects how many females can be monopolized by one male and how many males can

be attracted by a female. Within a single population of dunnocks, there may be monogamous pairs as well as birds in polygynous and polyandrous relationships.

Because of differences in the amount of energy invested in producing **gametes** (eggs are costly, sperm are not), finding a mate, and rearing offspring, the costs and benefits of a particular mating system may be different for males and females. In addition, not all individuals of the same sex in a population experience the same costs and benefits of a particular mating system (for example, some males in a polygynous mating system may have several mates whereas other males may have none). SEE ALSO BEHAVIOR PATTERNS; EVOLUTION; SEXUAL REPRODUCTION; SEXUAL REPRODUCTION, EVOLUTION OF; SEXUAL SELECTION; SOCIAL BEHAVIOR; SOCIOBIOLOGY

Susan Evarts

gamete reproductive cell, such as sperm or egg

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McClintock, Barbara

American geneticist
1902–1992

In the words of James Watson, codiscoverer of the structure of deoxyribonucleic acid (DNA), Barbara McClintock was one of the most important geneticists of the twentieth century. McClintock made major discoveries about **chromosome** structure and showed for the first time that movable elements within the chromosome (transposons) could control **gene expression**. In 1931, with her graduate student, Harriet Creighton, she showed that meiotic crossing over in corn separated formerly linked observable traits, thus proving that genes were located on chromosomes.

McClintock went on to study the genetic control of coloration in Indian corn. She discovered a genetic element whose presence would cause the chromosome to break where it occurred. McClintock termed this element *Ds*, for "dissociation." The breakage caused by *Ds* interrupted the normal expression of nearby genes, causing the color variegation. McClintock also discovered that after breakage, the chromosomal fragment containing *Ds* can reinsert itself elsewhere, interrupting other genes and causing different effects. She coined the term "transposition" to describe this new type of genetic mutation.

McClintock's discovery of the breakage and transposition of a genetic element conflicted with the then prevalent view of chromosomes as static blueprints, and her work was largely ignored throughout the 1950s. Her discoveries, however, laid the foundation for the dynamic view of the **genome**, and she was finally honored with the Nobel Prize in physiology

Barbara McClintock.

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

gene expression use of a gene to create the corresponding protein

or medicine in 1983. SEE ALSO LINKAGE AND GENE MAPPING; MEIOSIS; TRANSPOSON

<div align="right">*Richard Robinson*</div>

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genome total genetic material in a cell or organism

Medical Assistant

A medical assistant is a health care professional who provides administrative or clinical assistance to a doctor. Duties of the administrative medical assistant include general office responsibilities, such as answering the phone and making appointments, as well as more specialized skills, such as keeping medical records and processing insurance reimbursements. The clinical medical assistant may be responsible for obtaining a medical history from the patient, taking vital signs (temperature, blood pressure, and pulse), performing visual exams, obtaining specimens such as blood samples or throat swabs, or other medical procedures that assist in the diagnosis of a patient. All of these are done at the request of the physician, but are usually performed without direct supervision. In smaller clinics or private doctor's offices, the medical assistant may perform both types of duties.

To become a medical assistant, one should take high school courses in science, mathematics, computer skills, and business. Medical assistant training programs are available at junior colleges, community colleges, and private vocational schools. Programs may last from seven months to two years, depending on the breadth of skills involved. Personal and professional skills essential to the medical assistant include attention to detail, desire to work with people, and a professional and friendly manner. SEE ALSO DOCTOR, FAMILY PRACTICE; NURSE; NURSE PRACTITIONERS

<div align="right">*Richard Robinson*</div>

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Medical/Science Illustrator

Science and medical illustrators provide art for books, newspapers, magazines, advertisements, articles in scientific journals, online Web sites and other electronic references, and museum, zoo, and legal exhibits. Illustrators may draw an illustration of an arrowhead dug from an archaeological site, a diagram showing how **neurons** in the brain transmit signals, or an animation of a chemical reaction. Illustrations may be artistic (such as an artist's conception of the surface of a faraway planet), realistic, or diagrammatic.

Everything that science and medical illustrators draw is meant to communicate scientific or medical ideas or facts. Some science illustrators specialize in natural history, drawing a new species of fish or a coral habitat, for example. Medical illustrators specialize in human anatomy,

neuron nerve cell
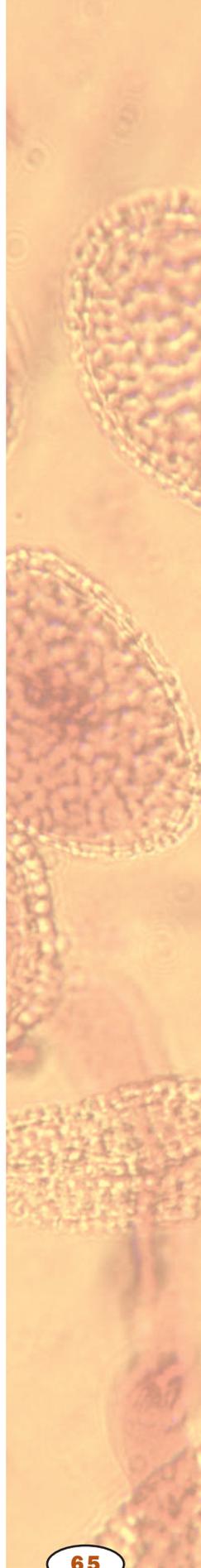
diseases, and surgical procedures. They may do anatomical drawings that help students and health professionals learn the structure of the human body, or they may make detailed drawings of how to perform a heart by-pass operation.

The audience for an illustrator's work can be laypeople who know little science, the kind of people who wander into a museum on their lunch break; students; or highly specialized professionals. Illustration can be simple pen-and-ink line drawings, airbrush paintings, computer-generated graphics, cartoons, or even three-dimensional models.

Many science and medical illustrators begin by getting a bachelor's degree in biology or some other science. They may then spend one to two years studying medical illustration or science illustration in a graduate program at a university. Such students can launch their career by taking an internship or job at a magazine or art studio, for example. Others get a degree in art and teach themselves science as they work. Still others are self-taught. If art has always been a hobby, they may start out working with a researcher they know, then gradually find more work. High school students interested in science illustration should take as much math as possible, in an effort to prepare for science classes in college.

Jennie Dusheck

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Meiosis

haploid having single, nonpaired chromosomes in the nucleus

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

gamete reproductive cell, such as sperm or egg

diploid having pairs of chromosomes in the nucleus

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

gametophyte a haploid plant that makes gametes by mitosis

mitosis separation of replicated chromosomes

Meiosis is the two-step series of specialized cell divisions that makes sexual reproduction possible. Meiosis produces **haploid** cells, which contain just one member of every **chromosome** pair characteristic of an organism. In all animals, specialized cells in the reproductive organs, called germ cells, undergo meiosis to produce haploid **gametes** (sperm and egg), which then fuse during sexual reproduction to create new **diploid** embryos. For example, human gametes are haploid and contain twenty-three different chromosomes. All other cells in the human body are diploid, containing two versions of each chromosome for a total of forty-six. Fusion of gametes to form a new embryo restores the diploid number characteristic of the organism, and it mixes maternal and paternal **genes** to give new combinations of traits. Meiosis itself also yields great genetic diversity in the resultant gametes through two mechanisms: (1) independent assortment of chromosomes at both of the meiotic divisions; and (2) physical exchange of chromosomal regions through a process called crossing over. Both processes create new chromosomal combinations, resulting in an array of genetically diverse gametes from a single individual.

Plants, fungi, and some protists also perform meiosis. In plants, meiosis creates a multicellular haploid organism, called a **gametophyte**, which in some groups is independent of the diploid plant. Gametes are produced by **mitosis** of the gametophyte, which then fuse to form the embryo. This cycle is called alternation of generations.

beginning of meiosis: prophase I

crossing over

metaphase I

anaphase I

telophase I

metaphase II

anaphase II

telophase II
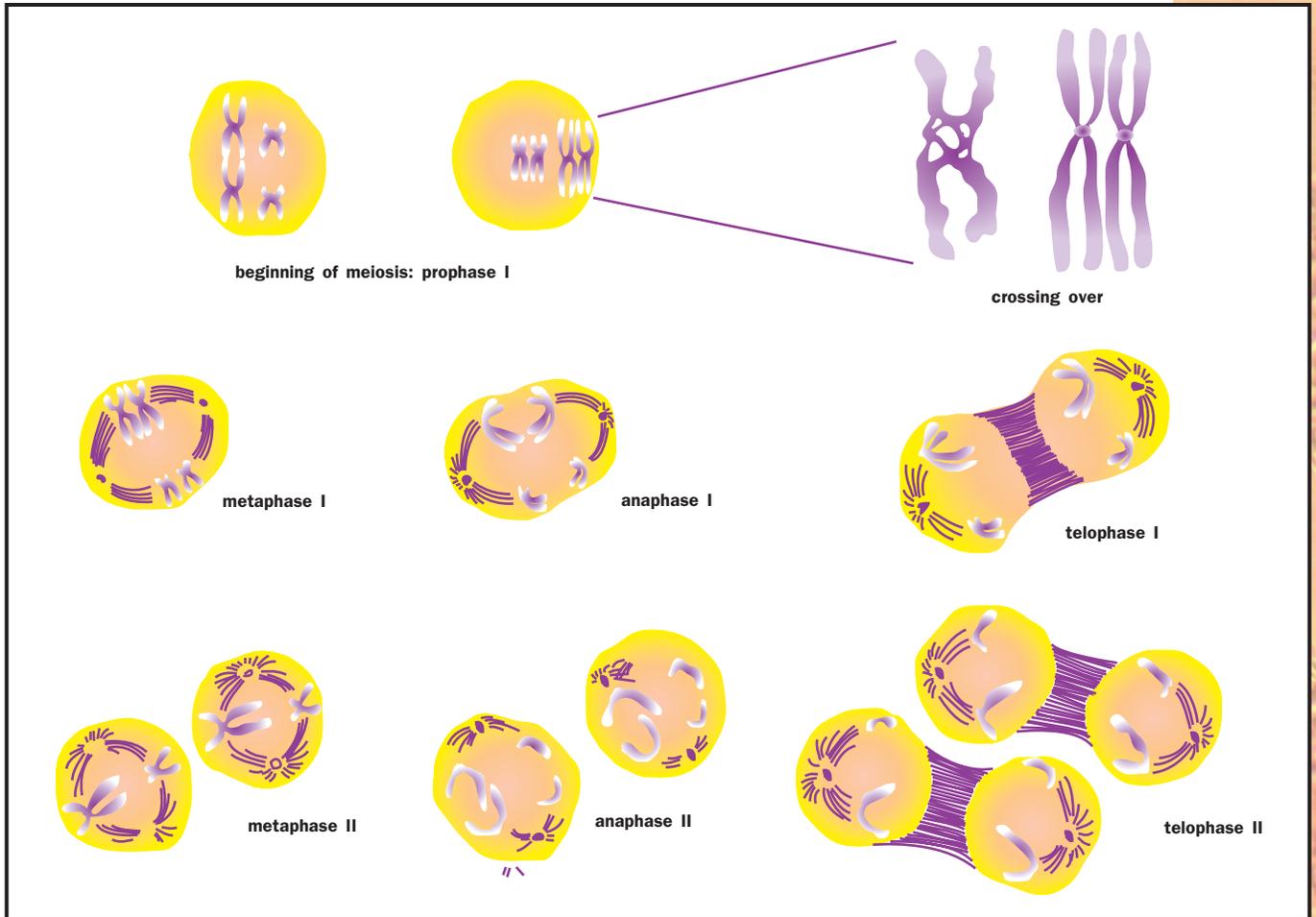
Chromosome Basics and Meiosis Overview

As noted, diploid cells contain pairs of chromosomes, each member of which carries the same set of genes. One member of each pair is inherited from the mother, and one from the father. The two pair members are called **homologous chromosomes**, or homologs.

Prior to meiosis, the diploid cell replicates its deoxyribonucleic acid (DNA). During replication, each chromosome duplicates itself to form two identical copies, which remain attached at a region known as the **centromere**. Each copy is known as a **chromatid**; thus, each chromosome is composed of two identical sister chromatids.

During meiosis, homologous chromosomes line up and exchange segments, a process called crossing over. Following this, homologs are separated from each other in the first meiotic division. Next, in the second meiotic division, chromatids are separated from each other, in a process which is mechanically identical to mitosis. The result is four haploid cells. The coordination of the two meiotic chromosomal divisions gives meiosis its distinctive characteristics: a reduction in the number of chromosomes by half, accompanied by mixing of parental chromosomes, and swapping of regions between homologous chromosomes.

Meiosis involves two divisions. During meiosis I, homologous chromosomes cross over, exchanging segments. By the end of telophase I the members of homologous pairs have separated from each other. During meiosis II, sister chromatids are separated, just as they are during mitosis.

homologous chromosomes chromosomes carrying similar genetic information

centromere region of the chromosome linking chromatids

chromatid a replicated chromosome before separation from its copy

Meiosis I

Consider a spermatocyte or oocyte about to embark on meiosis. This diploid cell contains one set of chromosomes contributed by its mother and one set of chromosomes contributed by its father. Following DNA replication, the unique aspects of the first division of meiosis (meiosis I) begin. Because meiosis reduces chromosome content, a mechanism must ensure that every final haploid gamete has both the correct number and the correct set of chromosomes, with one member of each homologous pair. Meiosis I guarantees this by keeping each chromatid pair together and aligning homologous pairs of duplicated sister chromosomes prior to the first chromosomal division. The alignment and subsequent separation of pairs of homologous chromosomes during meiosis I thus sets up the mechanism that ensures that all four haploid gametes will contain the correct complement of chromosomes. Interestingly, the mechanism whereby meiosis aligns homologs also results in reciprocal exchanges of DNA between aligned chromosomes.

Alignment of homologous chromosome pairs begins before meiosis I, when each duplicated set of chromosomes seeks its homologous partner pair within the oocyte or spermatocyte. The underlying DNA sequence homology of the similar maternal and paternal chromosome pairs guides this search and eventual alignment along the entire length of each chromosome. The alignment is further mediated and cemented by a three-dimensional zipperlike structure surrounding each set of paired homologous chromosomes, the synaptonemal complex. In the process of these alignment steps, specific **enzymes** nick and then rejoin DNA at different places along the paired chromosomes. This process of genetic exchange is called meiotic recombination, or crossing over. Crossing over provides an attachment that holds homologous chromosomes temporarily in place and, at the same time, produces **progeny** chromosomes consisting of a patchwork of material from each of the originals. Thus, the two central characteristics of meiosis, reduction in chromosome number and genetic rearrangements, are intimately intertwined.

Once all sets of chromosome pairs have established at least one such crossing over, correct assortment of chromosomes at meiosis I is ensured. The synaptonemal complexes dissolve and the newly rearranged chromosomes proceed through the second mechanism that generates genetic diversity at meiosis I: They assort independently of one another to opposite poles of the cell pulled by spindle fibers. Whereas one chromosome pair might divide so that its predominantly maternal chromosome moves to the cell's "north" pole, another pair of chromosomes will move its predominantly paternal chromosome to that same north pole. These chromosomal movements are randomly determined, yielding great genetic diversity of gametes in an organism with multiple chromosomes. In an organism with three homologous pairs, there are four different possible chromosome arrangements at the end of meiosis I. In humans there are more than 4 million possible arrangements.

Thus, overall, the first division of meiosis provides two major mechanisms for new genetic combinations: (1) cutting apart and pasting together various segments of homologous chromosomes to yield unique **hybrid** chromosomes; and (2) independent assortment of maternal and paternal chromosomes.

enzyme protein that controls a reaction in a cell

progeny offspring

hybrid combination of two different types

Meiosis II and Cytokinesis

As meiosis II begins, each daughter **nucleus** contains the haploid number of chromosomes (for humans, twenty-three). Each chromosome is composed of two chromatids attached at the centromere. The second division of meiosis separates the chromatids. Once again, spindle fibers provide the pulling power. Once chromatids are separated, they are called chromosomes, and so at the end of meiosis II, each of the four new cells has the haploid number of chromosomes. Following this, cytokinesis occurs, in which the **cytoplasm** of the original cell is divided and membranes form to separate the new cells. Cytoplasm is divided evenly in sperm, but unevenly in eggs. During egg formation, most of the cytoplasm is allotted to one of the cell products, leaving one functional egg and several "polar bodies" that contain DNA and membrane, but little else. This unequal division gives the single egg a larger store of food to supply the developing embryo after **fertilization**.

nucleus membrane-bound portion of cell containing the chromosomes

cytoplasm material in a cell, excluding the nucleus

fertilization union of sperm and egg

Meiosis versus Mitosis

The alignment of homologous chromosome pairs in meiosis I and the accompanying physical exchanges between aligned chromosomes is unique to meiosis. In mitosis, by contrast, homologous chromosome pairs never or very rarely interact. Each mitotic chromosome duplicates, forming two sister chromatids, and then these two identical sister chromatids separate to opposite poles. While mitosis is specialized to produce entirely identical progeny, meiosis is specialized to produce a wide range of distinctive haploid progeny.

Mistakes in Meiosis

Among the many potential causes of infertility are problems with meiosis. If a person's spermatocytes or oocytes consistently produce sperm or eggs that contain an incorrect number or complement of chromosomes, then there will be great difficulty in producing a viable embryo.

A much more common situation arises from the rare, sporadic occurrence in a normally fertile person of an improper chromosome separation. When two chromosomes fail to separate as they should, a "nondisjunction" event has occurred. Such **nondisjunctions** are almost always lethal to the egg or sperm, or to the resultant embryo. There are exceptions, however. For example, approximately one out of one hundred men is the result of such a nondisjunction, which gave him an extra X chromosome. Such XXY individuals have Klinefelter's syndrome, a sex chromosome trisomy (three sex chromosomes instead of the normal two) with minor outward manifestations. Down syndrome individuals possess three copies of chromosome twenty-one instead of the normal two; their extra copy resulted from a nondisjunction of those chromosomes during one of the meiotic divisions of one of the parents. SEE ALSO ALTERNATION OF GENERATIONS; CHROMOSOME, EUKARYOTIC; CYTOKINESIS; MITOSIS; SEX CHROMOSOMES; SEXUAL REPRODUCTION

nondisjunction failure of separation of homologous chromosomes during meiosis

Wendy E. Raymond

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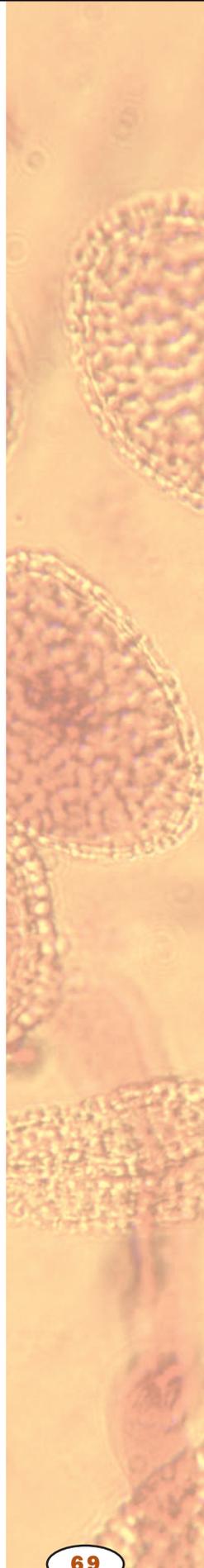
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organelle membrane-bound cell compartment

aqueous watery or water-based

lipid fat or waxlike molecule, insoluble in water

bilayer composed of two layers

A transmission electron micrograph of a Golgi apparatus, a membranous subcellular structure.

Membrane Proteins

Cells and their **organelles** are **aqueous** compartments bounded by thin membranes. The core of these membranes is a film of specialized **lipids**, two molecules thick. Attached to and embedded in this lipid **bilayer** are numerous proteins, each specialized to carry out a different function. Thus, each membrane has its own team of proteins. A typical membrane might be composed half of lipid and half of protein. However, this varies widely. For example, the envelopes of some viruses employ only a few protein species to gain entry into cells and later mediate the exit of new virus particles. In contrast, busy membranes are crowded with hundreds of different proteins; each type is present in a specified number—hundreds, thousands, or even
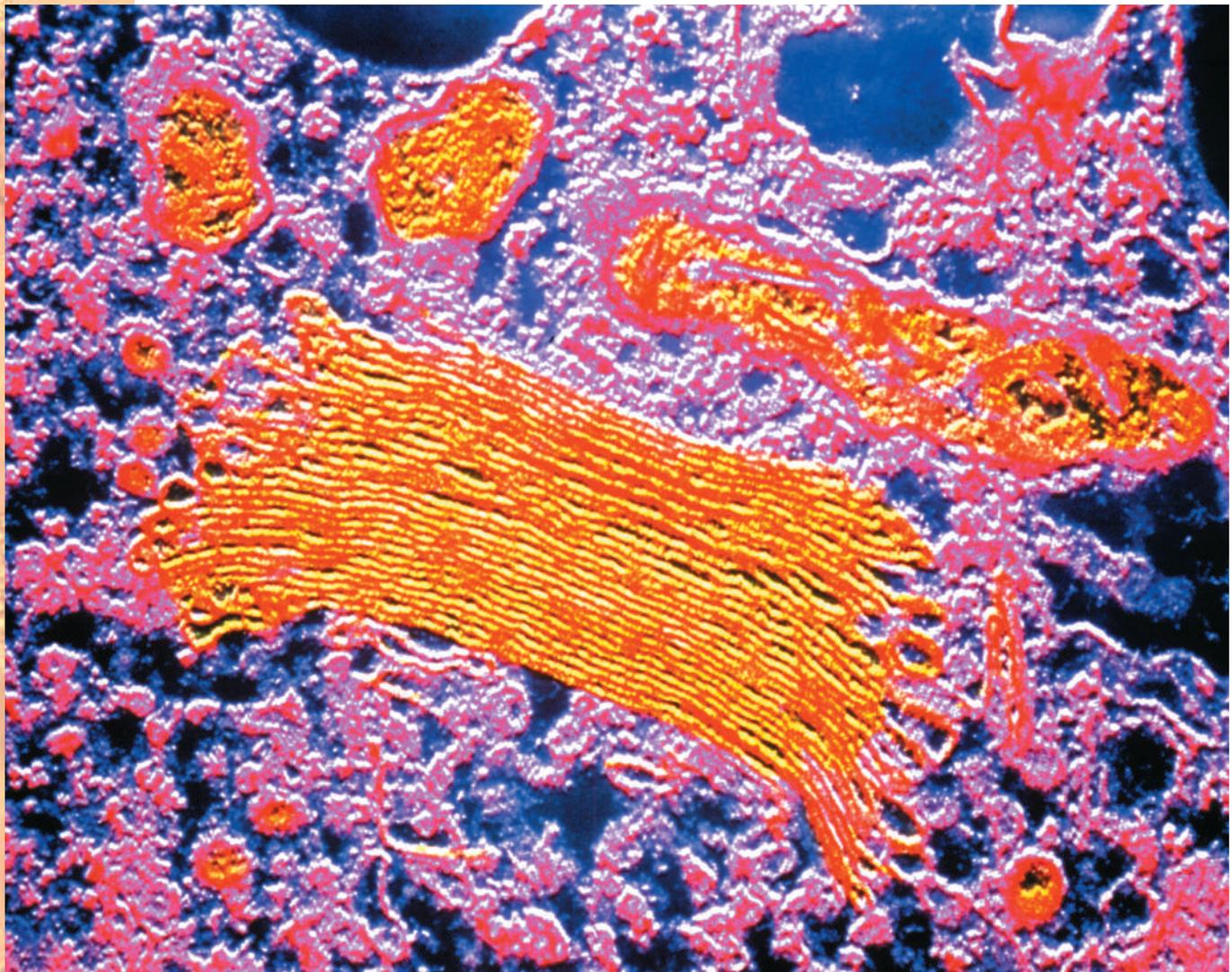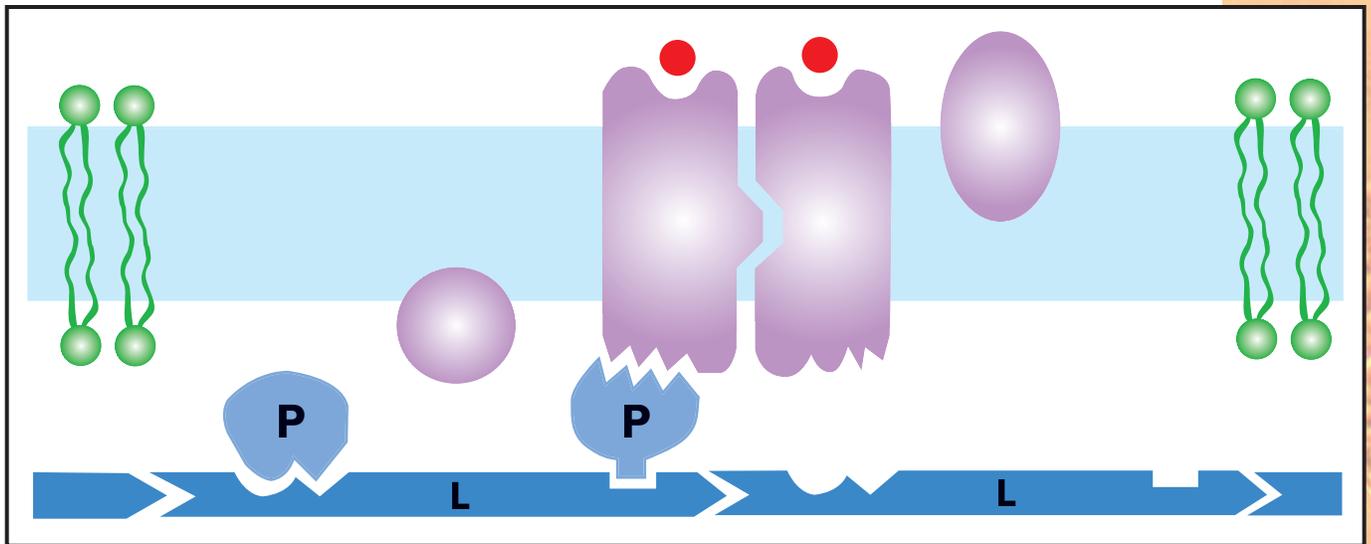
millions of copies per cell. Built into the structure of each of these proteins is molecular information directing the way it sits in its membrane and an address tag targeting it to its home.

What Membrane Proteins Do

Membranes do not simply serve as walls between cellular compartments but are also participants in their **metabolism**. Many membrane proteins are transporters, moving **solutes** between the aqueous compartments. Other membrane proteins serve as **enzymes** that **catalyze** vital processes; for example, the harvest of energy from food.

A variety of membrane proteins are receptors, signal **transducers** that transmit stimuli received outside the cell (for example, **hormone** or odor molecules) to functional proteins inside. The signals conveyed to the **cytoplasm** typically turn on complex circuits of response, adapting the metabolism of the cell to a perception of the outside world. Thus, receptors transport information rather than cargo across membranes.

There are two general ways this transfer of information occurs. First, in many cases, the binding of the external stimulus molecule to the receptor brings about a specific change in the shape of this protein. The altered form of the receptor is then recognized by a relay protein inside the cell because its new shape precisely matches a site on the relay protein, enabling them to fit together like a key in a lock. This association turns on the response. The second class of receptors uses a somewhat different strategy: the binding of extracellular signal molecules to these membrane molecules causes them to change shape, but, in this case, their altered contour allows them to associate with one another (once again, through lock-and-key recognition). These conglomerates are then recognized as a stimulus by the appropriate relay proteins at the cytoplasmic side of the membrane.

Most cells have **cytoskeletons**: protein scaffolds that lend mechanical support to both the watery interior of the cell and to their fragile and deformable membranes. Membranes are bound to the underlying cytoskeleton through linker proteins. Cytoskeletal proteins can tap adenosine

Membrane proteins can be integral (I) or peripheral (P), determined by their amino acid structure. Peripheral proteins bind to integral proteins and to cytoskeletal proteins (L).

metabolism chemical reactions within a cell

solute dissolved substance

enzyme protein that controls a reaction in a cell

catalyze aid in the reaction of

transduce proteins that convert a signal of one type into another type

hormone molecule released by one cell to influence another

cytoplasm material in a cell, excluding the nucleus

cytoskeleton internal scaffolding in a cell, composed of protein

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

pseudopod "false foot"; an extension of the plasma membrane during locomotion by an amoeba or similar crawling cell

polar partially charged

amino acid a building block of protein

hydrophobic "water hating," such as oils

hydrocarbon molecule or group composed only of C and H

triphosphate (**ATP**) or some other high-energy molecule to push and pull on the membrane so as to change its contour. Amebae and white blood cells, for example, are made to crawl as their plasma membranes are deformed into **pseudopods** by a dense mass of filaments in the underlying cytoskeletal array. In addition, some membrane-spanning proteins link the cytoskeleton inside the cell to filaments in the extracellular space and thereby manage the intricate relationships of the cells in human tissues.

Associations of Proteins with Their Membranes

Lipid bilayers are like oily liquid films. Their molecules diffuse about randomly within the membrane but avoid the aqueous environment, just as oil shuns water. This is because the chemical nature of lipids is mostly nonpolar, whereas that of water is **polar**. Some proteins destined for the membrane are designed so that groups of nonpolar **amino acid** side chains create a water-shunning (hydrophobic) region on their surface. This lodges the protein in the interior of the bilayer. Proteins that are anchored by dissolving in the bilayer core are said to be integral to the membrane. At the same time, the tops and/or bottoms of these integral membrane proteins make contact with the water space. Predictably, these exposed regions are covered with polar amino acid side chains, attracted to water, which help to orient and stabilize the protein in the membrane. Every copy of an integral membrane protein that spans the bilayer is oriented identically; for example, with the same end pointed inside or outside, as befits its function.

Other membrane proteins are entirely covered with polar amino acid side chains. Although these proteins are water soluble, they nevertheless associate with membranes. This they do by making specific lock-and-key attachments to the projecting portions of integral proteins. These docked water-soluble molecules are called peripheral membrane proteins because they reside outside the lipid bilayer. Their anchorage can be permanent or they may get on and off the membrane, randomly in some cases or else in response to a biological signal.

A third mode of membrane association is for the cell to attach **hydrophobic** tails to peripheral proteins. The tails then dissolve in the hydrophobic (nonpolar) core of the bilayer, thereby anchoring the protein. Typically, these tails are long **hydrocarbon** chains; frequently, they are the very same fatty acids that hold the lipid molecules in the bilayer.

Scientists can disassemble biological membranes in the laboratory, separate the component molecules from one another, and then recombine them. With any luck, the molecules will reassemble into a membrane that is reminiscent of the original and, to some degree, functional. This self-assembly demonstrates that membrane molecules carry information about their intended destination within their structures.

Constraining the Movement of Membrane Proteins

Membrane lipids and proteins can, in principal, diffuse freely by random (Brownian) motion, circumnavigating a cell within a few minutes. But some membranes have mechanisms to suppress this kind of freedom so as to segregate specified molecules into different domains, or regions of the membrane surface. For example, the epithelial cells that line the intestine,

separating the inside from the outside of the body, are polarized to perform distinctly different tasks at their two surfaces. To help maintain their two-faced existence, each cell surface has a belt of protein filaments around its waist called a tight junction that fences off the other membrane molecules into their proper compartments. SEE ALSO CELL JUNCTIONS; CELL MOTILITY; ENZYMES; HORMONES; ION CHANNELS; MEMBRANE STRUCTURE; MEMBRANE TRANSPORT; NUCLEAR TRANSPORT; PROTEIN TARGETING; SIGNALING AND SIGNAL TRANSDUCTION

Theodore L. Steck

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Membrane Structure

A membrane separates a cell from its environment or subdivides a cell into specialized regions or compartments. The structure of a membrane is best understood in light of its component parts and in the context of the specialized functions performed by the cell or by its various, membrane-bound compartments.

Molecular Structure

Cellular membranes consist mainly of phospholipid assembled into a stable, sheetlike structure called a **bilayer**. The process of assembly occurs spontaneously under normal cellular conditions once phospholipid has been synthesized. To understand this process and the important properties of all membranes, it is necessary to appreciate the **amphipathic** nature of phospholipid structure. An amphipathic **lipid** is structurally polarized into a molecular region that is **hydrophilic** and one that is **hydrophobic**. When the phospholipids in an **aqueous** environment like **cytoplasm** reach a critical concentration, they associate into **aggregates** that are more stable in an aqueous environment than are the individual lipids. These aggregates, or micelles, can assume several forms, but they all have two features in common: The polar "heads" of the phospholipids project into the aqueous environment, and the hydrophobic regions or "tails" are oriented away from water. At low lipid concentrations the micelles are spherical; at higher concentrations, the micelles aggregate to form an extended, two-dimensional sheet called a bilayer.

To understand the structure of a bilayer, imagine two single layers of phospholipid, each consisting of polar heads and nonpolar tails, aligned head with head and tail with tail. Then imagine these monolayers coming together in a symmetrical fashion, such that the tails of one monolayer touch those of the other, and the heads project outward away from the tails. The resulting structure is a stable bilayer, with a hydrophobic core and hydrophilic surfaces.

Such bilayers can be made in the laboratory. Moreover, compositional studies carried out in the early 1900s by Dutch scientists E. Gorter and F.

bilayer composed of two layers

amphipathic having both polar and nonpolar regions

lipid fat or waxlike molecule, insoluble in water

hydrophilic "water loving"

hydrophobic "water hating," such as oils

aqueous watery or water-based

cytoplasm material in a cell, excluding the nucleus

aggregate clump together
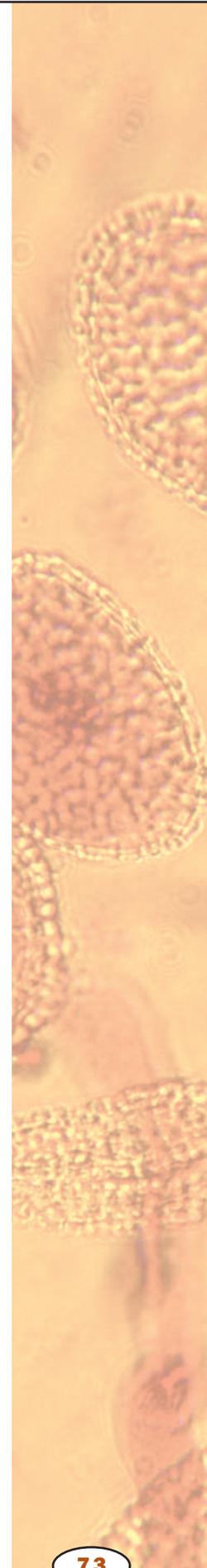
Three-dimensional view of a cell membrane.
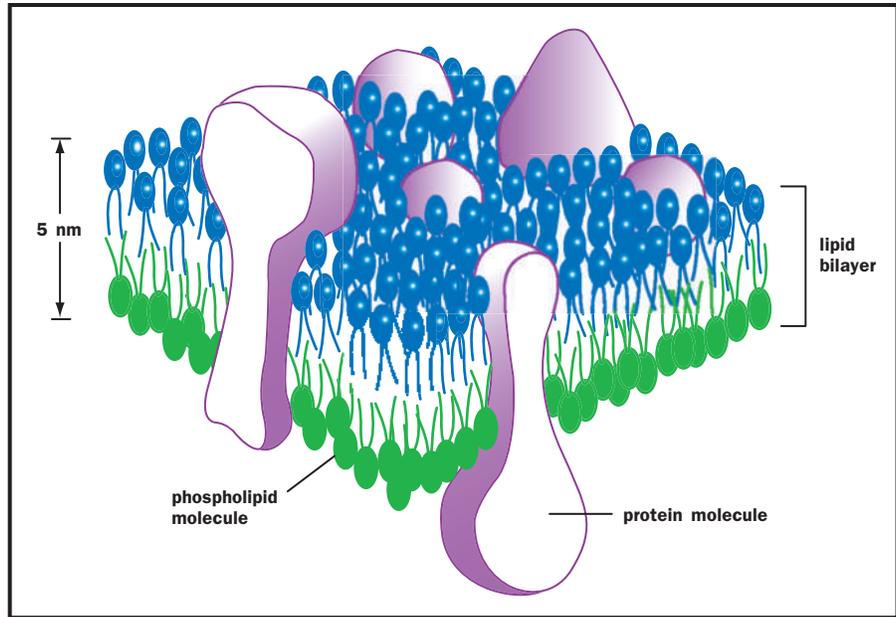
Grendel strongly suggested plasma membranes actually consist of lipid bilayers. When they extracted the lipid from plasma membranes of different mammals, they found just enough to make a monolayer with approximately twice the surface area of the cells from which the lipid was obtained. Thus, they concluded the cells were covered with a membrane consisting of a symmetrical lipid bilayer.

More recent studies indicate the lipid composition of one monolayer or leaflet of a membrane may differ somewhat from that of the other, introducing a degree of asymmetry into what is essentially a symmetrical structure. For example, phospholipid containing the sugar inositol as its polar head is found predominantly in that half of the bilayer facing the cytoplasm, whereas lipid containing longer, more complex saccharides (called glycolipids) are found exclusively in the extracellular half of the bilayer.

Membrane Properties

The amphipathic nature of the phospholipid components generates the bilayer organization of a cellular membrane and also provides its three basic properties. First, a bilayer lipid membrane is stable: that is, once formed it stays formed and is unlikely to disintegrate. Such stability results from the weak interactions among the nonpolar tail regions and from the tendency of highly dipolar water molecules to exclude nonpolar molecules from their midst. Thus, bilayers can be thought of as being formed, in part, by the self-adhesiveness of water and its tendency to compact and segregate any substance that is not equally polar.

Second, a lipid membrane tends to prevent passage of polar substances; thus, a membrane forms a boundary and compartmentalizes regions of cytoplasm containing relatively water-soluble and nonamphipathic **solutes**, such as **ions**, sugars, **amino acids**, and **nucleotides**, and much larger molecules, such as **proteins**, that are unable to pass easily across it. The third and perhaps most important property of membranes is their dynamic

solute dissolved substance

ion an electrically charged particle

amino acid a building block of protein

nucleotide the building block of RNA or DNA

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

nature. A membrane will bend and fold; it can be deformed without breaking. Under special circumstances, such as occurs in **vesicle** fusion or budding, a bilayer can be broken. When this happens, it very quickly reseals. Moreover, and most important, at room temperature a membrane's constituents are in constant, random motion. In brief, the amphipathic nature of its lipid constituents makes a membrane both a stable and a fluid boundary.

vesicle membrane-bound sac

Clearly, advantages are conferred on cells and **organelles** by their being compartmentalized and by the boundary nature of their membranes. Separated from each other, these compartments can differentiate to carry out specialized functions, precisely because the reactants, products, **enzymes**, and other factors appropriate for these functions are compartmentalized. Moreover, compartmentalized functions are more easily regulated and controlled.

organelle membrane-bound cell compartment

enzyme protein that controls a reaction in a cell

No benefit comes without a price, however, and although compartmentalization is a fundamentally important feature of cells, the boundary nature of membranes poses problems as well. For one, a completely impenetrable boundary would stifle cells and their organelles. Thus, lipid membranes are modified to allow various water soluble substances, such as nutrients and waste products, to move from one side to the other. For another, cells and their organelles receive signals across their membranes, and these signaling functions modify the basic phospholipid bilayer structure. Also, cells are anchored to their environments—to other cells or to the extracellular **matrix** (ECM)—and organelles are attached to various cytoskeletal elements. Directed movement of both cells and organelles are possible when these anchorages and attachments are transient rather than permanent. For the most part, the protein components of membranes serve these additional functions of transport, signal conduction, and anchorage and attachment.

matrix a network, usually of threadlike fibers

Membrane Proteins

Proteins are very important components of membranes, although molecule for molecule they may be relatively minor constituents compared to the vastly greater numbers of membrane lipids. There are three types of basic membrane proteins. Integral membrane proteins (IMP) completely span the bilayer and have regions exposed to both the cytoplasm and to the extracellular environment (or in the case of organelles, to the interior or lumen environment). IMPs may span the membrane once or multiple times, and typically they carry out transport, signaling, and anchoring/attachment functions. Peripheral membrane proteins (PMP) are attached to the membrane, usually to integral membrane proteins, by electrostatic or **hydrogen bonds** at either their cytoplasmic or extracellular (or lumenal) surfaces; these surfaces are often referred to, respectively, as the C- or the E-face of the membrane. Peripheral membrane proteins are involved primarily in anchoring or attachment.

hydrogen bond weak bond between the H of one molecule or group and a nitrogen or oxygen of another

Finally, lipid-anchored proteins (LAP), as their name implies, are covalently bound to membrane lipids and are found associated with either the C- or the E-face of the membrane. **Enzymatic** and signaling functions are performed by LAPs. In addition to facilitating specific functions, these modes of associations modulate the basic lipid bilayer structure of the membrane.

enzymatic related to function of an enzyme

Fluid Mosaic Model

The modern view of membrane structure, known as the fluid mosaic model, was developed in 1972 by S. J. Singer and G. L. Nicholson and reflects three basic features of membrane structure. Integral membrane proteins, when viewed from above one surface or the other, contribute a mosaic or "pebbled" pattern to a membrane, and these proteins and the membrane lipids are capable of **lateral** movement in the plane of the membrane, due to the fluid nature of lipid association. Lipid-anchored proteins are also potentially mobile as well, moving by virtue of their association with mobile lipids.

lateral side-to-side

Any lateral movement of IMPs or LAPs may be constrained, however, by their associations with peripheral membrane proteins in the form of cytoskeletal elements or, outside the cell, in the form of the ECM. Moreover, certain IMPs may be constrained by association with IMPs of adjacent cells in a tissue. These associations reflect the anchoring or attachment functions served by membrane proteins.

A third important feature of membrane structure is its asymmetry. Thus, different peripheral membrane proteins are found associated with the extracellular or cytoplasmic faces of membranes and, in turn, are attached to regions of IMP exposed, respectively, at the extracellular and the cytoplasmic membrane surfaces.

hormone molecule released by one cell to influence another

conformation three-dimensional shape

affinity attraction

Membrane asymmetry is also evident in the orientation of IMPs responsible for transmembrane signaling. For example, a **hormone** binding to the portion of an IMP exposed on the E-face of the plasma membrane can cause the transmembrane portion of the IMP to undergo a **conformational** change that results in a change in binding **affinity** in the portion exposed at the C-face. The cytoplasmic region of the IMP might then exhibit enzymatic activity, change the enzymatic activity of another protein with which it associates, or attach or detach from a cytoskeletal element as a result of extracellular hormone binding.

polysaccharide carbohydrate composed of many individual units of sugar

Bacteria and plant cells are surrounded by a relatively static and inflexible layer of **polysaccharides** called a cell wall, which is exterior to the plasma membrane and should not be confused with it. SEE ALSO BACTERIAL CELL; CELL WALL; CYTOSKELETON; LIPIDS; MEMBRANE PROTEINS; MEMBRANE TRANSPORT; PLASMA MEMBRANE; SIGNALING AND SIGNAL TRANSDUCTION

Chris Watters

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aqueous watery or water-based

organelle membrane-bound cell compartment

solute dissolved substance

vesicle membrane-bound sac

Membrane Transport

Biological membranes are the structures that divide biological space into functional **aqueous** compartments: cells and their **organelles**. To allocate hundreds of different **solutes** to their proper locations, cells equip their various membranes with multiple transport mechanisms, some simple and some complex. (Use of membrane **vesicles** for endocytosis and exocytosis is covered elsewhere.)

Membrane Diffusion

The simplest kind of transport is the unassisted diffusion of solutes across membranes (see Figure 1a). The kinds of molecules that transit in this fashion are more soluble in oil than water and so readily dissolve in and then spontaneously traverse the nonpolar **lipid** core of the membrane **bilayer**. Among these diffusible lipid-soluble molecules are **steroid hormones**, many kinds of drugs, the oxygen that cells **respire**, and the carbon dioxide they expire.

Motion of all kinds must be impelled by some form of energy. In the case of simple membrane diffusion, movement across the bilayer is a random walk driven by the kinetic (heat) energy provided by the collisions of the solute with surrounding molecules. This is the Brownian motion that agitates all molecules. Random diffusion causes the solute molecules to end up at equal concentrations on the two sides of the membrane no matter how great the initial difference (gradient) was. Solute transport by these means is thus said to be downhill.

Membrane Channels

Most cellular solutes have a **polar** chemical structure and are therefore strongly attracted to water. Consequently, these water-soluble molecules tend not to enter the lipid core of the membrane readily; indeed, the bilayer is designed keep them from doing so. To transport these solutes across the barrier, membranes are equipped with a variety of special **protein** structures.

The simplest way to convey water-soluble solutes across membranes is through channels: membrane-spanning proteins with central pores. By these means, selected solutes diffuse downhill across membranes, passing single file along a narrow column of water molecules in these pores. Driven by random Brownian diffusion, a solute will ultimately reach an equal concentration in the two aqueous compartments.

Channels can discriminate among solutes. They use the diameter of their pores as a sieve and place critical **amino acid** side chains along the pore to give it the proper shape and chemical profile. As a result, different channels strongly prefer Na^+ or K^+ or Ca^{++} or H^+ and pass cations much better than anions; another channel is specialized for Cl^-. Some channel families conduct larger solutes into cells; for example, nutrients like amino acids or sugars. There are also elaborate channels that enable newly synthesized

lipid fat or waxlike molecule, insoluble in water

bilayer composed of two layers

steroid hormone group of hormones that includes estrogen, testosterone, and progesterone

respire use oxygen to burn cellular fuel

polar partially charged, and usually soluble in water

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

amino acid a building block of protein
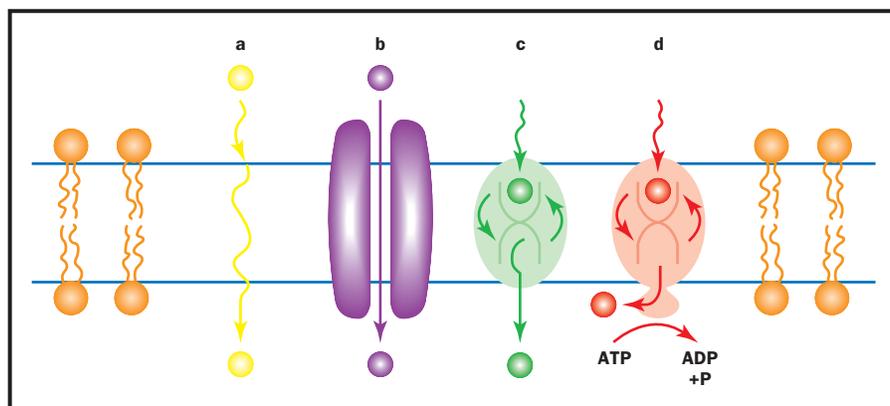
Figure 1. Modes of membrane transport. a) Some solute molecules can diffuse unassisted through the lipid bilayer. b) Certain solute molecules can diffuse though the aqueous pore of a specific channel protein. c) Reciprocating transporters can convey selected solute molecules across the bilayer by means of a fluctuating change in their shape. d) The energy released by the breakdown of ATP molecules can be coupled by a transport protein to pumping specific solute molecules against their concentration gradient.

polypeptide chain of amino acids

conformation three-dimensional shape

secretion material released from the cell

axon long extension of a nerve cell down which information flows

ion an electrically charged particle

gradient difference in concentration between two places

enzyme protein that controls a reaction in a cell

substrate the molecule acted on by an enzyme

cytoplasm material in a cell, excluding the nucleus

metabolite molecule involved in a metabolic pathway

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

polypeptide chains to slither across the membrane in an extended **conformation**; they then fold up into mature proteins on the other side. This is the basis for protein **secretion**.

Among the most interesting kinds of channels are those along the **axon** or at the synapses of nerve cells. When turned on for a few milliseconds by a stimulus, these proteins allow small numbers of Na⁺ or K⁺ to diffuse across the membrane. These pores open as the result of a change in the structure of the channel protein, typically brought about by one of two mechanisms: (1) the association of a specific neurotransmitter molecule to a binding site on the channel protein (at the synapse); or (2) a change in the electrical field across the membrane (along the axon). In both cases, the consequent movement of **ions** through these activated channels alters the electrical charge across the membrane, causing channels nearby to open. This electrical cascade is what propagates excitation along a nerve.

Reciprocating Transporters

Animal cells have membrane transporters that "carry" specific nutrients down their concentration **gradients**. These transport proteins work like an engine with a four-step cycle. The first step is for the membrane-bound transporter to bind a solute molecule outside of the cell. Each kind of transporter is selective for a specific solute family, just as an **enzyme** acts only upon certain **substrates**. Discrimination comes from the close-fitting association of the solute with a pocket in the protein, like a key in a lock or a hand in a glove. The shape of the transporter molecule fluctuates constantly; driven, once again, by Brownian (thermal) motion within the fluid membrane. In the second step, the right twists and turns cause the protein to "swallow" the solute, reorienting it from the outside to the interior of the cell. Third, the solute diffuses away from the transporter into the **cytoplasm**. Finally, the empty transporter reorients to its initial shape, so that its solute binding site again addresses the cell exterior. The protein is then ready for the next cycle.

Such transporters convey **metabolites** such as **glucose** and amino acids in the bloodstream (where they are at high concentration) to the cell's cytoplasm (where they are being consumed). Their activity can be regulated according to need, often through the action of hormones. For example, when excess glucose is available, the hormone insulin is released from the pancreas into the bloodstream. This hormone signals muscle cells to bring their glucose transporters into play; these convey the sugar into the cells, returning the blood glucose level to normal.

This mode of transport utilizes the energy of Brownian motion in two ways: molecular collisions not only propel solute molecules up to and away from the transporter but also drive the protein to change its shape, back and forth, between its two functional orientations. No matter how well designed, these reciprocating transporters can only equalize the concentration of a solute between the two compartments the membrane separates. That is, random motion cannot gather up every molecule of a nutrient outside a cell or expel every molecule of waste from the interior of a cell. If the cell needs to take up or pump out a solute beyond its equal distribution, it must apply energy. The methods of transport just described are therefore referred

to as "passive transport." Mechanisms requiring applied energy are often called "active transport."

Active Transport

Cells draw upon metabolic energy to drive solutes across membranes against their concentration gradients. For example, K^+ is continuously pumped into human cells as Na^+ is pumped out. One source of energy used by these active transporters is the universal cellular currency, adenosine triphosphate (**ATP**). To tap its energy, plasma membrane–spanning proteins split the ATP to a simpler form (adenosine diphosphate plus phosphate). Instead of allowing the released energy to dissipate as heat, the cleavage step is coupled to the movement of the solute. To accomplish this, the breakdown of the ATP is performed in a pocket of the transporter such that the release of its energy forces the protein into an altered shape. This strain in the protein drives the solute to move "uphill" against its concentration gradient across the membrane, opposite the direction it would spontaneously diffuse. Indeed, the ATP molecules will not be split by the protein unless the solute is being transported simultaneously; the two processes are inextricably coupled through the transporter. A significant fraction of cellular energy is expended in this way.

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

Membrane Energetics

The conversion of sunlight to electricity by solar panels is a new, "green" alternative to fossil fuels, but nature got there first. Billions of years ago, a membrane transport system evolved that converts solar energy into cellular energy. In this device, photons of sunlight are captured by chlorophyll and other pigments in the membrane. The energy trapped thereby is then used by membrane proteins to force negatively charged electrons away from positively charged protons, separating them across the bilayer. This charge separation turns the membrane into an electrical battery. The potential energy stored in these membranes can then be harvested by proteins that couple it to energy-consuming cellular processes, just as batteries can be used to power a flashlight.

One major use of the potential energy created by separating protons from electrons across membranes is to drive the synthesis of ATP. ATP then powers other metabolic processes, such as the formation of glucose (the major product of photosynthesis), or the transport of solutes discussed in the preceding section. In addition, the **membrane potential** can itself be directly coupled to pumping certain solutes against their concentration gradient (active transport). In those cases, the downhill diffusion of protons across the membrane provides the energy to pump other solutes uphill. (Picture a paddle wheel that taps a mountain stream for energy to grind grain.) Such membrane potentials also propel bacterial swimming by powering the rotation of their propellerlike flagella. Membrane potential energy is thus a currency as universal as ATP or glucose.

membrane potential electrical and chemical differences across a membrane leading to storage of energy and excitability

Finally, consider how the body's cells extract energy from glucose. On a gross level, glucose reacts with the oxygen the lungs breathe, yielding energy as well as the carbon dioxide and water the body respires. But this "burning" of glucose is tightly coupled by membrane transport proteins to the pumping of protons and electrons across membranes. Then, just as in
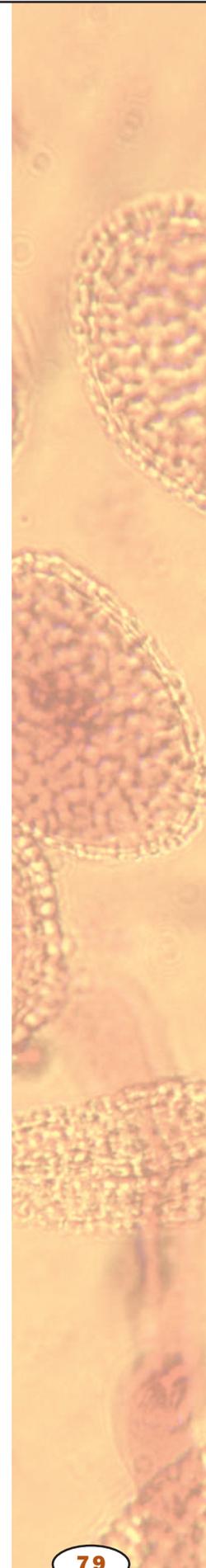
photosynthesis, the membrane potential is tapped by other membrane proteins to make ATP or to drive active transport or to enable bacteria to swim. SEE ALSO BLOOD SUGAR REGULATION; ENDOCYTOSIS; ENZYMES; EXOCYTOSIS; ION CHANNELS; MEMBRANE STRUCTURE; METABOLISM, CELLULAR; NEURON; NUCLEAR TRANSPORT; ORGANELLE; PHOTOSYNTHESIS; SYNAPTIC TRANSMISSION

Theodore L. Steck

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Mendel, Gregor

Czech geneticist
1822–1884

Gregor Johann Mendel was born on July 22, 1822, in what is now Hyncice, Czech Republic. He entered a monastery in what is now Brno, Czech Republic, and performed a famous and important series of breeding experiments while at the monastery. Mendel died on January 6, 1884, in Brno.

Mendel is often referred to as the father of genetics because his work set the foundation upon which modern biology, and especially genetics, is based. Numerous scientists during Mendel's time were studying the heritability of various traits. However, much of this science was descriptive and qualitative. Mendel's work, as reported in 1866, differed from that of others in four major ways: (1) his choice of material, (2) his careful observations, (3) his mathematical approach to the analysis of the data, and (4) his inductive leap used to explain his results.

In his genetic experiments, Mendel chose garden peas because they had many traits that appeared in two forms, because they grew quickly, and because he could perform both out-crosses (fertilization between two different plants) and self-crosses. He always began his crosses with plants that were **true breeding**, thus ensuring that all parents were uniform in their genetic contribution. Mendel usually followed the inheritance of only one trait in a given cross, and he was careful to distinguish parents and **progeny** in his analysis.

In all, Mendel examined seven different traits that each had two different forms, such as green versus yellow seeds. One form of each trait disappeared in the progeny of a cross; this form he referred to as recessive. The form that remained in the first generation of progeny was called dominant. However, when these progeny, all of whom expressed the dominant form, were allowed to self-pollinate, the recessive trait reappeared in about one-fourth of the progeny in the next generation. To explain these results, Mendel hypothesized that each individual had two bits of information for a trait, and that these bits of information separated from each other in the formation of the reproductive cells. This hypothesis has now become known as the Law of Segregation.

Gregor Mendel.

true breeding giving only offspring identical to the parents

progeny offspring

true-breeding
dominant

A   A

a   Aa   Aa

true-breeding
recessive

a   Aa   Aa

all identical
progeny

A   a

A   AA   Aa

a   Aa   aa

one-fourth show
the recessive trait
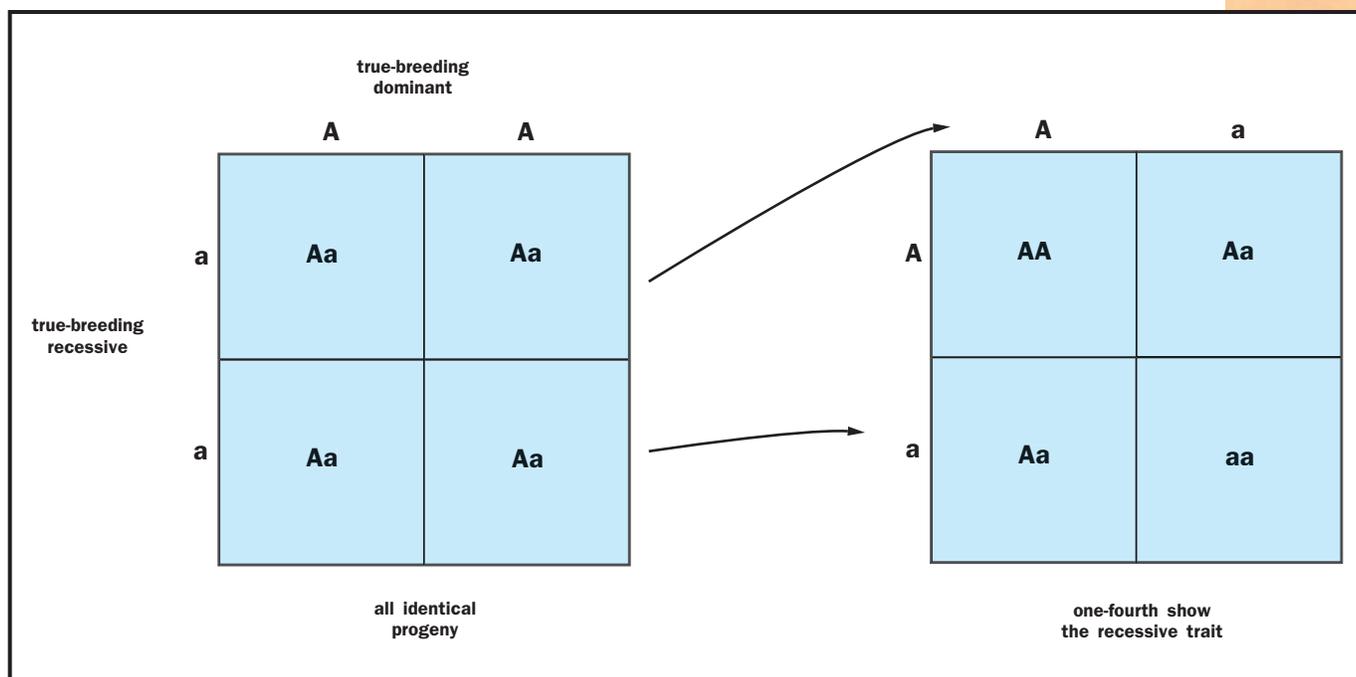
When Mendel crossed plants that differed in two traits, such as seed color and seed texture, he observed that each trait behaved independently of the other trait. This observation has become known as the Law of Independent Assortment. Scientists now know that not all traits assort independently. Some traits tend to stay associated because they are located on the same **chromosome**.

Mendel's theories went almost unread and uncited for thirty-five years, possibly because his mathematical explanations were foreign and confusing to many of the scientists of his time. In the early 1900s, three scientists independently rediscovered his work. Mendel's work now serves as the prototype and cornerstone for modern genetic analysis and much of modern biology. His work has allowed investigators to explain evolution in terms of changes in the frequencies of **alleles** and genes. SEE ALSO GENE; HISTORY OF BIOLOGY: INHERITANCE; MODEL ORGANISMS: CELL BIOLOGY AND GENETICS

William R. Wellnitz

Cross between true-breeding dominant and true-breeding recessive.

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

allele a particular form of a gene

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Meristems

Plants have the impressive abilities to reproduce asexually and regenerate damaged parts. The secret to these abilities lies within a tissue type called meristem. Meristematic cells are fully developed and functional at maturity,

but unlike other cells in the plant, they remain totipotent. This means that when induced, they can develop into any specific plant tissue at any point during the life of the plant. Other cells in the plant are fully differentiated (meaning that they are specialized in both form and function) and do not divide. Cells in the meristem, however, divide and produce all of the new cells in a plant.

While meristem tissue is the source of the regenerative potential of a plant, meristems also play a pivotal role in normal plant growth. Plants have the unique ability to continue to grow and develop new organs while functioning as a mature, reproducing organism. Plants grow larger via cell division and cell elongation. Simple plant growth is facilitated by meristem tissue because it is the primary site of cell division (mitosis) in the plant. Plants develop new organs (stems, leaves, flowers, roots) via cell division and cell differentiation. Because the source of all new cells in a plant is the meristem, this tissue plays an important role in organ development as well. While some of the cells of the **apical meristem** divide to generate new meristematic cells, most of the offspring cells differentiate into specialized cell types that stop dividing and function as a part of the organ in which they were generated.

Meristems and Simple Plant Growth

Plants have meristematic tissue in several locations. Both roots and shoots have meristematic tissue at their tips called apical meristems that are responsible for the lengthening of roots and shoots. The shoot apical meristem is formed during embryonic development, but after germination gives rise to the stem, leaves, and flowers. The root apical meristem is also formed during development, but during germination gives rise to the root system. Cell division and cell elongation in the apical meristem is called primary growth and results in an increase in plant height and root length. Increasing root length enables the plant to tap into the water and mineral resources of a new region or layer of soil. Increasing shoot length makes the plant taller, thus allowing it better access to sunlight for photosynthesis.

Many types of plants also increase the diameter of their roots and stems throughout their lifetime. This type of growth is called secondary growth and is the product of **lateral** meristem. Lateral meristem is called the vascular cambium in many of the plants in which it is found. Secondary growth gives a plant added stability that allows for the plant to grow taller. Lastly, some plants have intercalary meristem. These are areas of plants that help in the regeneration of parts of the plant that have been damaged by predators or the environment. Intercalary meristems produce growth at the base of grass blades, for instance.

Meristem tissue is not autonomous. Throughout the life of the plant, the rate of cell division and cell elongation in the meristems is regulated by plant **hormones**. For example, giberellins stimulate cell division in shoot apical meristem, causing the plant to grow taller. These hormones also cause cell elongation in intercalary meristem of grasses. Cytokinin and auxin are also important growth regulators. Auxin stimulates growth by inducing cell elongation, while cytokinins are thought to stimulate both cell division and cell elongation.
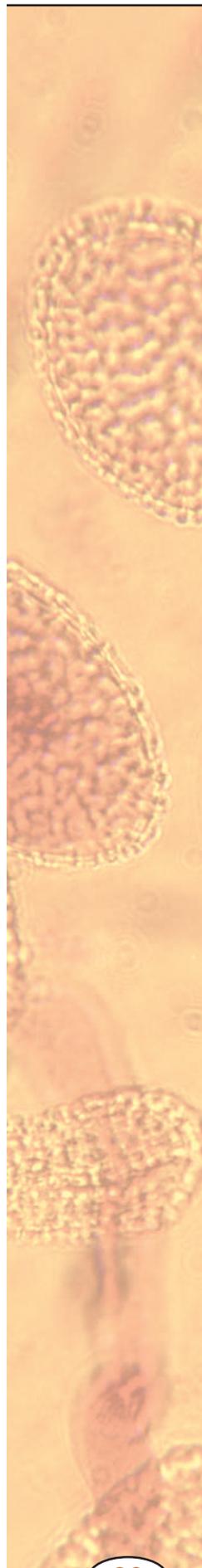
apical meristem growing tip from which all plant tissues arise

lateral side-to-side

hormone molecule released by one cell to influence another
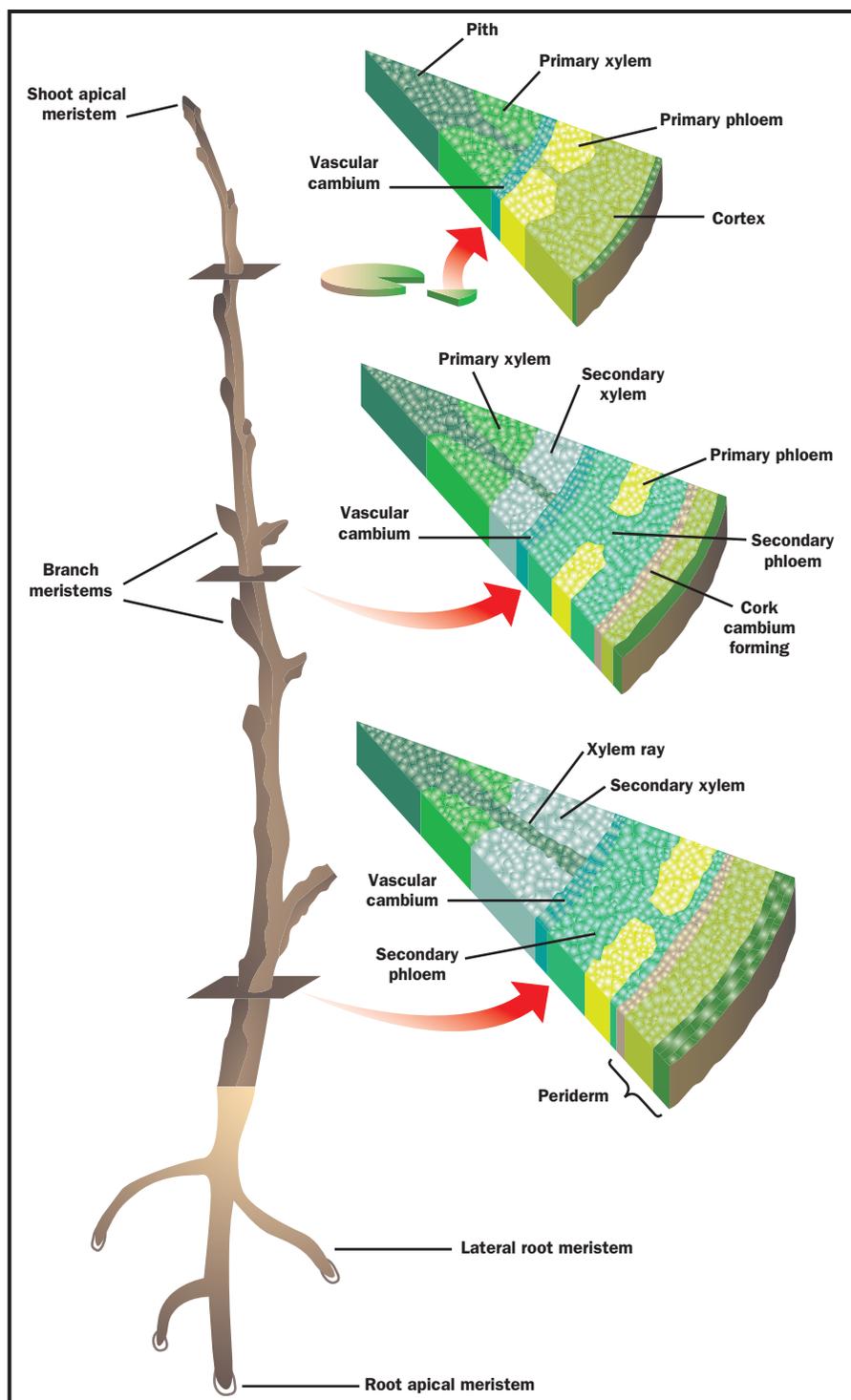
Meristem locations, with cross-sections of vascular tissues.

Shoot apical meristem

Pith

Primary xylem

Primary phloem

Vascular cambium

Cortex

Primary xylem

Secondary xylem

Primary phloem

Vascular cambium

Secondary phloem

Cork cambium forming

Branch meristems

Xylem ray

Secondary xylem

Vascular cambium

Secondary phloem

Periderm

Lateral root meristem

Root apical meristem

Apical Meristems and Pattern Formation

As the source for all new cells of the growing plant, the meristem plays an important role in the formation of new organs and in the correct placement of those organs within the plant body. The process by which this organization happens is called pattern formation and, in plants, is directed by the meristem. To accomplish this task, meristematic cells must be able to interpret their position in the plant and establish a certain fate.

For example, during the development of a new leaf, the dividing cells of the meristem must differentiate into several different functional types of epidermal cells and parenchyma cells. However, they do not need to differentiate into reproductive cells like those found in a flower. How is it that meristematic cells "know" what to become? The actively dividing cells of the apical meristem use positional cues such as hormones and cell-cell interactions as guides during differentiation. Moreover, these positional cues result in the activation of certain genes and the inactivation of other genes in a set of cells, thus initiating their specific differentiation pattern based on their spatial location in the plant. The specific genes that are initially activated in meristem cells during this process are called homeotic genes. These genes encode a family of **transcription factors** that, once activated, will determine the fate of a cell by activating and inactivating a whole host of other genes.

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

gene expression use of a gene to create the corresponding protein

transcription messenger RNA formation from a DNA sequence

translation synthesis of protein using mRNA code

One mechanism of differential **gene expression** (the activation and inactivation of genes during differentiation and organ development) is binding of plant hormones to the developing cell's surface. Hormones such as cytokinins have been shown to affect ribonucleic acid (RNA) **transcription** and **translation**. It is thought that the presence of both cytokinins and another class of hormones, called auxins, are important for proper root and shoot development. In the laboratory, if a set of undifferentiated meristem cells are grown in culture, they will not develop into a plant embryo unless they are stimulated with auxin and cytokinin. A high cytokinin/auxin ratio will stimulate the meristematic cells to develop stems, leaves, and flower buds. On the other hand, a high auxin/cytokinin ratio will stimulate the meristematic cells to develop roots. SEE ALSO ANATOMY OF PLANTS; DIFFERENTIATION IN PLANTS; GENETIC CONTROL OF DEVELOPMENT; HORMONES, PLANT; ROOTS; SHOOTS; WATER MOVEMENT IN PLANTS

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Metabolism, Cellular

Cellular metabolism is the sum total of all the biochemical reactions taking place within a cell. It includes all the reactions involved in degrading food molecules, in synthesizing **macromolecules** needed by the cell, and in generating small precursor molecules, such as some **amino acids**, for cellular needs. It also includes all reactions involving electron transfers (oxidation-reduction, or redox, reactions). Metabolism takes place in sequences of biochemical reactions called pathways.

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

amino acid a building block of protein

Metabolic Pathways

Metabolic pathways can be simple linear sequences of a few reactions, or they can be extensively branched with reactions converging on or diverging from a central main pathway. They can be cyclic, with a precursor of an early reaction regenerated at the end of a pathway (for example, the **Krebs cycle** of **aerobic** respiration, or the Calvin cycle of photosynthesis). Some pathways serve multiple purposes. For example, the Krebs cycle is best known for its role in oxidizing sugars and other **organic** molecules to provide adenosine triphosphate (**ATP**) for the cell, but it is also used as a source of precursor molecules for cellular biosynthesis. Clearly, evolution has repeatedly used existing metabolic pathways to provide novel functions.

All biochemical reactions are **catalyzed** by **proteins** called **enzymes**; for most reactions, there is one enzyme that catalyzes only that reaction. Enzymes can be exquisitely regulated by the cell, providing a high degree of control of cellular metabolism. The activity of enzymes is often sensitive to the amount of specific molecules in the cell. For example, enzymes involved in producing ATP are often inhibited by ATP; when the cell has sufficient amounts of this **metabolite**, therefore, the pathways that produce it are turned off, thereby preventing wasteful reactions. Alternatively, these same enzymes may be strongly activated by ATP's precursor, adenosine diphosphate (**ADP**), levels of which become elevated when the cell is doing work and needs rapid generation of ATP. This pattern of regulation by molecules that are either precursors of or products of a pathway is common in cellular metabolism.

Anabolism and Catabolism

Metabolism is divided into two broad categories. Catabolism, or the degradation of molecules, usually involves removing electrons from molecules (oxidation) and is generally accompanied by the release of energy. Anabolism, or the synthesis of complex molecules, usually involves enriching molecules in electrons (reduction) and generally requires the cell to expend energy in the form of ATP. Reactions that yield energy, such as most catabolic reactions, are called exergonic, whereas those that require an input of energy, such as most **anabolic** reactions, are called endergonic.

The main function of the anabolic pathways is to synthesize the four classes of macromolecules needed by the cell: **polysaccharides**, **lipids**, nucleic acids, and proteins. Although these four categories are chemically distinct, they are all synthesized by the same general type of reaction, condensation synthesis of individual small subunits (monomers) into the macromolecules (polymers). In a condensation reaction, a hydrogen atom is removed from one **monomer**, and a **hydroxyl** group from the other, forming water. A new bond is formed between the two monomers where the water was removed:

$$\text{—A—OH} + \text{H—A—} \rightarrow \text{H}_2\text{O} + \text{—A—A—}$$

For example, nucleic acids such as DNA and RNA are synthesized from their monomers, **nucleotides**, by condensation synthesis. Polysaccharides and proteins are produced in a similar fashion from their monomers, sugars and amino acids, respectively. Lipids, the fourth class of macromolecule, are somewhat different. Unlike the other macromolecules, which are

Krebs cycle central metabolic pathway in mitochondria

aerobic with oxygen, or requiring it

organic composed of carbon, or derived from living organisms

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

catalyze aid in the reaction of

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

metabolite molecule involved in a metabolic pathway

ADP adenosine diphosphate, the low-energy form of ATP

anabolic characteristic of a reaction that builds complex molecules from simpler ones, and requires energy

polysaccharide carbohydrate composed of many individual units of sugar

lipid fat or waxlike molecule, insoluble in water

monomer "single part"; monomers are joined to form a polymer

hydroxyl chemical group consisting of -OH

nucleotide the building block of RNA or DNA
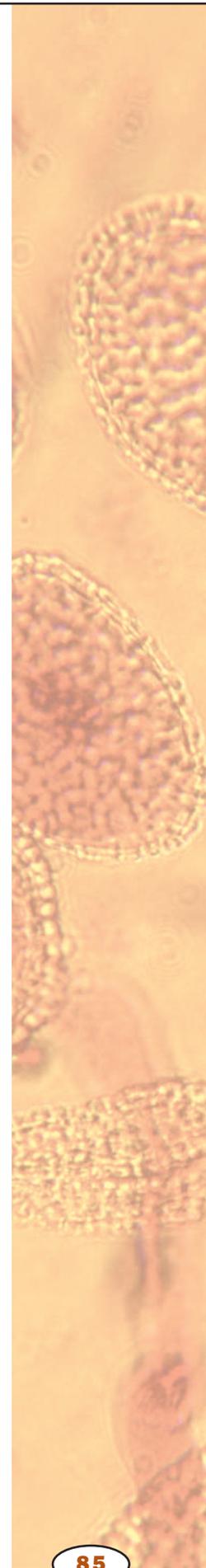
A scanning electron micrograph of an intestinal epithelial cell showing two lysomes that contain digestive enzymes that destroy damaged molecules. One category of metabolism is catabolism, the degradation of molecules.
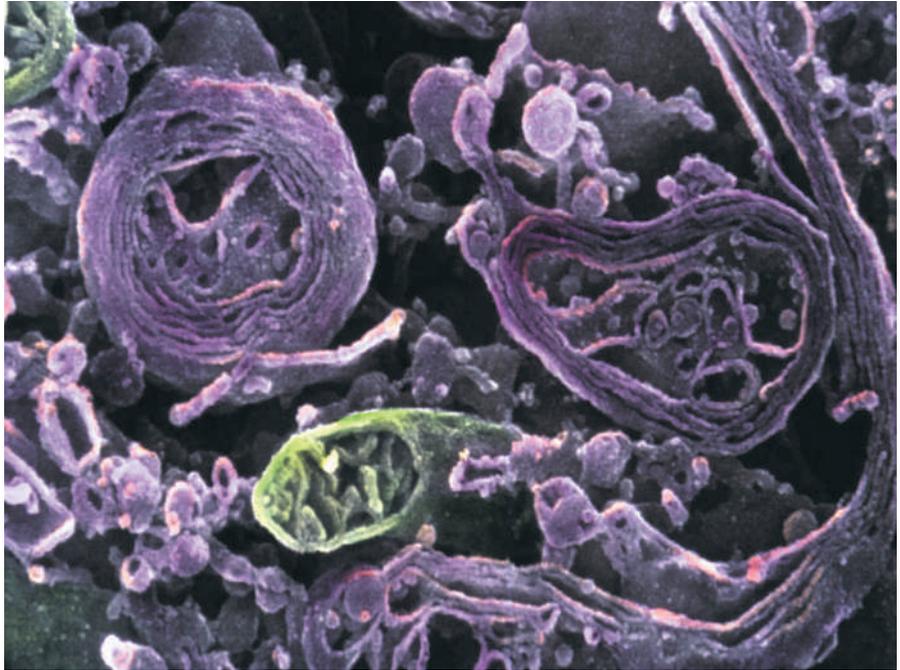
composed of long chains of monomers, most lipids have only three or four different molecular subunits, most important of which are the fatty acids. The fatty acids are not directly joined to each other, but are joined to another molecule such as glycerol (for fats and oils). However, the fatty acids are joined to glycerol by the same kind of dehydration reaction as in the other groups of macromolecules.

hydrolysis splitting with water

The reverse of condensation synthesis is **hydrolysis**, in which a water molecule is added to a bond between two monomers, breaking it and separating the monomers. One of the hydrogens from water becomes attached to one of the monomers, and the hydroxyl that remains is attached to the other:

$$H_2O + \text{—A—A—} \rightarrow \text{—A—OH} + \text{H—A—}$$
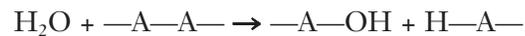
For example, nucleic acids are degraded to their monomers when water is inserted between the individual nucleotide monomers, breaking the bond that joins them. Hydrolysis reactions are a type of catabolic reaction, although they do not usually directly produce ATP; they do, however, produce monomers that often are further catabolized to generate ATP.

Turnover

Metabolism is a dynamic process. The cell is continuously degrading and synthesizing molecules. In general, the catabolic pathways are providing energy in the form of ATP that is used to drive the anabolic processes. This is necessary since endergonic reactions, in order to proceed, require an input of energy, which they obtain from ATP. This is accomplished by coupling the endergonic reaction to the hydrolysis of ATP to ADP and **inorganic** phosphate, an exergonic reaction. As long as the amount of energy required is less than the amount released by ATP hydrolysis, the coupled reactions will proceed.

inorganic not bonded to carbon

The dynamic nature of metabolism results in constant degrading and rebuilding of most cellular materials. For example, proteins exist in a cell for relatively brief times, ranging from minutes to weeks, with most proteins having average life spans of a few days. Structural proteins generally last longer than enzymes, but they too are eventually degraded and synthesized anew. Likewise, other cellular materials are turned over in a similar fashion. This constant turnover of cellular materials keeps the cell in good condition. Molecules that may have been damaged by, for example, being partially oxidized, will sooner or later be degraded and replaced.

Cellular metabolism is the most fundamental level where the dynamic properties of life begin to appear. The complex interactions of diverse pathways, their regulation, and their organization demonstrate the exquisite refinement of the biochemistry of life. All processes that occur within individual organisms can be traced to the pathways of cellular metabolism. SEE ALSO CARBOHYDRATES; CONTROL MECHANISMS; ENZYMES; GLYCOLYSIS AND FERMENTATION; KREBS CYCLE; LIPIDS; NUCLEOTIDES; PROTEIN STRUCTURE

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Metabolism, Human

Metabolism means the sum of all chemical changes in a cell or the body of an organism. It has two subdivisions: catabolism and anabolism.

Catabolism (from the Greek *cata*, meaning "down") consists of all those reactions in which large molecules are broken down into smaller ones, with a release of energy from their chemical bonds. Examples include the digestion of a **protein** into **amino acids** that the body can absorb from the diet and use in its own metabolism, and the breakdown of stored **glycogen** in the liver to supply energy between meals. These breakdown processes are known chemically as **oxidation** reactions.

Anabolism (from the Greek *ana*, meaning "up") consists of all those reactions that assemble small molecules into larger ones and store energy in the newly formed chemical bonds. Examples include the assembly of amino acids into muscle proteins and the synthesis of glycogen and fat for energy storage. These synthetic processes are known chemically as reduction reactions.

Metabolic Rate

Metabolic rate means the amount of chemical energy liberated in the body per unit time. Chemical energy is measured in calories (the amount of energy that will heat 1 gram [0.035 ounce] of water by 1 degree Celsius [1.8 degrees Fahrenheit]), although a calorie is such a small unit that it is more practical to think in terms of kilocalories (kcal). One kilocalorie is 1,000 calories, or what dietitians (and food labels) call a Calorie with a capital *C*. Metabolic rate is generally expressed in kcal/hour or kcal/day. A person's

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

amino acid a building block of protein

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

oxidation reaction characterized by loss of electrons, or reaction with oxygen
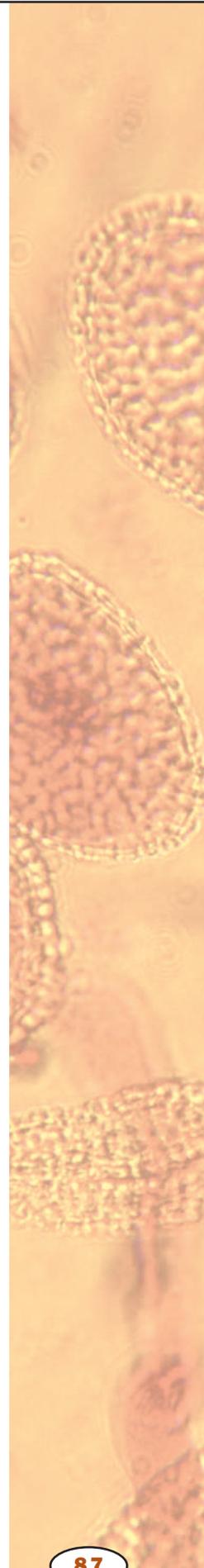
organic composed of carbon, or derived from living organisms

hormone molecule released by one cell to influence another

basal lowest level

metabolic rate can be estimated by having him or her breathe from a spirometer, a device that measures the person's rate of oxygen consumption. Every liter of oxygen consumed represents the release of approximately 4.82 kcal of energy from **organic** compounds such as fat and glycogen. This ratio varies, however, depending on what type of energy-storage molecules the person is oxidizing at the time of measurement.

Metabolic rate depends on such variables as physical activity, mental state, fed or fasting status, and **hormone** levels, especially thyroid hormone. The **basal** metabolic rate (BMR) is a standard of comparison that minimizes such variables. It is measured when a person has not eaten for twelve to fourteen hours and is awake, relaxed, and at a comfortable temperature. It is not the minimum rate needed to keep a person alive; the metabolic rate is lower than the BMR when one is asleep. Total metabolic rate (TMR) is the BMR plus the added energy expenditure for movement and other activities. Metabolic rate is elevated not only by physical activity but also by eating, anxiety, fever, pregnancy, and other factors. Factors that reduce the TMR below normal include depression, apathy, and prolonged starvation.

The TMR is higher in children than in adults. Consequently, as people approach middle age, they often gain weight even with no change in food intake. Weight-loss diets tend to be frustrating not only because most of the initial weight loss is water, which is quickly regained, but also because the TMR declines with time; as the diet progresses, fewer calories are burned and one begins to synthesize more fat even with a stable caloric intake.

The average young adult male has a BMR of 2,000 to 2,500 kcal/day, and the average female slightly lower. Thus, one must consume this many calories per day just to sustain such essential processes as the heartbeat, respiration, brain activity, **muscle tone**, renal function, and active transport through cell membranes. The **central nervous system** accounts for about 40 percent of the BMR and the muscular system for 20 to 30 percent. Even a relatively sedentary lifestyle requires another 500 kcal/day, and hard physical labor, as in farming or manufacturing, may require up to 5,000 kcal/day.

muscle tone low-level, constant muscle contraction

central nervous system brain and spinal cord

Metabolic States

Two metabolic states, absorptive and postabsorptive, are defined by the time elapsed since food intake and by corresponding changes in the body's energy processing.

The absorptive (fed) state lasts for about four hours during and after a meal. It is a time when the body is absorbing digested nutrients, using some of them to meet immediate energy needs, and converting the excess to energy storage products. This state is regulated mainly by the hormone insulin, which promotes cellular uptake of glucose (blood sugar) and amino acids; glucose oxidation; and the synthesis of glycogen (glycogenesis) and fat (lipogenesis). Because of the rapid cellular uptake of glucose, the blood glucose level falls under the influence of insulin. Insulin is thus called a hypoglycemic hormone (from *hypo*, meaning "low"; *glyc*, meaning "sugar"; and *em*, meaning "blood").

The postabsorptive (fasting) state prevails in the late morning, late afternoon, and overnight; that is, when one has not eaten for four hours or longer. During this time, the stomach and small intestine are empty, and the body's metabolic needs must be met from stored fuel. The postabsorp-
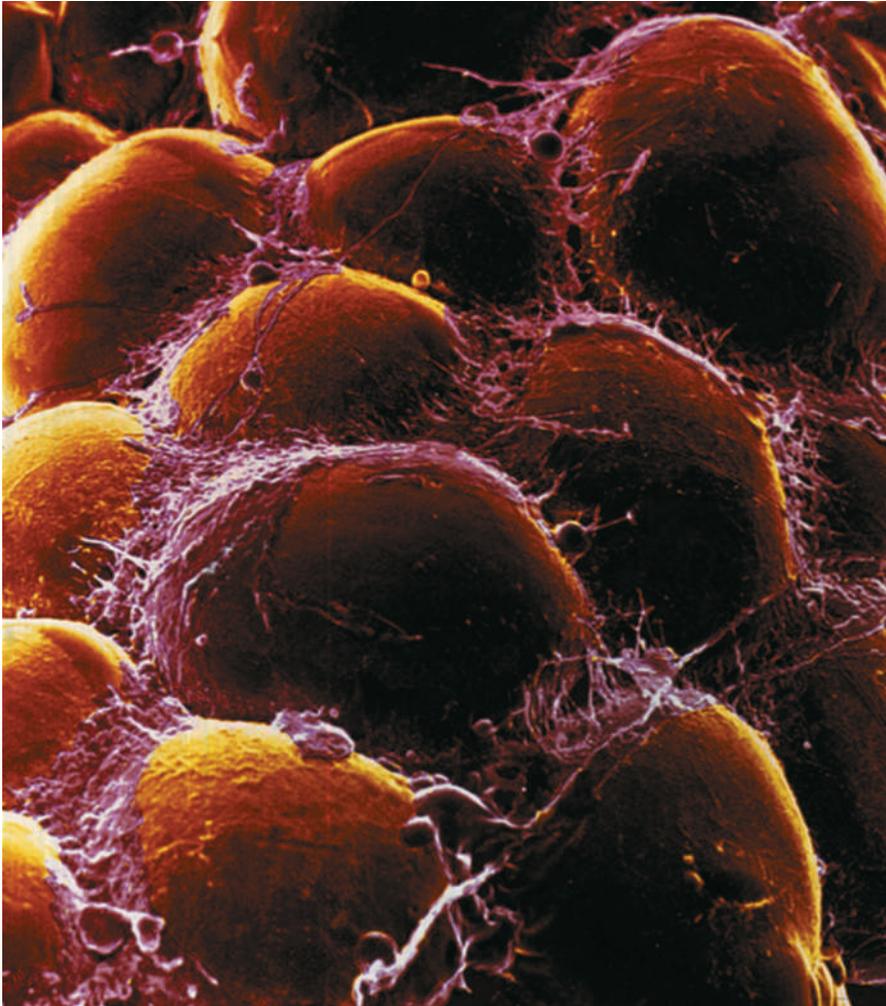
A scanning electron micrograph of fat cells that make up adipose connective tissue. The sympathetic nervous system issues commands to adipose tissue that mobilizes fuels such as glucose and fatty acids.

tive state is dominated by hyperglycemic hormones, which raise the blood glucose level and thus make glucose available to the brain and other organs that require it. Hyperglycemic hormones include glucagon, cortisol, growth hormone, epinephrine, and norepinephrine. Collectively, these hormones promote glycogen breakdown (glycogenolysis), fat breakdown (lipolysis), and the synthesis of glucose from amino acids and fats (gluconeogenesis).

The **sympathetic nervous system** also plays a major hyperglycemic role, issuing nerve fibers to liver, adipose tissue, and muscular tissue that directly stimulate glycogenolysis and lipolysis. The sympathetic nervous system is involved especially in conditions of fear, anger, injury, and other forms of stress. Thus, it mobilizes fuels such as glucose and fatty acids to meet the demands of the "fight or flight" state and tissue repair and recovery. SEE ALSO BLOOD SUGAR REGULATION; CARBOHYDRATES; DIGESTION; GLYCOLYSIS AND FERMENTATION; HORMONES; KREBS CYCLE; LIPIDS; METABOLISM, CELLULAR; OXIDATIVE PHOSPHORYLATION

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

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Microbiologist

Microbiologists are scientists who investigate the world of microscopic organisms including all bacteria, protozoa, and viruses, along with some algae and fungi. The microbes studied can be found everywhere from thermal hot springs (more than 100 degrees Celsius) to Antarctic ice shelves (less than 0 degrees Celsius). Therefore, microbiologists can be found everywhere.

Microbiologists are often associated with determining the microbes involved with causing disease, but their work extends into every other facet of life. Working variously as immunologists, epidemiologists, etiologists, chemotherapists, and microbial taxonomists, microbiologists identify, control, and prevent organisms from causing disease. Microbiologists can study transfer of genetic information from one organism to another (genetics) or the control of chemical **metabolism** inside organisms (physiology). Industrial applications using microbes can vary greatly. Microbiologists can use microscopic organisms for bioremediation (cleaning the environment), pharmaceutical uses (discovery and production of antibiotics), food microbiology (using microbes to produce/protect food and beverages), and fermentation technology (production/manufacture of products like vitamins and **enzymes**).

Microbiologists can work for a wide range of employers in either the public or private sector. Public sector employers include many federal governmental branches, along with state and county health departments. The private sector includes pharmaceuticals (e.g., Eli Lily), genetic engineering companies (e.g., Monsanto), biotechnology firms (e.g., Promega), food and beverage industries (e.g., Budweiser), and chemical supply/manufacture companies (e.g., Sigma).

Degrees held by microbiologists can vary greatly from a high school diploma to a doctorate degree. The majority of microbiologists have at least an undergraduate degree in biology. More specific degrees are available in fields such as epidemiology, microbiology, virology, mycology, biochemistry, and food microbiology. Associate degrees or training programs may

metabolism chemical reactions within a cell

enzyme protein that controls a reaction in a cell

A quality control microbiologist inspects a bacteria culture from ground meat processed at a slaughterhouse.

help train microbiologists to work in hospital departments such as microbiology (identifying organisms), chemistry (profiles of patient physiology), cytology (identifying abnormal cells), and blood banks.

In order to prepare, students in high school could take classes in the following subjects: microbiology, health sciences/terminology, basic and advanced biology and/or chemistry, and biochemistry. SEE ALSO BACTERIAL DISEASES; BIOTECHNOLOGY; EPIDEMIOLOGIST; PLANT PATHOLOGIST; PLANT PATHOGENS AND PESTS; PROTOZOAN DISEASES; VIRAL DISEASES

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Microscopist

A microscopist is any scientist or technician who routinely uses a microscope in his or her work. While beginning students usually have some experience with simple light microscopes, there are many types of more sophisticated microscopes for special purposes, such as phase contrast and fluorescence light microscopes, scanning and transmission electron microscopes, and tunneling electron microscopes that can see even down to the level of individual molecules. These types of microscopes require specialized training to be able to prepare specimens properly, use the microscope, and record the images.

Many scientists who work in anatomy, **cytology**, and other fields employ technicians to maintain and operate specialized microscopes, and employment opportunities for microscopists are abundant. Positions for technicians typically require a bachelor of science degree, although some are available with only a high school diploma and on-the-job training, an associate's degree, or certification from a training program in areas such as electron microscopy. Independent research in microscopy usually requires a master's degree or doctorate.

cytology study of cells

Microscopists are employed by universities, medical schools, hospitals, museums, industries, and government agencies. Microscopists work not only in biology but also in medicine, chemistry, geology, materials science, electronics, **forensic** science, food science, and other fields.

forensic related to legal proceedings

To prepare for a career in microscopy, one should take four years of high school science and mathematics; biology, chemistry, physics, and geology are all related to microscopy. Further training on the job or in college may involve physics (especially optics and electromagnetism), electronics, photography (for photomicrography and microcinematography), and histotechnique (slicing and staining tissues for microscopic examination). Biology, geology, chemistry, and physics are among the appropriate choices of a college major; a minor in photography or astronomy would also enhance one's qualifications. One's hobbies can also provide a good grounding for a career in microscopy; for example, photography (especially close-up nature photography), photoprocessing, and astronomy (which employs
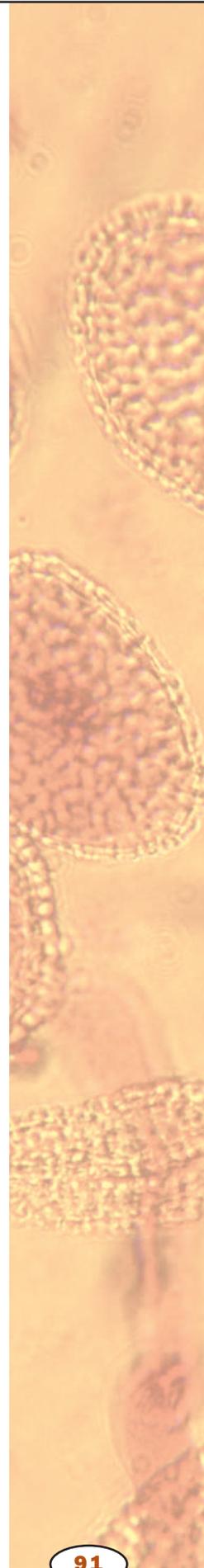
similar principles of optics). SEE ALSO ELECTRON MICROSCOPY; LEEUWEN-HOEK, ANTONY VAN; LIGHT MICROSCOPY

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Migration

Many animals move from one place to another at certain times of the year or during a particular period of their life cycle. These movements are often referred to as migration. Some animals, such as many species of insects, migrate only once during their lifetime, often just before they reproduce. Other animals, including many species of birds and many marine animals, such as sea turtles and whales, migrate long distances to their breeding grounds many times during their lives.

Animals migrate for several reasons. In some cases, animals can only reproduce in a particular habitat, such as sea turtles and sea birds that must return to land in order to lay their eggs. In other instances, animals are forced to leave an area when conditions in the environment deteriorate. Many bird species that nest in Canada and the northern regions of the United States migrate south as winter approaches. The ultimate reason these birds migrate south is because their food supply (including insects and fish) will not be available during the cold months. However, these birds normally begin migrating south before their food supply has disappeared, and often even before it has begun to decline.

In actuality, it is the changing length of the days (photoperiod) that stimulates hormonal and behavioral changes that result in migration. Such an environmental cue is often referred to as the proximate (or immediate) cause of migration, whereas the inevitable decline in food supply is referred to as the ultimate cause. A bird that waited until its food actually disappeared would not have sufficient body fat reserves to migrate a long distance. Thus, scientists believe that natural selection favored birds that used predictable environmental cues, such as the seasonal change in day length, to initiate migration before their food source disappeared.

Seasonal migrators exhibit obligatory migration, meaning they must migrate every year. For other animals, the decline in the conditions of their environment is not so predictable. For example, owls that live in the tundra and Canadian forests feed on small rodents that are abundant some winters and scarce during others. During winters when rodent populations are high, these owls remain in Canada and do not migrate. However, if rodent populations are low, these owls will migrate down into the northern regions of the United States. Animals such as these owls exhibit facultative migration, meaning migration is optional for them.

A spring tide of surfbirds surge from the mud flats of Alaska's Copper River delta. The strong-flying migrants winter as far south as the Strait of Magellan.

Scientists have been fascinated by how animals are able to navigate during their migration. Studies have shown that migrating species are able to use a wide variety of mechanisms to navigate, including the stars, the sun, olfactory (chemical) cues, and Earth's magnetic field. Some species learn their migration routes by first traveling with experienced individuals, but other species are able to migrate and navigate successfully without prior experience, an ability that still perplexes scientists. Migration requires a lot of energy and many individuals die during migration. Despite these heavy costs, the potential benefits of migration are great, which is why migration behavior has evolved in so many species. SEE ALSO BEHAVIOR PATTERNS; BIRD; FIELD STUDIES IN ANIMAL BEHAVIOR; TUNDRA; TURTLE

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Mimicry, Camouflage, and Warning Coloration

Many predators search for their prey with their eyes. As a result, many prey species have evolved special body coloration to reduce their chance of being eaten. For example, many prey species blend in with their environment, making it difficult for the predators to find them. These species use camouflage as their first line of defense. Another word for this type of defense is "crypsis" or "cryptic coloration." Cryptic coloration is especially common in small animals such as insects, lizards, snakes, and frogs. These animals are often the same color as the leaves or twigs on which they rest. Some insects even look like the twigs or leaves themselves. It is important to remember that crypsis is not just a morphological adaptation, but that behavior

An Indian leaf butterfly exemplifying cryptic coloration.

plays a very important part as well. Crypsis works only if the animal is resting on the appropriate background and usually only when the animal isn't moving.

Many small animals have evolved toxic chemicals that make the creature poisonous to eat. Interestingly, many of these species are brightly colored, making it easy for the predators to see them. Scientists believe that the bright coloration has evolved to help the predator, often birds, remember that the species is poisonous. For example, if a bird eats a poisonous butterfly or frog, it will get very sick. In some cases, the poison is released so quickly that the bird will spit the prey out and avoid swallowing it. In either case, it is probably easier for the bird to remember to avoid this species in the future if the prey is distinctively colored. Experiments have shown that it often takes only a single encounter with a toxic prey species for a predator to learn to avoid it. Warning coloration, sometimes referred to as aposematic coloration, is found in a wide variety of animals, including insects, mites, spiders, and frogs.

One problem with being defended by toxic chemicals is that the animal has to use energy to make the chemicals, energy that could otherwise be used for such things as growth and reproduction. Some animals have evolved a way to enjoy the benefits of warning coloration without the costs. These animals mimic the coloration of the poisonous animals. This type of mimicry is referred to as Batesian mimicry, named after the nineteenth-century British naturalist who first described it. The best-known example of Batesian mimicry in the United States and Canada is probably the Viceroy butterfly that looks remarkably like the poisonous Monarch butterfly. The two species are unrelated and the caterpillars feed on different plants and do not look anything like one another. However the adults of both species look so similar that most people, and more importantly, most birds, cannot tell them apart. It is important that the Batesian mimic be less common than the toxic model species. For example, if the Viceroy were more common than the Monarch, birds would end up eating a lot of Viceroys before eating a Monarch and would not "learn the lesson" the coloration acts to teach. SEE ALSO ADAPTATION; NATURAL SELECTION; POISONS; PREDATION AND DEFENSE

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Mitochondrion

organelle membrane-bound cell compartment

eukaryotic cell a cell with a nucleus

Mitochondria (singular mitochondrion) are abundant **organelles** present in nearly all **eukaryotic cells**. The main function of mitochondria is to produce adenosine triphosphate (ATP), the cellular energy source. Mitochondria are believed to be the evolutionary result of early anaerobic (nonoxygen-using) eukaryotic cells engulfing aerobic (oxygen-utilizing) bacteria, resulting in a symbiotic relationship between the two organisms. The eukaryotic cells received ATP in exchange for supplying nutrients to the engulfed bacteria, and the bacteria provided ATP and allowed the eukaryotic

cell to survive in the increasing oxygen atmosphere present early in Earth's history.

Evidence for Bacterial Origin

The bacterial origin of these organelles is evident in the structure of the mitochondrion, its method of reproduction, and its genetics. Mitochondria are generally oval to elongated in shape, like bacteria, and are approximately 0.5 to 1 **micron** in diameter. Two membranes like those present in many types of bacteria surround the mitochondrion.

Animal mitochondria possess an amazingly simple genetic system. The human mitochondrial **genome** is a circular deoxyribonucleic acid (DNA) molecule (like a bacterial **chromosome**) made up of only 16,569 **base pairs** of DNA encoding thirty-seven genes. The mitochondrial genome is too small to encode all of the genes necessary for the mitochondrion to function. Instead, most of the genes necessary for mitochondrial functions are contained in the nuclear genome. At some point in evolution, these genes were moved from the mitochondrion to the **nucleus** and integrated into the nuclear chromosomes. The mechanism by which this transfer occurred is unknown.

Mitochondria have their own **ribosomes** and transfer ribonucleic acid (tRNA) to make mitochondrial-encoded **proteins** within the mitochondrial matrix (the fluid enclosed by the membrane). The bacterial origins of the ribosome are most evident in the unique sequences of the ribonucleic acid (RNA) and proteins that comprise it. Mitochondrial ribosomes are more like bacterial ribosomes than they are like the **cytoplasmic** ribosomes made in the nucleus. The mitochondrial machineries that make proteins in the mitochondrial matrix and replicate the mitochondrial DNA are also sensitive to several antibiotics that inhibit bacterial growth. The other cellular systems for protein synthesis and DNA replication in the nucleus are not sensitive to these antibiotics, supporting the notion that the mitochondria have their origin in a bacterial ancestor.

Because many of the mitochondrial components are not encoded by the organelle's DNA, but by the nuclear DNA, mitochondria must have mechanisms to take up their components from the surrounding cytoplasm. The mitochondrial proteins encoded by nuclear genes and synthesized on ribosomes in the cytoplasm are transported into the mitochondria by specific machinery found in the mitochondrial membranes. The transport machinery recognizes unique sequences of **amino acids** found only in mitochondrial proteins.

Reproduction

During cell growth, the contents of the cell approximately double to ensure that both daughter cells receive a full set of organelles and cytoplasm in addition to the correct number of chromosomes at cell division. The growth and division of mitochondria is not linked to the **cell cycle**; instead, mitochondria replicate their DNA and divide mainly in response to the energy needs of the cell. When the energy use by a cell is high, the mitochondria grow and divide. When the energy use is low, mitochondria are destroyed or become inactive. At cell division, mitochondria are distributed to the daughter cells more or less randomly by partitioning of the cytoplasm when the cell divides. Mitochondria divide by binary fission similar to bacterial

micron one-millionth of a meter; also called a micrometer

genome total genetic material in a cell or organism

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

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

nucleus membrane-bound portion of cell containing the chromosomes

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

cytoplasm material in a cell, excluding the nucleus

amino acid a building block of protein

cell cycle sequence of growth, replication, and division that produces new cells
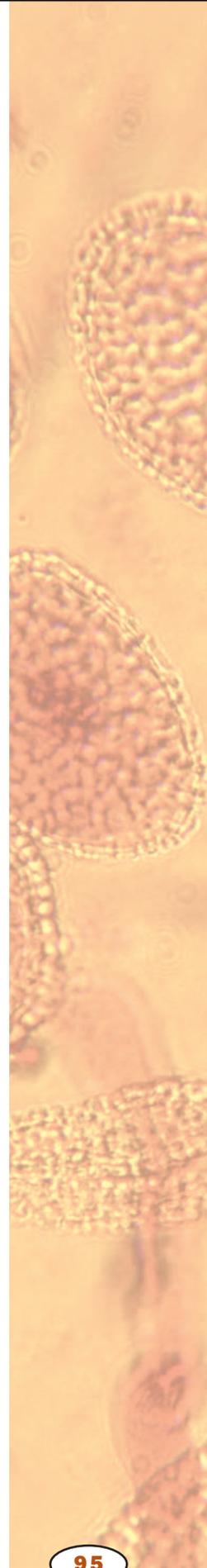
Three-dimensional drawing of the mitochondrion.

Matrix

Inner membrane

Outer membrane

Intermembrane space
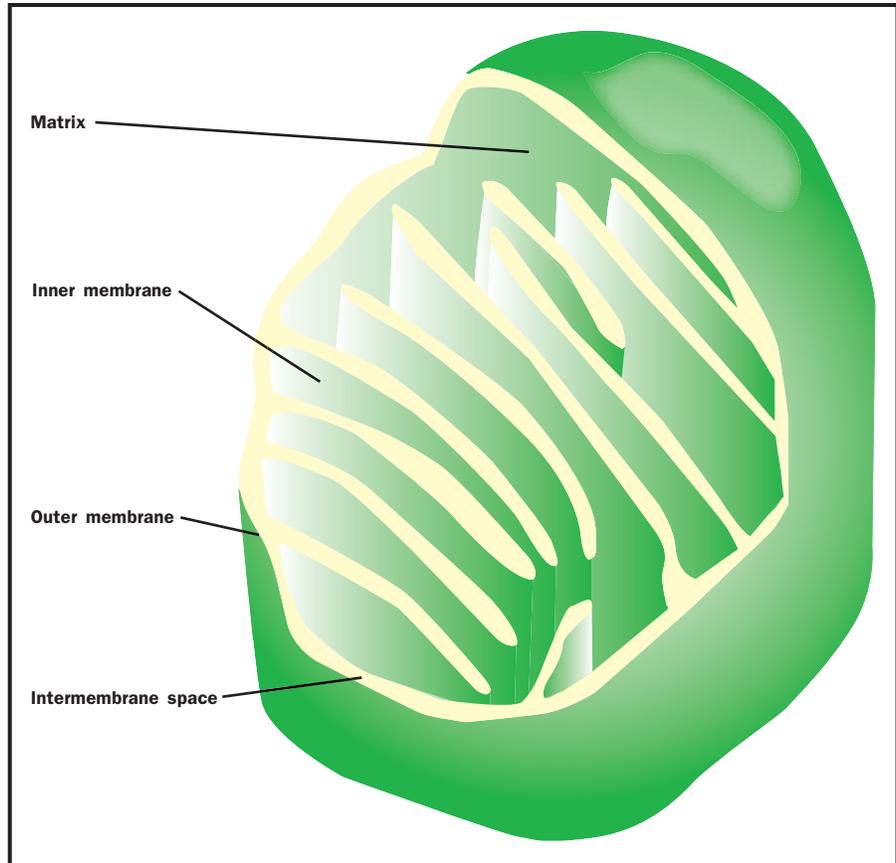
cell division. Unlike bacteria, however, mitochondria can also fuse with other mitochondria.

Membranes and Matrix

organelle membrane-bound cell compartment

The mitochondria are unique **organelles** in that they are surrounded by two membranes, rather than the single membrane that surrounds other non-nuclear organelles in the cell. The outer mitochondrial membrane completely encloses a large internal space called the matrix. The inner mitochondrial membrane is highly folded into structures called cristae, which significantly increase the surface area of the inner membrane. The narrow space between the inner membrane and the outer membranes is known as the intermembrane space. The outer membrane contains a large number of proteins that form pores or channels through the membrane allowing small molecules to pass freely between the intermembrane space and the cytoplasm. These pores make the outer membrane permeable to most **ions** and small molecules; therefore, the intermembrane space has the same ionic composition as the cytoplasm surrounding the mitochondrion.

ion an electrically charged particle

The inner membrane, on the other hand, is relatively impermeable and blocks the movement of ions and other small molecules. Both the inner and outer mitochondrial membranes contain specific transport proteins that can move large molecules or ions across each by both passive active transport. Only those large molecules that have specific membrane transporters are able to enter mitochondria. This allows the mitochondria to create a unique

biochemical environment within the matrix to carry out the energy production reactions.

Mitochondrial Metabolism

ATP is the main source of energy for most processes in the cell, and large quantities must be made for a cell to function. Most cells use simple sugars, such as **glucose**, as their primary energy source. The **metabolism** of glucose begins in the cytoplasm with a process called **glycolysis**. During glycolysis, glucose is processed from a 6-carbon sugar to two molecules of a 3-carbon compound called **pyruvate**. However, glycolysis is an inefficient process, yielding only two ATP molecules for each molecule of glucose metabolized. The pyruvate formed in glycolysis can be further metabolized in mitochondria to gain another thirty molecules of ATP from a single original glucose molecule. In addition to the metabolism of pyruvate, fatty acids derived from dietary fat can also be used by mitochondria to make ATP.

Krebs Cycle. The metabolic functions of the mitochondrion occur within the matrix and the inner mitochondrial membrane. The matrix contains a highly concentrated mixture of the **enzymes** of the Krebs, or citric acid, cycle and enzymes for the degradation of fatty acids. Pyruvate and fatty acids from the cytoplasm are actively transported into the mitochondrial matrix by specific membrane transporters that span both the outer and the inner membranes. Inside the matrix, both pyruvate and the fatty acids are first converted to an activated 2-carbon compound called acetyl-Coenzyme A that is the starting point of the **Krebs cycle**. The enzymes of the Krebs cycle process the acetyl CoA, removing high-energy electrons that will be used as an energy source to produce ATP. The high-energy electrons from the Krebs cycle are stored on the specialized carrier molecules that carry the electrons from the matrix to the inner mitochondrial membrane.

Electron Transport Chain. The high-energy electrons from the Krebs cycle are passed to a series of three large protein complexes located in the inner mitochondrial membrane, known as the electron transport chain. Each complex is made up of several proteins organized to form a pathway that moves electrons through the complex. The electrons from the Krebs cycle enter the chain at a very high energy and gradually give up part of their energy as they move through the electron transport chain. The energy from the electrons is used to pump hydrogen ions across the inner mitochondrial membrane from the matrix to the intermembrane space by active transport. This creates a chemical and electrical **gradient** across the inner membrane, storing energy in much the same way a battery does.

Low-energy electrons that emerge from the end of the electron transport chain are combined with an oxygen atom forming one molecule of water for every two electrons that pass through the chain. Because of the similarity to respiration by the body (inhaling oxygen and exhaling carbon dioxide), the Krebs cycle and the electron transport chain together are sometimes referred to as cellular respiration. The CO_2 that humans exhale is a product of the Krebs cycle, and the oxygen humans breathe in is used as the final electron acceptor in the electron transport chain.

ATP Synthesis. The electrochemical gradient is harnessed to produce ATP by an enzyme in the inner membrane called ATP synthase. As the

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

metabolism chemical reactions within a cell

glycolysis initial stages of sugar breakdown in a cell

pyruvate the ionized form of pyruvic acid, a key intermediate in cell metabolism

enzyme protein that controls a reaction in a cell

Krebs cycle central metabolic pathway in mitochondria

gradient difference in concentration between two places

Defects in mitochondrial genes are responsible for numerous maternally inherited diseases, including a number of muscle diseases (myopathies).

The maternal inheritance of mitochondria is being used to trace human evolutionary groups back to their African origins.

ADP adenosine diphosphate, the low-energy form of ATP

cytoskeleton internal scaffolding in a cell, composed of protein

fertilization union of sperm and egg

zygote fertilized egg

lineage ancestral line

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

eukaryotic cell a cell with a nucleus

cytoplasm material in a cell, excluding the nucleus

hydrogen ions flow back down their concentration gradient into the matrix through the ATP synthase complex, the energy released is used to add a phosphate group to adenosine diphosphate (**ADP**) to make adenosine triphosphate. Because the actions of the electron transport chain and ATPase are tightly linked, the combination of the two is referred to as oxidative phosphorylation. In fact, some types of mitochondria uncouple the movement of electrons through the electron transport chain from ATP syntheses by shuttling electrons back across the inner membrane. Since the energy is not used to make ATP it can be released as heat energy. Such mitochondria are found in "brown fat" in babies and hibernating animals, and are an important source of heat.

Within a cell, mitochondria are typically positioned near areas of high ATP use such as near the contractile apparatus of muscle cells or wrapped around the whiplike tail of the sperm. The positioning of mitochondria within a cell is at least partially due to attachment to the microtubule **cytoskeleton**. The cytoskeleton is a very dynamic scaffold within the cytoplasm, constantly growing and retracting. As it grows and retracts, it drags along attached organelles such as mitochondria. Destruction of the microtubules with specific drugs leads to a disorganized arrangement of the mitochondria that is restored when the cytoskeleton is allowed to reform.

Inheritance

Mitochondrial genes are not inherited by the same mechanism as nuclear genes. At **fertilization** of an egg by a sperm, the egg nucleus and sperm nucleus each contribute equally to the genetic makeup of the **zygote** nucleus. However, all of the mitochondria, and therefore all the mitochondrial genes, are contributed to the zygote by the egg. At fertilization of an egg, a single sperm enters the egg along with the mitochondria that it uses to provide the energy needed for its swimming behavior. However, the mitochondria provided by the sperm are targeted for destruction very soon after entry into the egg. The egg itself contains relatively few mitochondria, but it is these mitochondria that survive and divide to populate the cells of the adult organism. This type of inheritance is called maternal inheritance and is common to the mitochondria of all animals. Because mitochondria are inherited from the mother only, the sequence of mitochondrial DNA is sometimes used to trace the **lineage** of families. SEE ALSO CELL EVOLUTION; CYTOSKELETON; GLYCOLYSIS AND FERMENTATION; HISTORY OF BIOLOGY: BIOCHEMISTRY; HUMAN EVOLUTION; KREBS CYCLE; METABOLISM, CELLULAR; OXIDATIVE PHOSPHORYLATION; PRIMATE

Stephen A. Adam

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Mitosis

Mitosis is the process of dividing **chromosomes** during cell division in **eukaryotic cells**. Mitosis is followed by cytokinesis, the splitting of the **cytoplasm**. In cell division, a parent cell splits, producing two daughter cells that

are identical to the parent. Eukaryotic unicellular organisms like the protist *Amoeba* use cell division in the production of new individuals, propagating their species. Multicellular eukaryotic organisms, including plants, animals, and fungi, rely on cell division to grow larger by adding new cells. They also use cell division to repair injured or worn-out tissues by replacing damaged cells with new cells.

The function of mitosis is to divide a cell's **nucleus** with its chromosomes into two daughter cell nuclei, each of which inherits the same number of chromosomes as the parent cell. Consider mitosis in human cells, each of which contains forty-six chromosomes.

How does a parent cell with forty-six chromosomes divide to yield two daughter cells each with forty-six chromosomes identical to those of the parent? The eukaryotic parent cell first copies, or replicates, its chromosomes prior to mitosis. Rather than ninety-two chromosomes, however, this replication process yields forty-six chromosomes, each composed of two parts, called sister **chromatids**, that are genetically identical to each other. The sister chromatids are connected to each other at a point called the **centromere**.

During mitosis, the **nuclear envelope** dissolves, and sister chromatids separate at the centromere, becoming two individual daughter chromosomes, each now with only one chromatid. By the end of mitosis, these daughter chromosomes are segregated from each other to opposite poles of the cell and become enclosed within two separate daughter nuclei. Following mitosis, cytokinesis divides the cell into two, with two sets of **organelles** and two daughter nuclei, forming two separate but identical cells.

Specifics of Mitosis

Mitosis is a continuous process that is often divided into four sequential phases known as prophase, metaphase, anaphase, and telophase. These phases can be distinguished through microscopic analysis. Several critical steps in mitosis are controlled by **phosphorylation** or dephosphorylation of proteins.

Prophase. Prior to mitosis, chromosomes appear in the nucleus as a tangled mass of thin strands (chromatin) and are not distinguishable from each other as separate entities. During prophase, the chromosomes condense into shorter and thicker rodlike structures that can be easily seen to consist of two sister chromatids connected by a centromere. This is thought to be driven by addition of phosphate groups to the **histone** proteins of the chromosome.

Another major event in prophase is the organization of what is known as the mitotic spindle. This too is thought to be driven by phosphorylation. Prior to mitosis, a special area of the cytoplasm near the nucleus, known as the centrosome, contains a pair of small cylindrical bodies called centrioles. The centriole pairs replicate and then the two pairs of centrioles begin to move with their centrosomes to opposite poles of the cell. During prophase, they continue their migration to the cell's poles and organize parts of the cell's cytoskeleton (the scaffold that maintains the cell's shape) into the mitotic spindle. The spindle consists of microtubules that reach from each centriole pair across the cell toward the other pair.

FLEMMING, WALTHER (1843–1905)

German physician and cell biologist who first described the process by which cells divide and separate their chromosomes. He named this process "mitosis." At the time of his work, 1882, no one knew that the chromosomes carried the units of heredity, genes.

nucleus membrane-bound portion of cell containing the chromosomes

chromatid a replicated chromosome before separation from its copy

centromere region of the chromosome linking chromatids

nuclear envelope double membrane surrounding the cell nucleus

organelle membrane-bound cell compartment

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

histone protein around which DNA wraps to form chromosomes
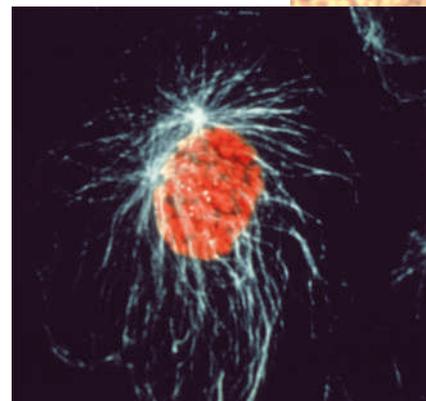
Prophase.
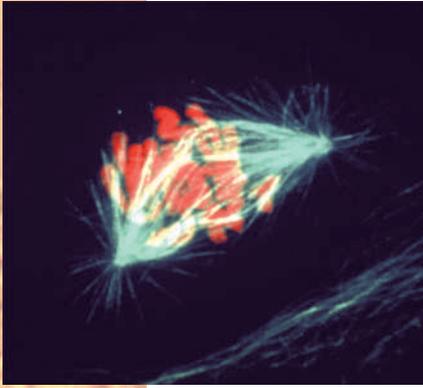
Metaphase.
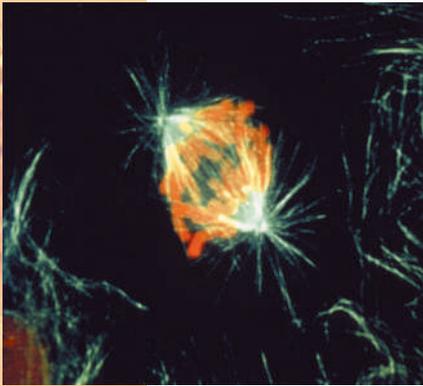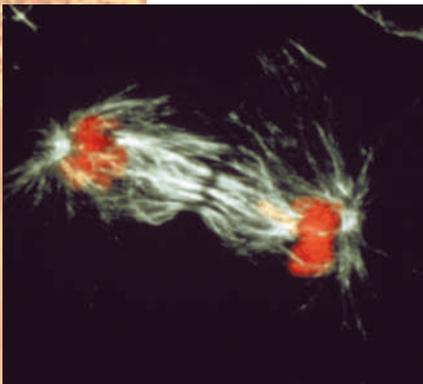
Anaphase.

Telophase.

Prometaphase

On either side of the centromere that connects the two sister chromatids of each chromosome, specialized complexes of proteins known as kinetochores form. These act as attachment points between chromosomes and the spindle fibers that are part of the mitotic spindle. Through these attachments, the spindle is able to physically move the chromosomes to opposite poles of the spindle. By the end of prometaphase, the nuclear membrane surrounding the chromosomes begins to break down (triggered by phosphorylation of membrane proteins) and the spindle fibers pull the chromosomes by their kinetochore attachments so that the chromosomes align at the midpoint between the spindle poles.

Metaphase.   During metaphase the chromosomes are fully aligned end to end at the cell's midline at what is known as the metaphase plate. Each kinetochore is attached to spindle fibers emanating from centrioles at opposite poles.

Anaphase.   The attachments between sister chromatids to each other split during anaphase, producing single-chromatid chromosomes. This is triggered by destruction of the phosphorylating proteins discussed earlier. For each pair of single chromatid chromosomes, one of the pair is pulled toward each of the two spindle poles. Meanwhile, the distance between the spindle poles also increases.

Telophase.   During telophase, the nuclear membranes are dephosphorylated and begin to reform around the two sets of chromosomes at either pole, enclosing and separating them from the rest of the cytoplasm. The mitotic spindle disappears. The chromosomes decondense and become thinner and more difficult to distinguish from each other. Cytokinesis begins the process of separating the two daughter cells and is nearly complete by the end of telophase. The end result is the production of two new cells that are genetically identical to each other and to the parent cell.

Differences Between Plants and Animals

Plants use a similar process with a few differences. For example, although a plant cell creates a mitotic spindle and has a centrosome, it lacks centrioles. The other major difference in plants is the way in which cytokinesis occurs. In animal cells, the plasma membrane pinches in along the midline of the cell, creating a cleavage furrow that will separate the cytoplasm in two. Plant cells have rigid cell walls that prevent this. Instead, they use two different approaches for cytokinesis. The plasma membrane and cell wall grow inward together, eventually separating the parent cell into two. Alternatively, the cell wall that will separate the two daughter cells starts growing in the middle of the cell between the two nuclei and continues toward the periphery. This is known as the cell plate. It continues growing until its edges reach the cell's outer surface, separating the parent cell into two daughter cells. SEE ALSO CELL CYCLE; CHROMOSOME, EUKARYOTIC; CYTOKINESIS; CYTOSKELETON; MEIOSIS; NUCLEUS; REPLICATION; SEXUAL REPRODUCTION

Michele D. Blum

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Model Organisms: Cell Biology and Genetics

Model organisms are used to study basic mechanisms common to many forms of life and to experiment with biological processes that may be difficult or unethical to study in humans. Model organisms are usually chosen for some combination of ease of study (for example, the transparent bodies of the **nematode** *Caenorhabditis elegans* or the zebrafish *Brachydanio rerio*), ability to grow and reproduce quickly in a small space (*Arabidopsis thaliana*, a four-inch plant with a life cycle of four to six weeks), prominent cell struc-

nematode worm of the Nematoda phylum, many of which are parasitic

Scanning electron micrograph of the head of a fruit fly (*Drosophila melanogaster*).

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

genome total genetic material in a cell or organism

cell cycle sequence of growth, replication, and division that produces new cells

transduction conversion of a signal of one type into another type

gene expression use of a gene to create the corresponding protein

hormone molecule released by one cell to influence another

ture of interest (the giant **chromosomes** of the fruit fly *Drosophila melanogaster*), or ability to closely model some aspect of human biology (the mammalian **genome** and complex brain of the mouse). Most model organisms combine many if not all of these characteristics.

Escherichia coli bacteria provide an especially important model for studies of gene regulation. Yeast (*Saccharomyces cerevisiae*) are used for a wide variety of studies in eukaryotic chromosome structure and gene regulation, as well as virtually every aspect of cell function, including the control of the **cell cycle** and signal **transduction**. The slime mold *Dictyostelium discoideum* is used to study cell motility and other aspects of cell function, especially those with applications to cancer. *C. elegans* has provided a window on the fate of individual cells during development, as each cell can be followed as it is formed, takes its place, and begins to function. *Drosophila* is central in the study of chromosomes and molecular aspects of development, especially development of the nervous system. Zebrafish and the frog *Xenopus laevis* are used most often to study vertebrate development. *Arabidopsis* is the major model of plant cell biology and genetics. Finally, cultures of human cells are often used to examine response to drugs, effects of genetic mutations, and other aspects of health and disease.

The genomes of each of these organisms are either fully sequenced or soon will be, allowing further investigation of the links between **gene expression** and cell function. This will make these models even more valuable, and also allow investigation of fundamental questions about the similarities and differences among all types of organisms. SEE ALSO MODEL ORGANISMS: PHYSIOLOGY AND MEDICINE

Richard Robinson

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The WWW Virtual Library: Model Organisms. <http://ceolas.org/VL/mo/>.

Model Organisms: Physiology and Medicine

A model organism is a member of an easy-to-study species that is used in experiments to learn how a more complex organism functions. Biomedical research relies heavily on model organisms as stand-ins for humans, but other types of research use these organisms too. For example, the small mustard relative *Arabidopsis thaliana* is a favorite model organism of biologists who work with plants. Most models of the human are vertebrates, such as rodents and primates, but even an organism as simple as a yeast can provide valuable insights and information about life at the molecular and cellular levels.

Model organisms typically have very short life cycles, enabling researchers to observe them over many generations. *Arabidopsis*, for example, has a life cycle of just six weeks or less, giving plant scientists peeks at such activities as flowering, reproduction, defense against pests, and **hormone** signaling. In addition, model organisms can be bred for genetic uniformity and the environmental conditions manipulated, so that researchers can pinpoint the sources of particular responses. Model organisms have been sta-

ples of biomedical research for decades, but they are even more valuable in the twenty-first century because they can be engineered to harbor human genes in each of their cells. An organism that has genes of a different species is termed **transgenic**.

A Rich History

The story of the discovery of the cause of Type I diabetes mellitus illustrates the role of model organisms in human health care. In this condition, the pancreas does not secrete the hormone insulin, leading to **glucose** buildup in the bloodstream, which causes weight loss, weakness, and many other signs, symptoms, and complications. It was once swiftly lethal.

In October 1921, a young surgeon at the University of Toronto named Frederick Banting was pondering earlier work that had shown that removing a dog's pancreas leads to symptoms identical to those of diabetes in humans. Would giving such a dog an extract from a pancreas reverse the symptoms? If the dog's predicament was similar to people with diabetes, might an extract help them, too? Banting and an assistant, Charles Best, addressed these questions in a small lab, with ten dogs. They removed the pancreas from one dog, and it soon developed symptoms. From a second dog, they tied off the pancreas, then removed it and obtained an extract, which they injected into the first dog. It recovered, although only for a day (diabetes requires daily insulin injections). A friend of Banting's became the first person to receive insulin, derived from fetal calves, and within two years insulin replacement therapy was in widespread use. Today, people with Type I diabetes mellitus obtain insulin not from cows or dogs, but from *Escherichia coli* bacteria given genetic instructions to produce human insulin.

Experiments on dogs led to other advances in medical technology, including open heart surgery, cardiac pacemakers, heart transplants, and coronary bypass surgery. Dogs haven't been alone. Diphtheria vaccine was tested on horses, polio vaccine on rabbits, and AIDS (acquired immunodeficiency syndrome) vaccines on chimps, macaques, cats, and mice. Using nonhuman animal models of human genetic diseases is commonplace (dogs for muscular dystrophy, and mice for sickle cell disease, for example).

Choosing an Appropriate Model

Researchers must choose model organisms carefully, or their use can lead to misinterpretations. For many years, microbiologists extrapolated from the widely studied *E. coli* to other microorganisms, missing a great deal of natural microbial variation. Similarly, some vertebrates given human disease-causing genes nevertheless do not develop similar symptoms, due to differences in physiology or **metabolism** between the species. For example, Lesch-Nyhan syndrome in humans causes self-mutilation, yet the same metabolic defect in mice has no apparent effect.

An organism's development must be considered too in selecting a model. Mice, for example, are three thousand times smaller than humans, grow about one hundred times as fast, and age thirty times faster. These differences may explain why cancer treatments that work in mice do not necessarily help people.

transgenic characterized by the presence of one or more genes from a different organism

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

metabolism chemical reactions within a cell
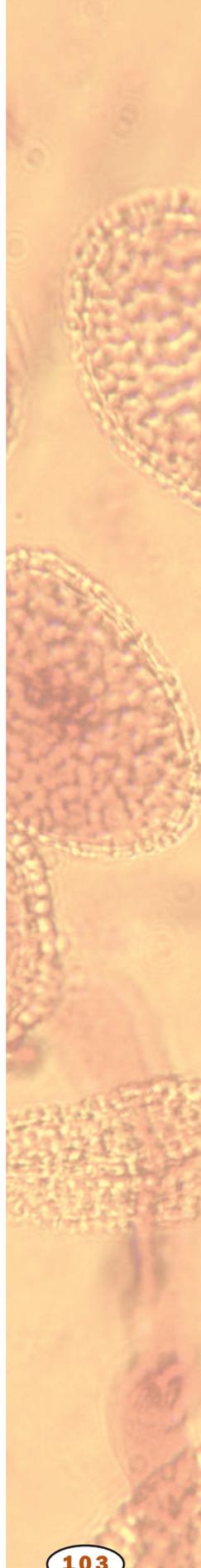
Mice have helped in developing treatments for seizures, multiple sclerosis, AIDS, and rejection of organ transplants.

Mice also do not live long enough to develop degenerative conditions associated with aging in humans. Still, mice are routinely used in preclinical investigations. They have helped in developing treatments for seizures, multiple sclerosis, AIDS, and rejection of organ transplants.

Different species provide different types of information, depending upon how closely they approximate the corresponding human condition. For example, pigs were used to pioneer heart surgery because their cardiovascular systems are remarkably like that of humans, and their organs are similar in size to those of humans. Mice are models for various forms of hereditary deafness, because their inner ears are structurally very similar to those of humans. A varied list of organisms has revealed the earliest stages in building an animal body, including sea urchins, frogs, worms, and fruit flies.

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

In pharmaceutical research, rats have modeled human reproduction, **endocrine** function, nutrition, and cancer. The rat's larger size compared to a mouse enables researchers to sample blood from the same animal over time, and to maintain the animal's body temperature and anesthesia level during surgery, which is much more difficult to do in mice. Rats are also more intelligent, making them useful in behavioral studies, and they tend to have more consistent litter sizes than mice.

Clues in Genomes

genome total genetic material in a cell or organism

Model organisms have proven so integral to research that in the late 1980s, the planners of the human **genome** project insisted that several nonhuman genomes be sequenced first. This enabled researchers to perfect deoxyribonucleic acid (DNA) sequencing technologies, and also provided a treasure trove of genes to which human genes can now be compared. Understanding how a gene functions in one species can provide clues to what it does in the human body, information that can be valuable in developing new ways to diagnose and treat disease.

Since 1995, several dozen genomes have been sequenced, including those of many model organisms. The first step in investigating the function of a human gene is to seek matches in databases of gene sequences from other species. Consider long QT syndrome, an inherited cardiac arrhythmia that causes sudden death in otherwise healthy young adults, usually athletes. Investigation of the nearly identical gene in the fruit fly revealed the cause of the defect-abnormal channels for potassium **ions** in the cell membranes of heart cells. As genomes continue to be sequenced, researchers will be able to ask more questions, and to seek the answers using model organisms. SEE ALSO BLOOD SUGAR REGULATION; DISEASE; HEART AND CIRCULATION; HISTORY OF MEDICINE; HUMAN GENOME PROJECT; ION CHANNELS; MODEL ORGANISMS: CELL BIOLOGY AND GENETICS; PANCREAS; PHARMACOLOGIST; TRANSPLANT MEDICINE; ZOOLOGY RESEARCHER

Ricki Lewis

ion an electrically charged particle

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Mollusk

The Mollusca (mollusks) are a large **phylum** of animals that includes the snails, slugs, clams, squids, and octopi, among others. Most are marine, many are freshwater, and some snails and slugs are terrestrial. The phylum name refers to their soft, pulpy bodies (*mollis* means "soft"). In many cases, the body is protected by a hard shell of calcium carbonate—the seashells familiar to beachcombers and "half shells" familiar to oyster lovers.

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

The shell is secreted by a membrane called the mantle that envelops the body like a cloak. In species without an external shell, such as octopi, the mantle forms an outermost skinlike body covering. The mantle encloses a space, the mantle cavity, which usually contains comblike gills for respiration. In some seemingly shell-less species—squids and cuttlefish—the shell is embedded in the mantle and can be found only by dissection. Most mollusks also have a radula. In snails, this is a tonguelike belt equipped with a few hundred to thousands of chitinous teeth, used to scrape food from surfaces such as rocks.

The most behaviorally sophisticated of all invertebrate animals are the cephalopod mollusks: the octopi, squids, cuttlefish, and nautilus. Cephalopods have long, flexible arms, equipped in most cases with suckers for prey capture. They are active swimmers; some have eyes remarkably similar to human eyes; they have more complex brains than any other invertebrate; and, correspondingly, they exhibit remarkably subtle social behaviors and learning capabilities. SEE ALSO ANIMALIA; OCEAN ECOSYSTEMS: HARD BOTTOMS; OCEAN ECOSYSTEMS: OPEN OCEAN; OCEAN ECOSYSTEMS: SOFT BOTTOMS; VISION

Kenneth S. Saladin

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Monocots

Monocots, or monocotyledons, are a class of the flowering plants, or angiosperms. Monocots are named for and recognized by the single **cotyledon**, or seed leaf, within the seed. The first green blade emerging from the seed upon germination is the cotyledon, which contains sugars and other nutrients for growth until the leaf is able to photosynthesize.

Monocots comprise about 67,000 species, or one-quarter of all flowering plants. They include not only the very large grass family (Poaceae, 9,000 species), but also the orchid family (Orchidaceae, 20,000 species), and the sedge family (Cyperaceae, 5,000 species), as well as palms, lilies, bromeliads (including pineapple), and the Araceae, which includes skunk cabbage and philodendron. The angiosperms have traditionally been divided into monocots and **dicots** alone, but recent work has shown that while monocots form a natural evolutionary group, dicots do not, and so the angiosperms are now grouped into monocots, **eudicots**, and basal angiosperms.

In addition to the single cotyledon in the seed, monocots can be recognized by the arrangement of vascular tissue in the stem. Vascular tissue includes **xylem**, used for water transport from the roots, and **phloem**, which carries sugars and other nutrients from the leaves to other tissues throughout the plant. Unlike other angiosperms, whose vascular tissue is arranged in rings around the periphery, the vascular bundles of monocots are scattered throughout the stem. One consequence of this is that monocots cannot form annual rings of hardened tissue—wood—and so are limited in the strength of their stems. Nonetheless, some monocots, notably the palms, do attain significant height. Leaves of monocots have parallel veins, as seen in grass.

The roots of monocots also differ from other flowering plants. In monocots, the first root to emerge from the seed dies off, and so no strong, central tap root forms. Instead, monocots sprout roots from shoot tissue near the base, called **adventitious** roots. The familiar fibrous root system of grasses is an example of this rooting pattern. Many monocots form bulbs, such as onion, gladiolus, and tulips. These are not root structures, but rather modified stems, made of compact leaves. This can be easily seen in the layers of the onion.

Most monocot flowers have flower parts in sets of three, so that there may be three or six petals, for instance, along with three egg-bearing carpels and pollen-bearing stamens in some multiple of three. The pollen grains of monocots have a single slit, or aperture, which splits open to allow the pollen tube to grow during **fertilization**. In contrast, the pollen grain of eudicots has three apertures.

Orchid flowers are among the most beautiful and complex of all flowers, due in part to their long and specialized relationship with specific pollinators. Some orchid flowers have evolved to resemble the female of the

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cotyledon seed leaf, which stores food and performs photosynthesis after germination

dicot plant having two cotyledons, or seed leaves

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

xylem water-transporting system in plants

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

adventitious growing from a nonstandard location

fertilization union of sperm and egg

An Eastern prairie fringed orchid (*Plantanthera leucophaea*), a type of monocot.
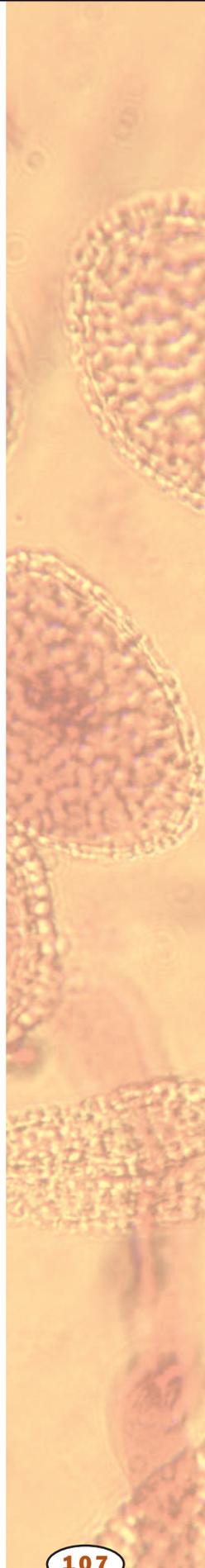
bee species that pollinates them, luring the male in to attempt copulation. During this process, the pollen, all of which is retained in a single, sticky mass, is transferred to the male bee, who will carry it to the next flower in another fruitless attempt to find a mate.

In contrast to the showy orchids, grass flowers are rather simple and dull, in keeping with the absence of any need to attract insects. Grass flowers are suspended at the tip of the plant, where wind can carry the pollen away to land on the female flower of a neighboring plant. Three grasses—corn, wheat, and rice—provide the vast majority of calories consumed by humans throughout the world. Their seeds, called grain, are rich in **carbohydrates** and contain some **protein** and vitamins as well. SEE ALSO ANGIOSPERMS; EUDICOTS; EVOLUTION OF PLANTS; FLOWERS; GRAIN; GRASSES; LEAVES; ROOTS; SEEDS; SHOOTS

Richard Robinson

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

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

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lineage ancestral line

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

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

cloaca common exit cavity for intestinal, genital, and urinary tracts

cranial related to the cranium, or brain cavity

Monotreme

Monotremes are an ancient group of mammals in the order Monotremata, which probably split from the **lineage** leading to **marsupials** (those with no placenta and having a pouch in the abdomen) and **placental** mammals early in mammalian evolution. The earliest fossil occurrence of monotremes is in the lower Cretaceous, approximately 110 million years ago.

Monotremes retain some of the primitive characteristics of mammalian ancestors, the therapsids. Monotremes lay eggs, have a somewhat reptilian posture, and retain a **cloaca**, a body cavity into which the reproductive, urinary, and excretory systems empty. Monotremes lack teeth as adults and have an unusual **cranial** shape. However, monotremes possess several critical mammalian features. They have fur, four-chambered hearts, single dentary (lower jaw) bones, and mammalian ear structure, and they lactate, or produce milk. Females lay one to three small, leathery eggs and incubate them outside of the body. Upon hatching, the young lap milk from the mother's mammary glands, which lack a nipple.

There are two families and three species of monotremes. The family Tachyglossidae includes two species: the spiny anteater, found in Australia, Tasmania, and southern New Guinea; and the long-nosed anteater, found only in New Guinea. The family Ornithorhynchidae includes a single species, the duck-billed platypus, an aquatic species that is found in eastern Australia and Tasmania. All three species eat primarily invertebrates and are prodigious burrowers. Populations of the long-nosed anteater are currently threatened by overhunting. Platypus is a protected species, and both the spiny anteater and platypus populations seem stable as of 2001. SEE ALSO Mammal; Marsupial

Tanya Dewey

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Muscle

Muscle can be categorized into three types based on structure, function, and location in the body. The specific details of muscle, including structure, physiology of contraction, energy requirements, muscle conditioning, and disease, can be illustrated using skeletal muscle.

Three Types of Muscle

The three types of muscle are skeletal, cardiac, and smooth muscle. Skeletal muscle is attached to the skeleton and moves the body and its components. It appears striated (striped) under the microscope and is under voluntary control. The biceps of the arm is an example of skeletal muscle. Cardiac muscle is only located in the heart. Cardiac muscle is also striated, but is not normally under voluntary control. Smooth muscle surrounds blood

vessels and other passageways and alters the size of openings or passageways and propels material through body tubes. Smooth muscle is distributed throughout the body. It lacks striations and is involuntary. The respiratory and digestive tracts have layers of smooth muscle in their walls.

Muscle Ultrastructure

A skeletal muscle fiber is formed from the fusion of many embryonic cells during development to form slender cells that extend from one end of the muscle to the other. Each muscle fiber normally has one nerve fiber that extends to the cell membrane, forming the neuromuscular junction. There is a 100-nanometer space, the synaptic cleft, between the nerve fiber and the muscle fiber.

The muscle cell membrane forms inward projections, the **transverse tubules**, associated with the cell's smooth **endoplasmic reticulum** (here called sarcoplasmic reticulum). The sarcoplasmic reticulum stores calcium and surrounds bundles of contractile **proteins**. The contractile proteins, which do the work of contraction, are parallel and arranged in an overlapping pattern that gives rise to the muscle striations. The pattern of striations is repeated many times down the length of the muscle fiber in segments called sarcomeres.

The proteins of the sarcomere are grouped in thick filaments and thin filaments. Contraction occurs when thick and thin filaments slide past each other, pulling the muscle ends closer together. A thick filament is a bundle of approximately two hundred myosin proteins. A portion of each myosin protein projects outward to form myosin heads.

transverse situated or lying across

endoplasmic reticulum network of membranes within the cell

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

plasma membrane

myofibril

transverse (T) tubules formed from invaginations of plasma membrane

sarcoplasmic reticulum
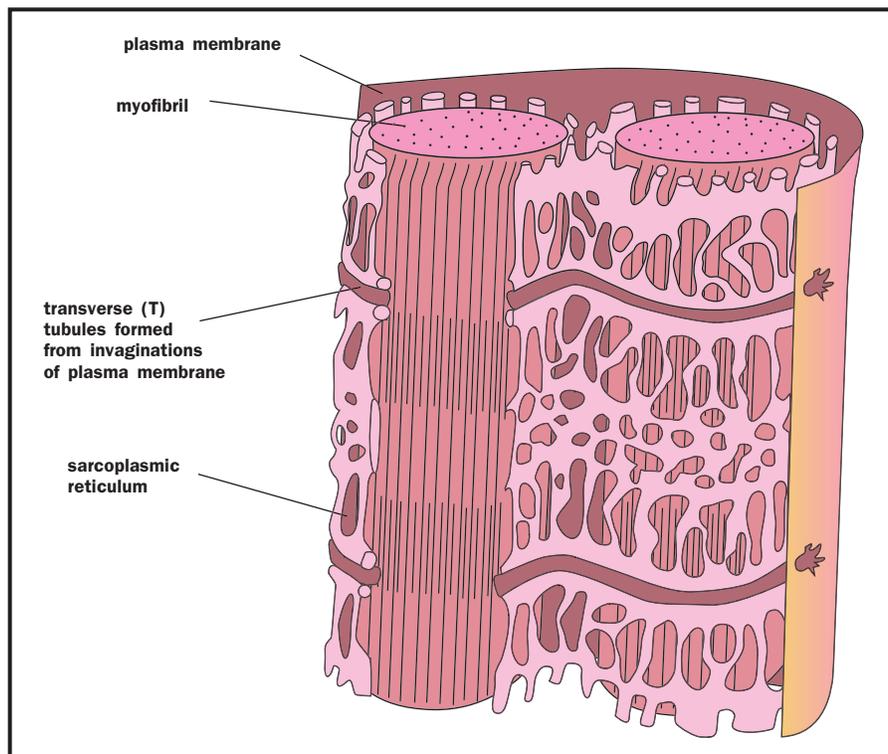
Microstructure of a muscle cell showing the close association of the sarcoplasmic reticulum and the myofibrils.

active site surface region of an enzyme where it catalyzes its reaction

polypeptide chain of amino acids

action potential wave of ionic movement down the length of a nerve cell

neuron nerve cell

Thin filaments overlap the thick filaments and are composed of three types of protein molecules. The main protein is actin. Three hundred to four hundred molecules of globular actin (G actin) link like beads in a necklace to form a strand called fibrous actin (F actin). Two such "necklaces" are then intertwined into a loose double helix. In the groove between the two F actins, much like a string, is the protein tropomysin. Each G actin contains an **active site** to bind the myosin head. When the muscle is at rest, tropomysin covers the active sites of actin. Attached to tropomysin is troponin, a small complex of three **polypeptides**. This structural arrangement allows muscle to contract.

Muscle Contraction

Muscle contraction begins when the nerve fiber releases the neurotransmitter acetylcholine into the synaptic cleft. Acetylcholine moves across the synaptic cleft and binds to receptors on the muscle fiber. This indirectly initiates an **action potential**, a change of electrical charge at the membrane that is similar to events in a **neuron**. The action potential spreads across and into the muscle fiber via the transverse tubules and triggers the release of calcium from the sarcoplasmic reticulum. Next, calcium binds to troponin, causing the troponin to change shape. Since troponin is attached to tropomysin, as troponin changes shape the tropomysin is pulled away from the active sites of actin, which become exposed. The myosin head, which was previously blocked by tropomysin, now binds to the active site of actin, forming a cross-bridge between the thick and thin filament.

In a ratchetlike movement, myosin pulls the thin filament past the myosin as the myosin head repeatedly flexes, lets go of the actin, extends and attaches to a new active site, and flexes again. As the many myosin heads continue to repeat this process, thin filaments slide past the thick filaments and the sarcomere is shortened. Shortening of all sarcomeres within the muscle fiber results in contraction of the whole fiber.

Muscle relaxes and returns to its original form when tropomysin covers up the active sites of actin, preventing the formation of cross-bridges. Relaxation also involves the destruction of acetylcholine by acetylcholinesterase in the synaptic cleft, ending muscle stimulation, and the reuptake of calcium into the sarcoplasmic reticulum. Without calcium, troponin returns to its original shape, pulling tropomysin back over the active sites of actin. Myosin no longer forms cross-bridges, so the muscle re-

Depolarization of the T-tubule membrane causes a release of calcium ions from the sarcoplasmic reticulum, triggering muscle contraction.

myosin heads

10 nm

bare zone

myosin heads
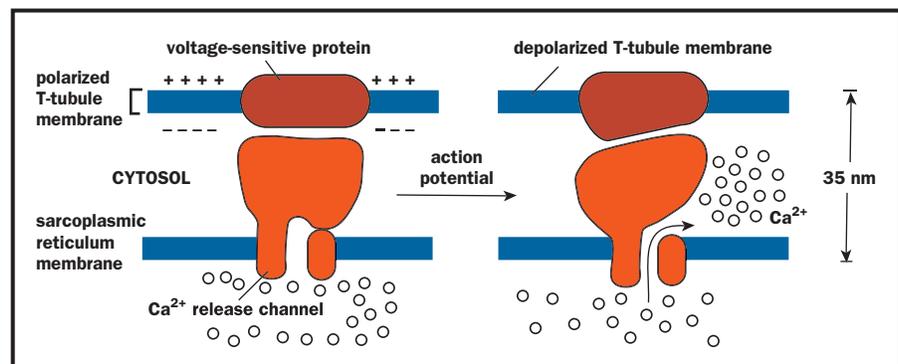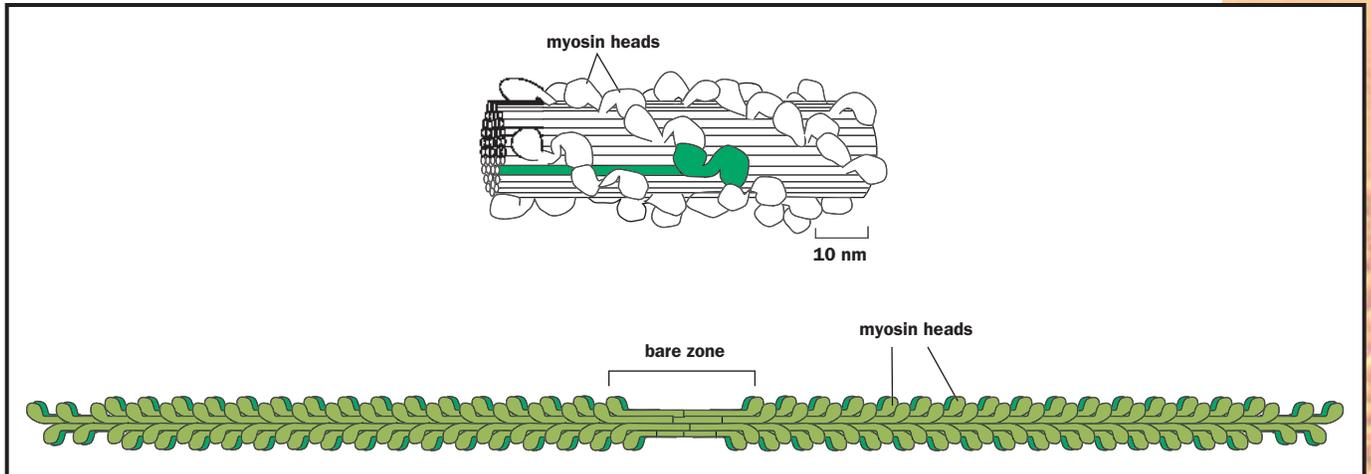
laxes. Note that a muscle can actively contract but cannot actively extend itself. For the releasing, muscles are usually present in pairs, each working against each other.

Energy (ATP) Requirements

The contraction of muscle fibers requires a large amount of energy in the form of adenosine triphosphate (ATP). ATP is made available through various mechanisms. A limited amount of ATP is stored in the muscle cell. ATP is also produced by a phosphate transfer from creatine phosphate to **ADP**; muscles do store larger amounts of creatine phosphate. The stored ATP and the ATP created from creatine phosphate are available for immediate use and provide approximately enough ATP for about six seconds of exercise.

Additional ATP can be produced through **anaerobic** and **aerobic metabolism**. Aerobic respiration provides a larger production of ATP but depends on sufficient oxygen delivery. Myoglobin, a protein in muscle cells that binds oxygen, contributes some of the oxygen for aerobic respiration. Aerobic ATP production also requires **mitochondria**. Muscles packed with mitochondria give meat a darker color ("dark meat") than muscles with fewer mitochondria ("white meat"). Anaerobic fermentation provides less energy but can produce ATP in the absence of oxygen. A serious drawback of anaerobic fermentation is the production of lactic acid, a product that can alter cell **pH**. Both processes can use **glucose** released from glycogen, which is stored in muscles as a reserve fuel.

Muscle Fatigue

A decrease in the ability of muscle to contract is muscle fatigue. Muscle fatigue can result from short burst of maximum effort, such as a 50-meter swim, or sustained long-term activities such as marathon running. The cause of fatigue depends on the activity. Fatigue from short, extensive burst of activity can result from depletion of ATP or buildup of lactic acid. Muscle fatigue from sustained activities can result from depletion of fuel molecules or depletion of acetylcholine at the neuromuscular junction.

Myosin heads in a myosin thick filament cluster to the outside, with the tails lining up inside. The heads on either end point in opposite directions. During muscle contraction, the heads pull actin filaments together toward the center bare zone, contracting the muscle fiber.

ADP adenosine diphosphate, the low-energy form of ATP

anaerobic without oxygen, or not requiring oxygen

aerobic with oxygen, or requiring it

metabolism chemical reactions within a cell

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

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

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

autoimmune disease
disease in which the immune system attacks the body's own tissues

ARTHRITIS AND GROWTH OF CARTILAGE

Arthritis is a breakdown of articular hyaline cartilage, often increased by enzymes of inflammation. Rheumatoid arthritis is an autoimmune disease, in which one's own immune system attacks healthy tissue. Osteoarthritis may be caused or accelerated by obesity, joint injuries, defective cartilage, lack of exercise, or biomechanical defects. Defects of only 1 square centimeter will alter the functioning of the articular cartilage.

Osteoarthritis is a major cause of joint replacements. A process to harvest and grow articular cartilage outside the body, called autologous chondrocyte implantation, is under investigation as of 2001. It is expensive and not exactly like real cartilage. However, in the future, replacement may employ stimulating growth factors, cartilage cells taken from an accessible place in the patient's body, and a synthetic matrix (scaffolding).

Hypertrophy and Conditioning

Through training, a muscle can become larger (hypertrophy) and have greater endurance. A muscle grows mainly by increasing the number of thin and thick filaments within the fibers. Growth results from repeated contractions of muscle, as in weight lifting. Muscle conditioning is the increased ability of the muscle to perform a task, either because of greater strength or better fatigue-resistance. Many changes in muscle performance, however, result from changes in the cardiovascular and respiratory systems, enabling them to deliver fuel and oxygen to muscle fibers more efficiently. Many changes specific to muscle fibers involve enhancing energy production, including an increase in number of mitochondria and myoglobin and greater storage of glycogen.

Muscle Disease

Diseases affecting muscle can result from loss of neurons that stimulate the muscle, such as polio; changes in the neuromuscular junction that result in loss of ability to stimulate the muscle, such as myasthenia gravis (an **autoimmune disease**); or loss of structural integrity of the muscle fiber, such as muscular dystrophy. All result in decreased ability of the muscle to contract and sometimes the complete loss of the muscle's function. SEE ALSO AUTOIMMUNE DISEASE; GENETIC DISEASES; METABOLISM, CELLULAR; MITOCHONDRION; MUSCULOSKELETAL SYSTEM; NEURON; NUCLEOTIDES; SYNAPTIC TRANSMISSION

Theresa Stouter Bidle

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Musculoskeletal System

The musculoskeletal system includes bones, joints, skeletal muscles, tendons, and ligaments. Muscles generate force; tendons transfer it to bones; and the bones move if enough force is transmitted. The force must be enough to overcome the weight of the moving body part, gravity, and other external resistance. Motion occurs at joints associated with one or both ends of the bone.

The force is produced in the muscle belly, which consists of muscle tissue. Tendons are basically connected bundles of collagen. They are classified as dense regular connective tissue and arise partially from the connective tissue coverings of muscle fibers and fiber groups. Tendons attach to the external membrane of a bone, the periosteum, which covers the bone except at joint surfaces. A few muscles bypass tendons and attach directly to the periosteum. Other muscles attach to skin (muscles of facial expression),

(a) (b) (c)

Classes of levers. (a) In a first-class lever, the fulcrum (F) is set up between the resistance (R) and the effort (M). (b) In a second-class lever, the resistance is between the fulcrum and the effort. (c) In a third-class lever, the effort is between the fulcrum and the resistance.
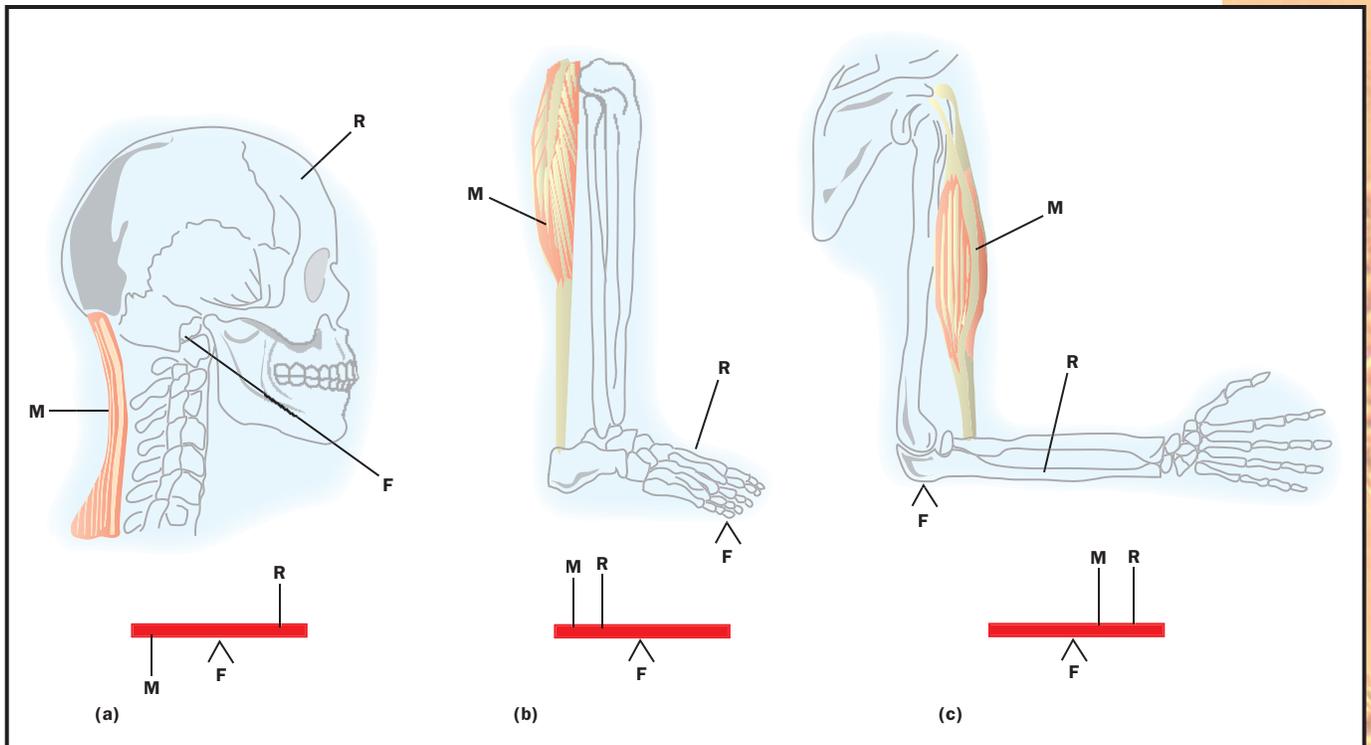
to other muscles, or to fascia, which are connective tissue sheets between muscles.

The surfaces of the bone making up the joint have a layer of hyaline cartilage, the articular cartilage, which forms a smooth surface for easy movement. Bone ends may be surrounded by a joint capsule, which secretes fluid for lubrication and nutrition. Joint motion is usually pain free, but age, injury, and some diseases damage the articular cartilage, resulting in arthritis.

Biomechanics applies the principles of physics to human movement. Some joints work like levers, others like pulleys, and still others like a wheel-axle mechanism. Most motion uses the principle of levers. A lever consists of a rigid "bar" that pivots around a stationary **fulcrum**. In the human body, the fulcrum is the joint axis, bones are the levers, skeletal muscles usually create the motion, and resistance can be the weight of a body part, the weight of an object one is acting upon, the tension of an antagonistic muscle, and so forth.

fulcrum pivot point of a lever

Levers are classified by first, second, and third class, depending upon the relations among the fulcrum, the effort, and the resistance. First-class levers have the fulcrum in the middle, like a seesaw. Nodding the head employs a first-class lever, with the top of the spinal column as the fulcrum. Second-class levers have a resistance in the middle, like a load in a wheelbarrow. The body acts as second-class lever when one engages in a full-body push-up. The foot is the fulcrum, the body weight is the resistance, and the effort is applied by the hands against the ground.

Third-class levers have the effort (the muscle) in the middle. Most of the human body's musculoskeletal levers are third class. These levers are built for speed and range of motion. Muscle attachments are usually close

An X ray of the human knee joint with the patella, the bone located within the quadriceps tendon, which wraps over the front of the knee, forming the kneecap.

to the joint. As the length of the lever increases, the possible speed increases, but so does the force required to produce it. For instance, the forearm is a third-class lever, controlled by the biceps muscle. A longer forearm can produce faster motion of the hand, but requires more effort to move than a shorter forearm.

A few muscle-bone connections work on the principle of a pulley, which changes the direction of an applied force. A classic example is the patella (kneecap), which alters the direction in which the quadriceps (patellar) tendon pulls on the tibia.

Muscles play four roles in producing joint movements: agonist (prime mover), antagonist, synergist, and fixator. A given muscle can play any of these roles, often moving from one to the next in a series during an action. Agonists and antagonists are opposing muscles. This means that when an agonist creates tension, the antagonist produces an opposing tension, thereby contributing to control at the joint. When one lifts a glass of water from the table to one's mouth, for example, the biceps brachii muscle acts as an agonist to flex the elbow, while the triceps brachii acts as an an-

tagonist to keep the elbow from flexing too fast or too far. Synergists aid the motion of an agonist.

Although every musculotendinous unit (muscle belly and tendons attaching it to the bone) has a specific name, it is common to group muscles according to the motion they create. Flexors create motion that would bring the **distal** segment closer to the torso, while abductors cause a limb to move **laterally**, away from the body. SEE ALSO BONE; MUSCLE; SKELETONS

Karen Jensen

distal away from

laterally side-to-side

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Mutation

Mutations are physical changes in **genes** and **chromosomes**. They may be confined to a single cell or may be transmitted from one cell to another within a multicellular organism (somatic cell mutation), or may be transmitted from one generation to another through mutation in the **gametes** (germ-line mutation). Mutations may be caused by natural events within the environment, by action or inaction of deoxyribonucleic acid (DNA) repair **enzymes**, and by human production of chemicals or high-energy radiation (mutagens). Mutation rates vary from organism to organism, from gene to gene, from time to time, and from place to place. They can have a significant effect not only on the individual, but on the evolution of species.

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

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

gamete reproductive cell, such as sperm or egg

enzyme protein that controls a reaction in a cell

Causes of Mutations

Since genes are composed of DNA, nearly anything that can change the structural composition, sequence, physical integrity, or length of a DNA molecule can cause mutations. Breakages may be caused by physical damage such as being severed by ice crystals in a frozen cell or violent agitation from high temperature. Exposure to high-energy radiation (bombardment by alpha, beta, or gamma particles) or ultraviolet light can have a similar effect. A variety of chemicals act as mutagens. Some chemicals, such as bromouracil, are structurally similar to DNA bases, and are inserted in place of normal bases. Ethidium bromide has a structure that allows it to wedge within the DNA double helix (intercalation), and is used as a stain for DNA. Many other chemicals, such as peroxides and mustard gas, chemically modify DNA.

Mutagens, which affect DNA, are distinct from **teratogens**, which influence the embryological development of an individual without necessarily affecting DNA structure. For example, thalidomide, a tranquilizer, causes nongenetic birth defects such as shortened limbs. Sensitive tests for identifying mutagens, like the Ames test, frequently also identify teratogens.

teratogens substances that cause birth defects

Spontaneous mutations can appear in DNA for many reasons, including faulty proofreading during replication. The fidelity of replication is

A white American alligator shows a genetic mutation known as leucism. This allele controls migration of pigment cells during development; absence in cells leads to white patches on the skin.

nucleotide the building block of RNA or DNA

greatly influenced by the cutting activities of DNA polymerases, which usually cut out incorrectly added **nucleotides**. Study of bacteria with high mutation rates (mutator strains) has shown they often have DNA polymerases with limited 3′ to 5′ (three-prime to five-prime) exonuclease activity. An exonuclease removes nucleotides at the end of the DNA chain. Low exonuclease activity means they are less able to remove incorrect nucleotides once added. On the other hand, antimutator strains often have DNA polymerases with very efficient 3′ to 5′ exonuclease activity. Due to these and other enzymes, a large number of different rates of mutation occur in different systems. Normally, the rate of change is about one in ten billion nucleotides per cell division, but the variance is wide and can be as high as one in ten thousand per generation. Human cells have approximately nine billion nucleotides, and so on average, about one mutation should occur in each round of DNA replication.

Types of Mutations: Structure and Information

Mutations can be classified in terms of the structural changes they cause, and in terms of the changes in the genetic information they produce. Point mutations are those affecting a single nucleotide. Point mutations may be deletions or insertions of nucleotides, or changes from one nucleotide to another (substitutions).

To understand the types of changes, it is useful to remember that the DNA nucleotides are adenine, thymine, cytosine, and guanine (abbreviated A, T, C, G). Canonically, A pairs with T, C pairs with G. Because of their chemical structures, A and G are referred to as purines, while C and T are pyrimidines. Substitutions, then, may be from purine to purine or from pyrimidine to pyrimidine (transitions), or purine to pyrimidine or vice versa (transversions).

amino acid a building block of protein

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

The DNA within a gene codes for the **amino acid** sequence in a **protein**, and so DNA mutations can lead to protein changes. The code is read in triplets, sequences of three nucleotides. From this, it is readily seen that any insertion or deletion will change the triplet groups, and so may have

major effects on the amino acids coded for. This is called a frame-shift mutation. Frame-shift mutations almost always result in nonfunctional proteins.

Transitions and transversions often have less drastic effects. In some cases, there is no effect at all. This occurs when the change is from one "synonym" to another in the **genetic code**; that is, when the new triplet codes for the same amino acid as the old one. A "nonsense" mutation is much more serious, since this converts a triplet coding for an amino acid (sense) into one with no corresponding amino acid (nonsense). This causes protein synthesis to stop (such triplets are called stop **codons**). A **missense mutation** is also potentially serious, since this changes one amino acid to another. When the new amino acid is chemically similar to the old one, there may be little effect on the protein structure and function. When they differ in size, polarity, or charge the effect may be profound.

Such is the case with the sickling variant of the **hemoglobin** gene. In the 1940s, Nobel laureate Linus Pauling suggested, and, in the 1950s, Verne Ingram demonstrated, that the first well-described "molecular disease" namely sickle cell disease, was due to a mutation that affected just one position in the amino acid sequence of the hemoglobin (Hb) molecule that carries iron in human blood. The underlying mutation was later shown to be a transversion from thymine to adenine. This converts an amino acid near one end of the beta chain of human hemoglobin from a glutamic acid side to a valine. This change, from a negatively charged **hydrophilic** side chain to a **hydrophobic** side chain, converts HbA to HbS. This alters the way hemoglobin molecules **aggregate** at low oxygen concentrations; HbS molecules cause the red blood cells that contain them to bend into a sickle shape. When these misshapen cells obstruct blood flow, an affected individual experiences great pain.

Mutation in Evolution

Mutation is one of the four forces of evolution; the others are selection, migration, and genetic drift. For a century after the publication of *The Origin of Species* by English naturalist Charles Darwin in 1859, mutation was often discussed as a source of new variation, but it was seldom considered to be highly important except in rare instances. However, in the 1960s, mutation became a major focus of evolutionary research.

The central question regarding mutation in evolution is to what extent mutations are harmful, harmless, or useful. In two experimental papers in 1966, Richard Lewontin and John Hubby demonstrated that many more individual fruit flies are **heterozygous** (meaning they have two different **alleles** at a genetic **locus**) and their populations had many more polymorphisms (the number of genes with more than one allele present) than could be accounted for by classical population genetic theory. R. K. Selander and others then extended this work for a broad **phylogenetic** spectrum of organisms. This gave strong support to the ideas of two population geneticists from Japan, Motoo Kimura and Tomoka Ohta, who hypothesized that most mutations were selectively neutral instead of being deleterious, as the standard view was at the time. In their view, mutations increase genetic diversity by giving rise to harmless differences in a gene that can be maintained in a population over long periods. These changes are reflected in the number of alleles (gene forms) within the population.

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

codon sequence of three mRNA nucleotides coding for one amino acid

missense mutation nucleotide change that causes a change in the amino acid normally added to the protein

hemoglobin oxygen-carrying protein complex in red blood cells

hydrophilic "water loving"

hydrophobic "water hating," such as oils

aggregate clump together

heterozygous characterized by possession of two different forms (alleles) of a particular gene

allele a particular form of a gene

locus site on a chromosome (plural, loci)

phylogenetic related to phylogeny, the evolutionary development of a species

An African clawed frog (*Xenopus laevis*), mutated, with three hind legs.

intron untranslated portion of a gene that interrupts coding regions

Neutralists (such as Kimura and Ohta) argued that most alleles at a genetic locus were either neutral or likely to have nonsignificant deleterious consequences. If alleles are principally neutral, then changes in alleles frequencies will be driven fundamentally by random forces (principally genetic drift). On the other hand, selectionists thought that alleles are predominantly harmful (with a view that only rare alleles have beneficial contributions), and, hence, natural selection would act to change allele frequencies in a predictable fashion, eliminating most new ones.

Kimura and Ohta's recognition of the neutral value of most mutations allowed the estimation of divergence times between related species by analyzing accumulated gene changes; the so-called molecular clock. Parts of proteins that were indispensable to function would be very well preserved and hence have few preserved mutational changes in their related gene sequences. Dispensable portions would have many more mutations. Changes in noncoding DNA regions, such as **introns** and "junk DNA," can accumulate even more mutations without effect.

In the last two decades of the twentieth century, two other major advances were made in the understanding of mutation. First, site-specific mutagenesis allowed molecular biologists to mutate genes almost letter by letter. With this approach, they can look at the impact of changing single amino acids on the structure and function of proteins.

Second, a debate on the role of mutation rate and the direction of mutations has been rekindled. In the 1940s, Salvador Luria and Max Delbrück showed definitively that mutations did not arise that specifically addressed some biochemical inability of the organism, such as an ability to metabolize a new food source or to resist **pathogenic** infection. Instead, random mutations are produced, and those populations with beneficial adaptations survived better than other populations.

However, in the 1980s, John Cairns and others challenged the orthodoxy of this view with a variety of new experiments, which they thought indicated that mutations with adaptive value preferentially arose in some bacterial populations.

The response from the majority scientific community was rapid. In 1999, Croatian scientist Miroslav Radman, working in Paris, provided the most widely accepted resolution to this conflict. Namely, he and others believe that some selective agents (in many experiments stress was induced by starvation) led to an increase in the overall rate of mutation rather than to an increased production of adaptive mutations. This increases the rate of all types of mutations, including adaptive ones. SEE ALSO BLOOD; CHROMOSOME, EUKARYOTIC; CHROMOSOME ABERRATIONS; DNA; GENE; GENETIC CODE; GENETIC DISEASES; NUCLEOTIDES; REPLICATION

John R. Jungck

Mutation rates and genetic adaptability (fitness). Redrawn from Radman, 1999.

pathogen disease-causing organism

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Mycorrhizae

Symbioses are intimate associations between two unrelated organisms. Mycorrhizae are very common but largely unseen symbioses between plant roots and fungi that are important in plant nutrition, community structure, and nutrient cycling. Throughout the course of their evolution, plants and fungi have formed many different types of mycorrhizal partnerships involving most plant families and thousands of fungal species.

These diverse symbioses have been grouped into general types: arbuscular mycorrhizae, ectomycorrhizae, orchid mycorrhizae, and mycorrhizae

Endotrophic mycorrhizae in an orchid root. Mycorrhizae are very common but largely unseen symbioses between plant roots and fungi.

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

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

forb broad-leaved herbaceous plant

in plants in the order Ericales including ericoid, arbutoid, and monotropoid mycorrhizae.

Mycorrhizae are critical for the mineral nutrition of many plants because threadlike fungal hyphae can exploit soil much more extensively than plant roots, and thus mycorrhizal associations greatly increase the absorption of **minerals** and water. Usually, mycorrhizal fungi supply minerals to their host plants, which reciprocate by supplying **carbohydrates** to their fungal associates, but there are a few exceptions. In orchids, and some chlorophyll-free plants in the order Ericales, the flow of carbon is reversed, and mycorrhizal fungi supply the plant with organic carbon derived from dead plant matter or from neighboring living plants.

Arbuscular mycorrhizae, the most common type, are associations between most crop plants, grasses, **forbs**, and many trees and fungi in the division Zygomycota, order Glomales. Both fossil and molecular evidence indicate that the earliest land plants had arbuscular mycorrhizal partnerships 450 million years ago. Ectomycorrhizae are commonly formed by woody shrubs and trees and a diverse array of fungi in the divisions Basidiomycota

and Ascomycota. Pines and other forest trees often grow poorly or cannot survive in the absence of ectomycorrhizae.

Taxa of mycorrhizal fungi differ greatly in their effects on plant fitness. Consequently, interactions between communities of mycorrhizal fungi and plants may have strong impacts on the structure and function of communities and **ecosystems**. SEE ALSO COMMUNITY; CONIFERS; FUNGI; SYMBIOSIS

Nancy Collins Johnson

ecosystem an ecological community and its environment

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Natural Selection

Natural selection is the process by which individuals with characteristics that are advantageous for reproduction in a specific environment leave more offspring in the next generation, thereby increasing the proportion of their genes in the population gene pool over time. Natural selection is the principal mechanism of evolutionary change, and is the most important idea in all biology. Natural selection, the unifying concept of life, was first proposed by Charles Darwin, and represents his single greatest contribution to science.

Natural selection occurs in any reproducing population faced with a changing or variable environment. The environment includes not only physical factors such as climate or terrain, but also living factors such as predators, prey, and other members of a population.

Mechanism of Natural Selection

The mechanism of natural selection depends on several phenomena:

- Heredity: Offspring inherit their traits from their parents, in the form of genes.

- Heritable individual variation: Members of a population have slight differences among them, whether in height, eyesight acuity, beak shape, rate of egg production, or other traits that may affect survival and reproduction. If a trait has a genetic basis, it can be passed on to offspring.

- Overproduction of offspring: In any given generation, populations tend to create more progeny than can survive to reproductive age.

- Competition for resources: Because of excess population, individuals must compete for food, nesting sites, mates, or other resources that affect their ability to successfully reproduce.

Given all these factors, natural selection unavoidably occurs. Those members of a population that reproduce the most will, by definition, leave more offspring for the next generation. These offspring inherit their parents' traits, and are therefore also likely to succeed in competition for resources (assuming the environment continues to pose the same challenges as those faced by parents). Over several generations, the proportion of offspring in a population that are descended from the successful ancestor
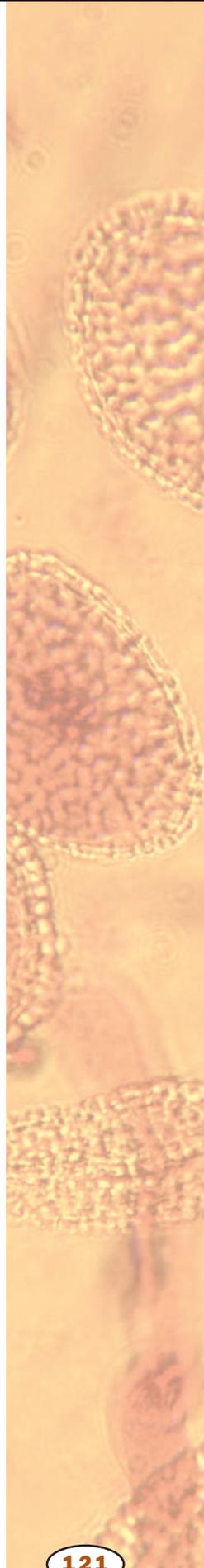
Uloborid spider eggs and spiderlings. In any given generation, populations tend to create more offspring than can survive to reproductive age.

increases, and traits that made the ancestor successful therefore also increase in frequency. Natural selection leads to adaptation, in which an organism's traits conform to the environment's conditions for existence.

Consequences of Natural Selection

Natural selection is truly the ultimate inventor. A short list of some of its many "inventions" includes flight, celestial navigation, echolocation, insulation, infrared sensors, hypodermic needles, plus all sorts of useful biologically active chemicals such as antibiotics, analgesics, emetics, diuretics, laxatives, tranquilizers, contraceptives, hallucinogens, pain killers, and many, many more. Each of these has been fashioned by natural selection to meet the needs of particular organisms in specific environments.

Pesticide-resistant insects and antibiotic-resistant bacteria are well-documented examples of natural selection in action. In each case, humans have provided the environmental challenge in the form of poisons acting on the population. Preexisting variations in susceptibility to the poison

mean that some organisms survive while others die without reproducing. Offspring of survivors have the same variation, and the most resistant of those survive best to reproduce. Over time, populations of resistant insects or bacteria are formed. (This is why taking the full prescription of an antibiotic is important; it kills the entire microbe population, preventing any from reproducing.)

Misconceptions About Natural Selection

Natural selection is easy to understand, but it is misunderstood much too often. Natural selection is not synonymous with evolution. Evolution refers to any genetic change in a population, whereas natural selection specifies one particular way in which such changes are brought about. Natural selection is the most important agent of evolutionary change simply because it results in adaptation of an organism to its environment. Other possible mechanisms of evolution besides natural selection include gene flow, meiotic drive, and genetic drift.

A persistent misconception is that natural selection occurs mainly through differences between organisms in death rates, or differential mortality. Differential mortality can be selective but only to the degree that it creates differences between individuals in the number of reproductive offspring they produce. Reproductive rate, rather than death rate, drives natural selection. A cautious tomcat that seldom crosses busy streets might live to a ripe old age without leaving behind as many descendent kittens as another less staid tomcat killed on a highway at a much younger age. If the short-lived cat leaves more descendants, its genes will spread faster than those of the long-lived cat, and natural selection will favor a short life span. Unless living longer allows or results in higher reproductive success, long life is not favored by natural selection.

Adaptations fashioned by natural selection suit an organism to its particular environment. For instance, a maple tree's broad leaves are well adapted to temperate climates, but unsuited to arctic cold. Similarly, a human's ability to store fat is an adaptation to environments in which fat is scarce, but is poorly suited to the modern fast-food environment. In this respect, natural selection is somewhat shortsighted, since it cannot "see" beyond the next generation.

Natural selection cannot preferentially create favorable variations, but instead must work with what is at hand. For instance, treatment with antibiotics does not create antibiotic-resistant mutants. Instead, it favors microbes that, by chance, already have genes for resistance.

Phrases such as "the struggle for existence" and "survival of the fittest" have had an unfortunate consequence. They tend to emphasize predation and fighting for food as the prevalent means of selection. This reinforces erroneous emphasis on differential death rates, with the strongest and fastest individuals being considered as having a selective advantage over weaker and slower individuals. But if this were true, every species would continually gain in strength and speed.

Because this is not happening, selection against increased strength and speed (counterselection) must be occurring and must limit the process. Animals can sometimes be too aggressive for their own good; an extremely
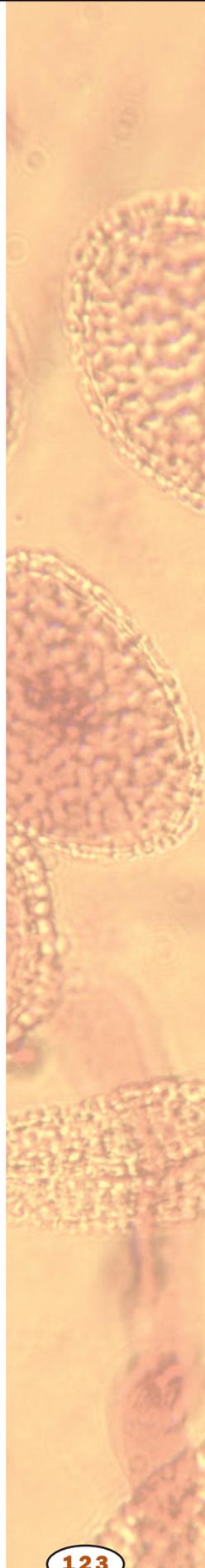
aggressive individual may spend so much time and energy chasing its prey that it spends less than average time and energy on mating and reproduction, and as a result, leaves fewer offspring than average. Likewise, an individual could be too submissive and spend too much time and energy running away from others. Usually, intermediate levels of aggressiveness result in the highest fitness.

Natural selection does not operate "for the benefit of the species." Birds lay fewer eggs during drought years. Is this because competition for limited food supplies would be detrimental to the species, and do birds hold back "for the good of their species"? Such arguments have a fatal flaw: "cheaters" that laid as many eggs as possible would reap a higher reproductive success than individuals that voluntarily decreased their clutch size. Over time, cheater genes would spread through a population, and genes for holding-back would become rare.

However, the same phenomenon can be interpreted more plausibly in terms of natural selection at the level of individuals. During droughts, parental birds cannot bring as many insects to their nest and therefore cannot feed and fledge as many chicks as they can when food supplies are more ample. Laying extra eggs means most chicks would die of starvation. Birds can actually leave more surviving offspring to breed in the next generation by laying fewer eggs.

Any individual that sacrifices its own reproductive success for the benefit of a group is at a selective disadvantage within that group to any other individual not making such a sacrifice. Classical selection will always favor individuals that maximize their own selfish reproductive success. Natural selection recognizes only one currency: babies. Although we might wish otherwise, beauty, brains, or brawn need not be favored unless such traits are translated into more offspring than average. If ugly, dumb, weak individuals pass on more genes, those traits will prevail in future generations.

Whenever one organism leaves more successful offspring than others, in time its genes will come to dominate the population gene pool. Ultimately, natural selection operates only by differential reproductive success. An individual's ability to perpetuate itself as measured by its reproductive success is known as its Darwinian fitness. SEE ALSO ADAPTATION; CONVERGENT EVOLUTION; EVOLUTION; POPULATION GENETICS; SEXUAL SELECTION

Eric R. Pianka

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Nematode

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

Nematodes, also called roundworms, are members of the animal **phylum** Nematoda. These worms have a complete digestive system and are more complex than the flatworms (phylum Platyhelminthes) but lack a circulatory system and other advanced features found in the annelids (segmented worms). The Nematoda is one of the largest animal phyla, with over 15,000

described species. Many more species remain to be discovered because most nematodes are microscopic in size and not easily observed.

Nematodes are an extremely diverse group and are common in most habitats. These aquatic worms are abundant in freshwater and marine **ecosystems** but also inhabit the moisture film around soil particles. A small handful of soil may contain several thousand individuals. Nematodes even occur in desert soils and in Antarctica.

Many kinds of nematodes are **parasites**, inhabiting vertebrates (including humans) or invertebrates. Others are parasites of plants and feed on or live within roots, tubers, bulbs, and other below-ground plant parts. A few unusual species live inside leaves, stems, or seeds. Some of the nonparasitic, free-living nematodes are predators of other minute organisms. Most free-living nematodes feed on bacteria or fungi. Their activities are important in the decomposition of **organic** matter and recycling of nutrients. SEE ALSO ANIMALIA; PARASITIC DISEASES; PLATYHELMINTHES; SYMBIOSIS

Robert McSorley

ecosystem an ecological community and its environment

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

organic composed of carbon, or derived from living organisms

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Nervous Systems

The nervous system is a network of nerve cells and, in most animals, a brain. In vertebrates, it also includes a spinal cord. The primary cell type found in the nervous system is the **neuron**, which has a cell body, containing the **nucleus**, and long extensions to carry information from one part of the body to another.

neuron nerve cell

nucleus membrane-bound portion of cell containing the chromosomes

The nervous system has two primary functions that are critical in maintaining the life of the organism. First, sensory receptors allow the organism to monitor its external environment and detect changes that occur (for example, an increase in temperature). The nervous system then activates structures such as muscles and glands, which permit the organism to respond appropriately to the environmental changes (moving out of the sun or activating sweat glands). Second, the nervous system also monitors the organism's internal environment, controlling heart rate so that enough blood is delivered to organs, or measuring nutrient levels to signal when an organism needs to obtain food.

While all nervous systems carry out these basic functions, the structure and complexity of the nervous system varies tremendously in different organisms. In vertebrates, it is divided into the **central nervous system** (CNS), which contains the brain and spinal cord, and the **peripheral** nervous system (PNS), which is composed of the nerves that carry information to and from the CNS. Invertebrate nervous systems may or may not have distinct peripheral and central regions, but communication with and response to the environment still occurs. Overall, invertebrate systems are much less complex. A vertebrate nervous system may contain a trillion neurons, whereas an invertebrate may have as few as 305.

central nervous system brain and spinal cord

peripheral outside the central nervous system (brain and spinal cord)

dendrites

OUTPUT

axon

INPUTS

cell body, or soma

Specialized cells, called Schwann cells, or oligodendrocytes, wrap around an axon to form a multilayered membrane sheath.
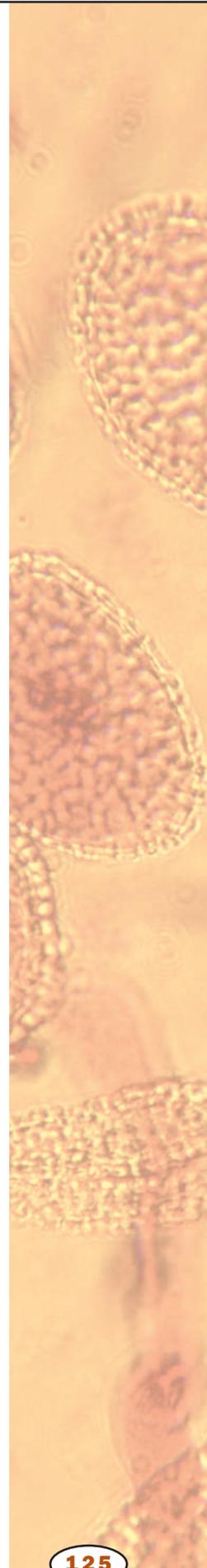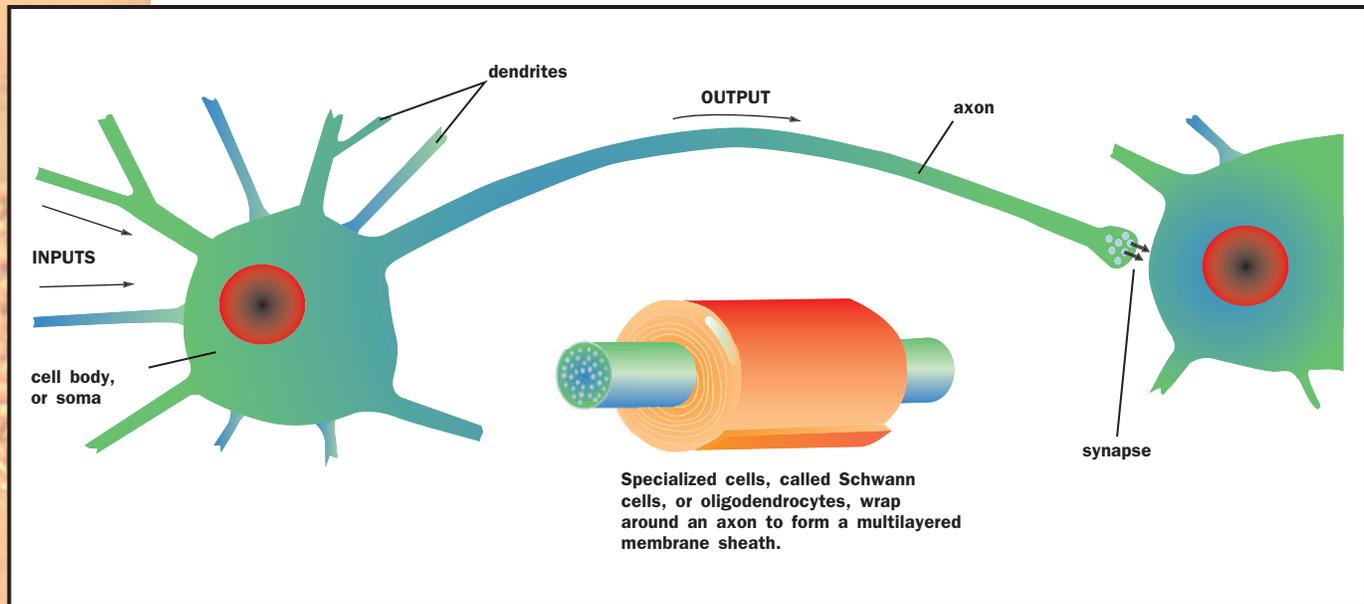
synapse

Neurons relay messages by accepting inputs at the dendrite and cell body, passing waves of electrochemical activity down the axon, and releasing chemical neurotransmitters from the axon to the next neuron at the synapse.

ganglia cluster of nerve cell bodies

Invertebrate Nervous Systems

Although the invertebrate nervous system is usually much simpler than the nervous systems found in vertebrates, there is still a broad range in complexity depending on the type of invertebrate.

The simplest type of nervous system is found in hydras and jellyfish (cnidarians) and is referred to as a "nerve net." Nerve nets do not have distinct central or peripheral regions, and lack anything that resembles a brain. Instead, the scattered nerve cells form loose networks in each cell layer of the body wall. Some of these neurons carry information from sensory organs that detect touch, light, or other changes in the environment. These neurons in turn contact neurons that control movement of the organism, such as swimming.

Unlike the hydras and jellyfish, invertebrates such as sea stars (echinoderms) display some centralized organization of the nervous system. A ring of neurons is located in the center of the sea star, and simple bundles of neurons called radial nerves extend from the ring to the tip of each arm. In each arm, extensions of the radial nerves form nerve nets as in the jellyfish. This arrangement permits coordinated movement of each arm and the tube feet located on the surface of the arm.

A distinct separation of peripheral and central nervous systems is found in invertebrates such as worms, insects, and mollusks, like the squid. Neuron cell bodies are grouped into clusters called **ganglia**, which are usually located along the animal's midline. The peripheral component of the nervous system is formed by the extensions of the cells in these ganglia; some carry sensory information from the environment to the ganglia, while others carry signals from the ganglia to produce a response (such as movement). This type of organization permits segmentation, in which each ganglion responds to and controls an individual segment of the body. To coordinate the segments, these ganglia are connected to each other in a chainlike fashion by a nerve cord, which is a bundle of neurons that runs the length of

(a) (b) (c) (d)
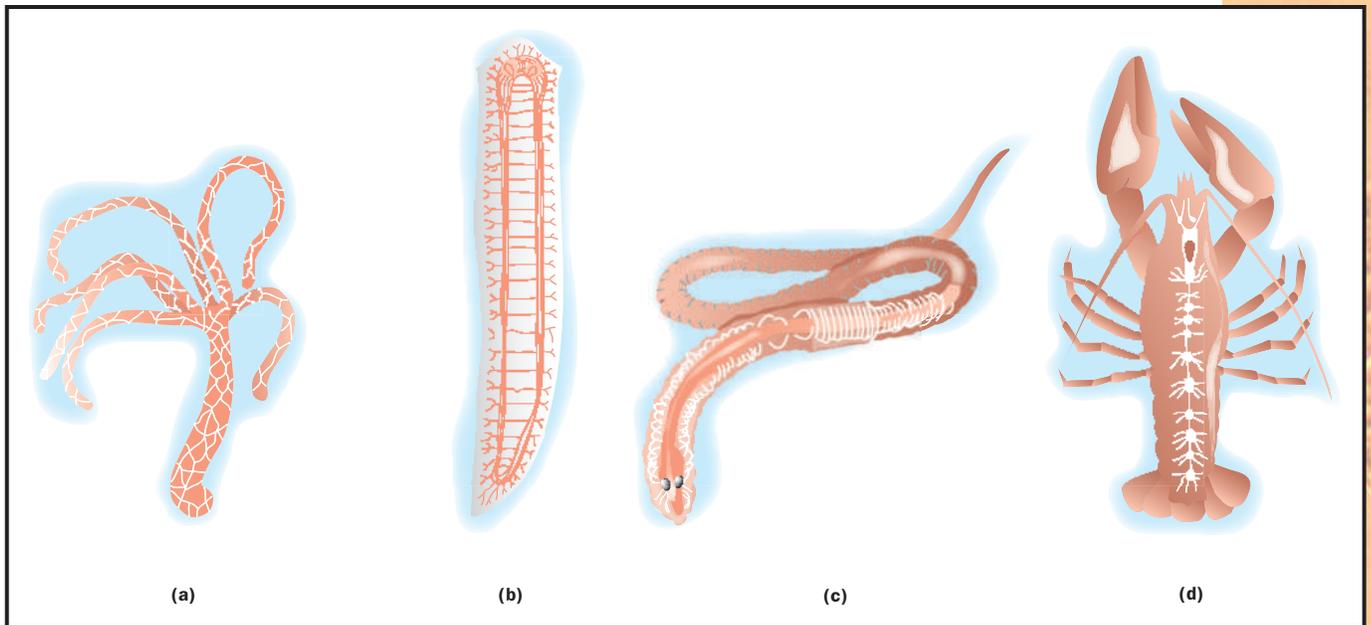
the animal. Some organisms have more than one nerve cord connected by **transverse** nerves, resembling a ladder.

In many invertebrates, the nerve cord is enlarged at the **anterior** (or head) end of the organism. This enlargement can be considered a primitive brain, and together with the nerve cord comprises the central nervous system. Without any type of brain, the coordination between different segments of the organism is limited at best, and the nervous system primarily produces simple reflexive movements. The presence of a brain allows the organism to receive a wide array of information from the environment, analyze it, and generate a coordinated and complex response. For example, the large brain of a squid enables it to process visual information and rapidly generate coordinated responses to capture prey. In fact, this invertebrate nervous system is so specialized, it closely resembles some vertebrate nervous systems.

Vertebrate Nervous Systems

Many of the features observed in more complex invertebrate nervous systems are also present in vertebrates. All vertebrates have a distinct central component that consists of a brain and spinal cord, as well as peripheral structures such as ganglia and nerves. The primary difference from invertebrates is in the number of neurons and the size of nervous system structures. However, just as variety exists among the nervous systems of the invertebrates, there are also diverse levels of complexity from one type of vertebrate nervous system to another.

Regardless of complexity, vertebrate brains all contain three regions: the hindbrain, midbrain, and forebrain. The hindbrain is located at the junction of the brain and spinal cord, and is dedicated to coordination of motor (movement) reflexes and regulation of **autonomic** processes such as blood pressure and heart rate. An extension of the hindbrain called the cerebellum assists in coordinating motor movement in response to sensory

The nerve signal can travel in both directions in the hydra (a), a cnidarian. A planarian (b) has two nerve cords and two clusters of nerve cell bodies at its anterior end. In annelids, such as the earthworm (c), two cords are fused and run down the ventral surface of the body. Arthropods such as the crayfish (d) also have a double ventral nerve, in addition to clusters of nerve cells in the area of the head.

transverse situated or lying across

anterior toward the front

autonomic independent; involuntary actions

input. The midbrain is concerned with visual processing and some motor control. The forebrain (the region closest to the anterior end of the organism) shows the most variability among vertebrates. It can be divided into two distinct regions. The telencephalon is concerned with associative activity, that is, combining or integrating all incoming sensory information and directing an appropriate response. The diencephalon contains the thalamus and hypothalamus, regions important in processing sensory input and autonomic responses, respectively. The size of these regions varies depending on the vertebrate class.

The spinal cord is similar to the invertebrate nerve cord, but is usually enclosed in a protective column of vertebrae (with the exception of the most primitive vertebrates, the lampreys and hagfishes). Information is carried to and from the brain and spinal cord by the peripheral nervous system, which contains ganglia located adjacent to the spinal cord. Spinal nerves enter and exit the spinal cord to carry information to and from the body; **cranial** nerves carry similar information about the head directly into the brain.

cranial related to the cranium, or brain cavity

Variety in Vertebrate Brains

In primitive vertebrates such as fish, the hindbrain is the largest of the three regions. The cerebellum is relatively well developed for swimming and balance, although not in the lampreys and hagfishes. Fish have a small midbrain (just above the hindbrain) for the processing of visual information, and a small forebrain primarily concerned with the sense of smell (olfaction).

The hindbrain is more enlarged in amphibians compared to fish, but the cerebellum is often reduced in size, which reflects the relatively simple locomotion of amphibians. The forebrain is still small and functions primarily in olfaction.

In reptiles and birds, the size of the cerebellum is increased over amphibians, reaching massive proportions in birds where it regulates the complex muscle activity and spatial coordination needed for flying. The midbrain is enlarged as well, which permits interpretation of more complex visual images. This is particularly true of birds, which also have relatively large eyes. In addition, the sense of hearing becomes more developed, and, beginning with reptiles, the midbrain shows a distinct region dedicated to auditory processing. Reptiles and birds also possess forebrain regions that are much larger than those of more primitive vertebrates; the more complex motor skills and sensory input require a larger telencephalon to process input and coordinate responses. The regions devoted to the sense of smell diminish in size, especially in most birds, which have a very poor sense of smell.

Birds possess a component of the forebrain called the hyperstriatum, which scientists believe could be the source of bird intelligence.

In mammals, including humans, the most striking change is in the size of the cerebellum (again for more complex movements) and the telencephalon, which may be so large that it covers the diencephalon, midbrain, and part of the cerebellum. As specialization of the telencephalon increases, the increased size is correlated with the appearance of convolutions or folds in the surface. This specialization reaches its highest level in humans; the highly wrinkled **cerebral cortex** completely covers all but the cerebellum in humans. In addition to integrating all types of sensory information and coordinating voluntary movement, all **cognitive** functions (speech, math, learning, memory) are located here as well. SEE ALSO BRAIN; CENTRAL

cerebral cortex outermost wrinkled portion of the brain

cognitive related to thought or awareness

Nervous System; Cnidarian; Echinoderm; Neurologic Diseases; Neuron; Peripheral Nervous System; Synaptic Transmission

Sheri L. Boyce

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Neurologic Diseases

Neurological disease is a structural disturbance or a malfunction of the **central nervous system**. Common neurological disorders include stroke, Alzheimer Disease, migraine headaches, epilepsy, Parkinson's disease, sleep disorders, multiple sclerosis, pain, brain and spinal cord injuries, brain tumors, and **peripheral** nerve disorders. According to the National Institute of Neurological Disease and Stroke (NINDS), neurological disease is "a burden borne by every age group, by every segment of society, by people all over the world" (www. http://ninds.nih.gov).

central nervous system brain and spinal cord

peripheral outside the central nervous system (brain and spinal cord)

Causes and Costs

The most common causes of neurological disorders include genetic, developmental, or **congenital** abnormalities; various peripheral diseases such as diabetes, high blood pressure, or a variety of infectious diseases; problems of the immune system (such as multiple sclerosis); brain or spinal cord injury; and environmental toxins. Neurodegenerative diseases affect brain cells, usually later in life, often for unknown reasons. Alzheimer Disease and Parkinson's disease are examples. Huntington's disease is a neurodegenerative disease known to be caused by inheritance of a mutant gene. Mental disorders have traditionally been distinguished from neurological diseases by their lack of evidence for an apparent mechanism as well as their principal symptom, maladaptive behavior.

congenital present at birth; inherited

However, this distinction is misleading because it suggests that mental disorders lack an underlying physical cause, which is increasingly being contradicted by research. Furthermore, many neurological diseases produce maladaptive behaviors, making this division less meaningful.

Taken together, neurological diseases are among the most destructive and costly public health problems for any society. Cerebrovascular accidents, more commonly called strokes, account for approximately half of all neurological problems in adults. Traumatic brain and spinal injuries constitute one of the leading causes of disability and death in the United States, particularly for young males. Epilepsy, chronic pain, and migraine headaches are widely diagnosed, and there is an increased incidence of Alzheimer Disease and Parkinson's disease due to the aging of society and greater exposure to environmental toxins.
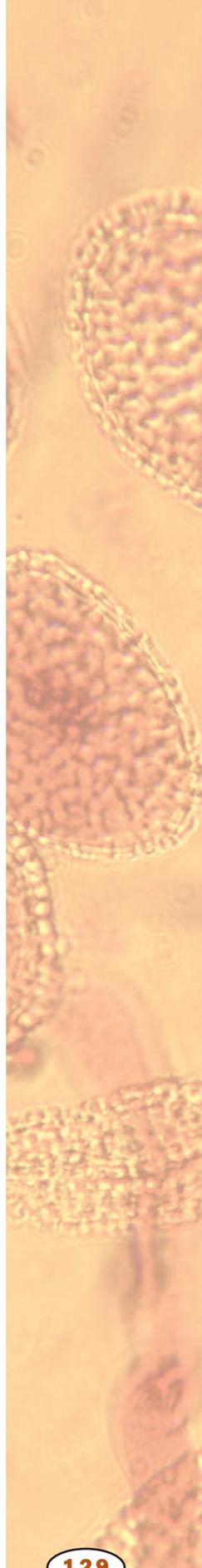
A computerized axial tomography (CAT) scan of a human brain with Parkinson's disease, showing atrophy. Neurodegenerative diseases such as Parkinson's affect brain cells, usually later in life.
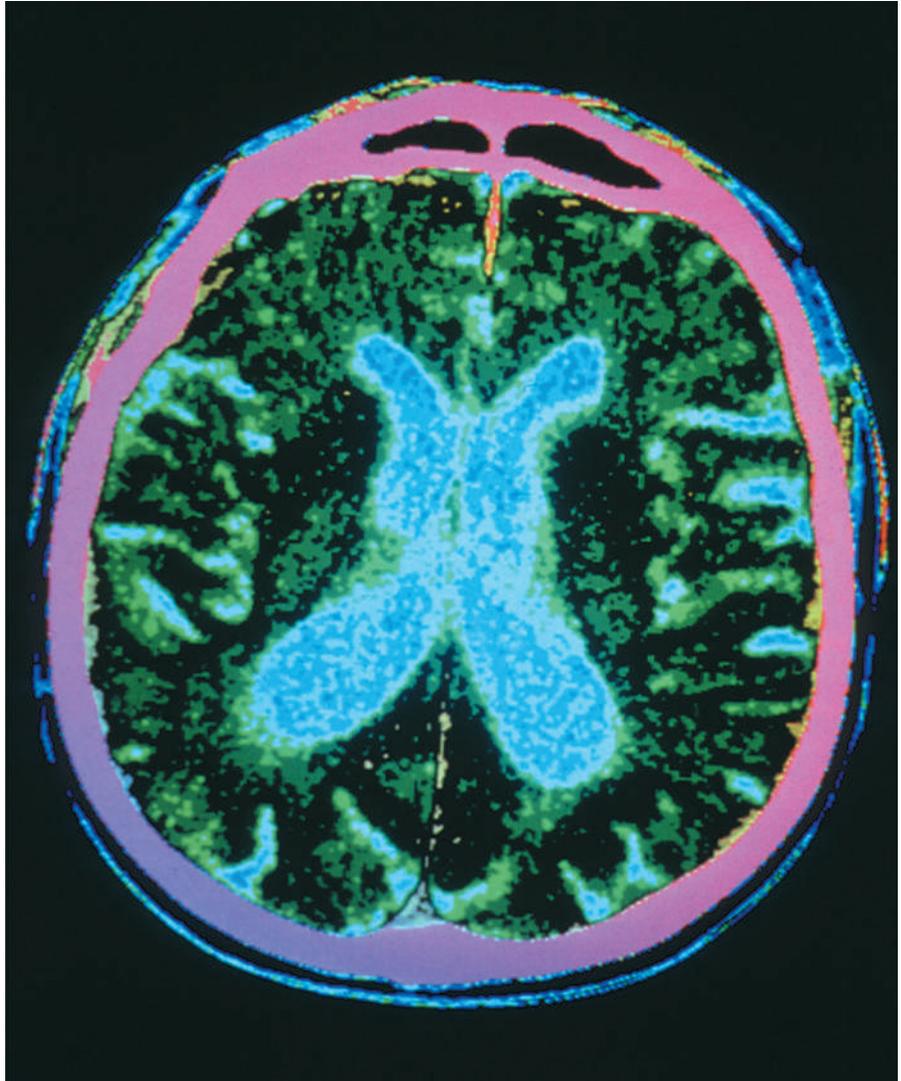
agnosia "not knowing"; loss of ability to recognize familiar objects

aphasia loss of the ability to form ideas into words

dementia neurological illness characterized by impaired thought or awareness

lethargy lack of excitability; torpor

neurologist doctor who treats brain disorders

cranial related to the cranium, or brain cavity

autonomic independent; regulating involuntary actions

Symptoms and Diagnosis

The diagnosis and treatment of neurological diseases is the medical specialty of neurology. Neurosurgery is a medical specialty related to neurology. A variety of tools is available for the diagnosis and treatment of neurological diseases. Typically, the practitioner performs an initial evaluation, and tests for a variety of conditions that could be indicative of the underlying pathology.

Neurological symptoms can be quite variable. Common symptoms include chronic pain, impaired reflexes, tremors, motor coordination problems, localized muscle weakness, paralysis, numbness, tingling, loss of vision, **agnosia**, and **aphasia**, as well as confusion, mental retardation, **dementia**, delirium, **lethargy**, seizure, tremor, stupor, and coma. The **neurologist** uses both the symptoms and the patient's history to begin to determine a diagnosis. Neurological examinations include tests for mental status, **cranial** nerve performance, and motor systems functioning; assessment of muscle strength and coordination; and examination of reflexes and sensory systems as well as **autonomic** nervous system responses.

Other noninvasive diagnostic tools include the electroencephalograph (EEG), which records electrical brain activity; computerized axial tomography (CAT) or computerized tomography (CT) scan, which is often used to locate lesions and tumors; magnetic resonance imaging (MRI) scans, which provide a more detailed map of brain functioning; and, finally, cerebral angiography, which allows for the visualization of blood flow to and from the brain. Spinal taps (lumbar punctures) permit the withdrawal of cerebrospinal fluid for chemical and microbiological analysis. Despite the advances in diagnostic procedures, dramatically improved treatments with **psychotropic** drugs, neurosurgery, and various rehabilitative measures, many of the neurological diseases cannot be effectively treated or reversed. SEE ALSO BRAIN; CARDIOVASCULAR DISEASES; CENTRAL NERVOUS SYSTEM; DOCTOR, SPECIALIST; NEURON; PSYCHIATRIC DISORDERS, BIOLOGY OF; SYNAPTIC TRANSMISSION

Arne Dietrich

psychotropic affecting consciousness, thought, or emotion

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Neuron

The neuron (nerve cell) is the fundamental unit of the nervous system. The basic purpose of a neuron is to receive incoming information and, based upon that information, send a signal to other neurons, muscles, or glands. Neurons are designed to rapidly send signals across physiologically long distances. They do this using electrical signals called nerve impulses or **action potentials**. When a nerve impulse reaches the end of a neuron, it triggers the release of a chemical, or neurotransmitter. The neurotransmitter travels rapidly across the short gap between cells (the synapse) and acts to signal the adjacent cell.

action potential wave of ionic movement down the length of a nerve cell

Functions and Classification

Communication by neurons can be divided into four major steps. First, a neuron receives information from the external environment or from other neurons. For example, one neuron in the human brain may receive input from as many as one hundred thousand other neurons. Second, the neuron integrates, or processes, the information from all of its inputs and determines whether or not to send an output signal. This integration takes place both in time (the duration of the input and the time between inputs) and in space (across the surface of the neuron). Third, the neuron propagates the signal along its length at high speed. The distance may be up to several meters (in a giraffe or whale), with rates up to 100 meters (328 feet) per second. Finally, the neuron converts this electrical signal to a chemical one and transmits it to another neuron or to an **effector** such as a muscle or gland.

effector organ at the end of a nerve, such as a muscle or gland

Parts of a neuron.

Dendrites

Soma

Nucleus

Nucleolus

Trigger zone
Axon hillock
Initial segment

Axon collateral

Axon

Direction of
signal transmission

Node of
Ranvier

Internodes

Myelin sheath

Schwann cell

Terminal
arborization

Synaptic
knobs
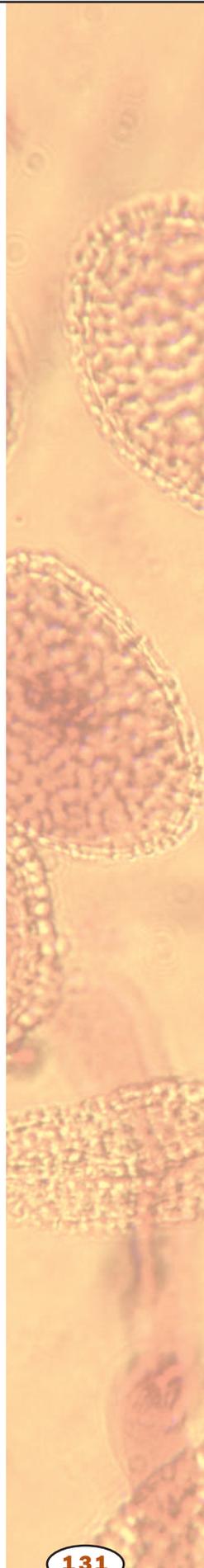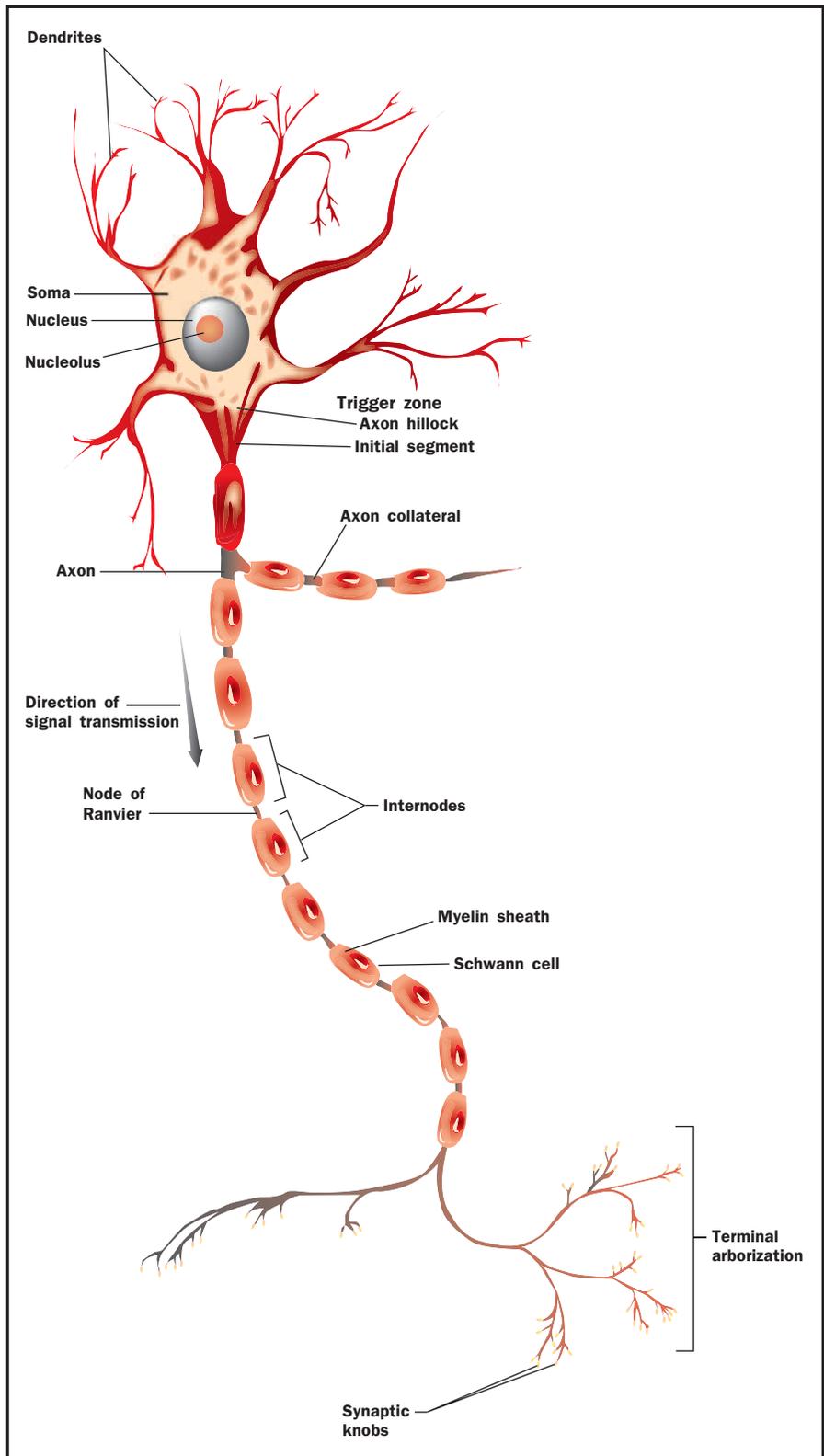
When combined into networks, neurons allow the human body memory, emotion, and abstract thought as well as basic reflexes. The human brain contains an estimated one hundred billion neurons which relay, process, and store information. Neurons that lie entirely within the brain

or spinal cord are referred to as interneurons and make up the **central nervous system**. Other neurons, receptors, and afferent (sensory) neurons are specialized to receive signals from within the body or from the external environment and to transmit that information to the central nervous system. Efferent neurons carry signals from the central nervous system to the effector organs (muscles and glands) of the body. If an efferent neuron is connected to a muscle, it is also called a motor neuron.

The ability of a neuron to carry out its function of integration and propagation depends both upon its structure and its ability to generate electrical and chemical signals. While different neurons have different shapes, all neurons share the same signaling abilities.

The Structure of a Typical Neuron

Neurons have many different shapes and sizes. However, a typical neuron in a vertebrate (such as a human) consists of four major regions: a cell body, dendrites, an **axon**, and synaptic terminals. Like all cells, the entire neuron is surrounded by a cell membrane. The cell body (soma) is the enlarged portion of a neuron that most closely resembles other cells. It contains the **nucleus** and other **organelles** (for example, the **mitochondria** and **endoplasmic reticulum**) and it coordinates the metabolic activity of the neuron. The dendrites and axon are thin **cytoplasmic** extensions of the neuron. The dendrites, which branch out in treelike fashion from the cell body, are specialized to receive signals and transmit them toward the cell body. The single long axon carries signals away from the cell body.

In humans, a single axon may be as long as 1 meter (about 3 feet). Some neurons that have cell bodies in the spinal cord have axons that extend all the way down to the toes. Axons generally divide and redivide near their ends and each branch gives rise to a specialized ending called a synaptic knob (synaptic terminal). It is the synaptic terminals of a neuron that form connections either with the dendrites or cell body of another neuron or with effector cells in muscles or glands. Once an electrical signal has arrived at the end of an axon, the synaptic terminals release a chemical messenger called a neurotransmitter, which relays the signal across the synapse to the next neuron or to the effector cell.

Classifying Neurons by Shape

Neurons can be classified according to the number of processes that extend from the cell body. Multipolar neurons are the most common type. They have several dendrites and one axon extending from the cell body. Bipolar neurons have two processes extending from the cell body, an axon and a single dendrite. This type of neuron can be found in the retina. Unipolar neurons are generally sensory (afferent) neurons that have a single process, which then divides into two. One of the two processes extends outward to receive sensory information from various areas of the body, while the other process relays sensory information towards the spinal cord or brain.

Electrical Signals in Neurons

All living cells have a separation of charges across the cell membrane. This separation of charges gives rise to the resting **membrane potential**.

central nervous system brain and spinal cord

axon long extension of a nerve cell down which information flows

nucleus membrane-bound portion of cell containing the chromosomes

organelle membrane-bound cell compartment

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

endoplasmic reticulum network of membranes within the cell

cytoplasm material in a cell, excluding the nucleus

membrane potential electrical and chemical differences across a membrane leading to storage of energy and excitability

Scanning electron micrograph of two types of neurons: a bipolar neuron (top) and a developing neuron (bottom).

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 and is the building block of cellulose in plants

mitosis separation of replicated chromosomes

HYDE, IDA HENRIETTA (1857–1945)

American physiologist who invented the microelectrode, a tiny needle used to measure electrical activity in living cells. The microelectrode was fundamental to studies of nerve and muscle cells. Hyde was the first woman elected to the American Physiological Society and the first woman to conduct research at Harvard Medical School.

Neurons and muscle cells both use brief changes in this resting membrane potential to quickly send signals from one end of the cell to the other. In neurons, electrical signals called action potentials propagate from the cell body down the axon to the synaptic terminals, where stored neurotransmitter is released. Action potentials are transient, all-or-none changes in resting membrane potential that travel along the axon at rates of 1 to 100 meters per second.

Myelin, a fatty insulating material derived from the cell membranes of **glial** cells, covers the axons of many vertebrate neurons and speeds the conduction of action potentials. The importance of this myelin covering to normal nervous system function is made painfully obvious in individuals with demyelinating diseases in which the myelin covering of the axons is destroyed. Among these diseases is multiple sclerosis, a demyelinating disease of the central nervous system that can have devastating consequences, including visual, sensory, and motor disturbances.

Although neurons share many of the features found in other cell types, they have some special characteristics. For example, neurons have a very high metabolic rate and must have a constant supply of oxygen and **glucose** to survive. Also, mature neurons lose the ability to divide by **mitosis**. Until the late twentieth century it was thought that no new neurons were produced in the adult human brain. However, there is evidence that, at least in some brain areas, new neurons are produced in adulthood. This finding suggests an exciting avenue for possible approaches to treating such common neurological diseases as Parkinson's disease and Alzheimer Disease, which are characterized by the loss of neurons in certain brain areas. SEE ALSO AUTOIMMUNE DISEASE; BRAIN; CENTRAL NERVOUS SYSTEM; CHEMORECEPTION; EYE; HEARING; MUSCLE; NERVOUS SYSTEMS; NEUROLOGIC DISEASES; PERIPHERAL NERVOUS SYSTEM; PSYCHOACTIVE DRUGS; SPINAL CORD; SYNAPTIC TRANSMISSION; TOUCH

Katja Hoehn

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Nitrogen Cycle

The nitrogen cycle is the series of biogeochemical transformations in which the element nitrogen is transferred among organisms and nonliving reservoirs such as the soil, the oceans, and the atmosphere. Nitrogen is an essential element for all living things because it is a principal component of **proteins** and nucleic acids. Whereas animals generally have access to abundant nitrogen, it is often in short supply for plants.

Ammonification

Most of the world's nitrogen is in the atmosphere, in the form of nitrogen gas (N_2), which is extremely unreactive. Atmospheric nitrogen is ammonified, or converted to ammonia (NH_3) or ammonium **ion** (NH_4^+), in several ways. It occurs through **enzymatic** nitrogen fixation, which is carried out by either free-living or symbiotic bacteria; through lightning, volcanic eruptions, and other high-energy events in the atmosphere; and finally by industrial processes. Industrial ammonification, which requires large amounts of energy, is used to create ammonia and nitrate for use as agricultural fertilizer. Industrial processes convert approximately 80 million metric tons of nitrogen per year, whereas bacterial nitrogen fixation converts slightly more, with about half of that carried out by crop plants. Ammonia is also produced through the action of fungus and bacteria breaking down **organic** compounds in the soil.

Nitrification, Denitrification, and Assimilation

Aerobic soil bacteria convert ammonia and ammonium to nitrate (NO_3^-), which can be absorbed by plants. This process, called nitrification, is counterbalanced by denitrification, which forms N_2 and N_2O, carried out by **anaerobic** bacteria. Nitrate is assimilated, or absorbed by plants, through their roots. Within the plant, nitrate is reconverted to ammonium for use in building organic compounds. Nitrogen moves through the food chain in these compounds and is eventually returned to the environment through urine, feces, or the decomposition of the organism.

Human nitrogen use has had a major impact on the nitrogen cycle. The agricultural use and overuse of nitrogen fertilizer has caused pollution of water bodies both near farms and more distantly. Nitrate in the soil is easily washed out and can become a pollutant of both groundwater and surface water. Nitrogen is usually a limiting nutrient in aquatic **ecosystems**, and therefore its runoff often produces overgrowth, or "eutrophication." Chronic eutrophication can change species composition of lakes, streams, and rivers. SEE ALSO Biogeochemical Cycles; Cyanobacteria; Ecology; Eubacteria; Nitrogen Fixation; Pollution and Bioremediation

Richard Robinson

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions
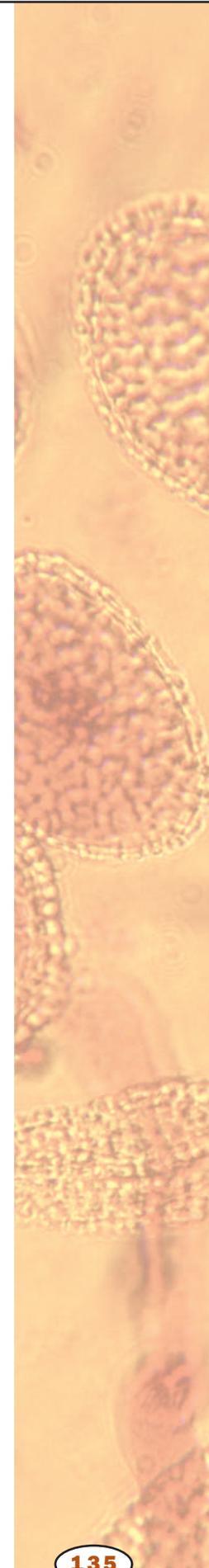
ion an electrically charged particle

enzymatic related to function of an enzyme

organic composed of carbon, or derived from living organisms

anaerobic without oxygen, or not requiring oxygen

ecosystem an ecological community and its environment

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Human Alterations of the Global Nitrogen Cycle. <http://esa.sdsc.edu/tilman.htm>.

Nitrogen Fixation

symbiotic cooperative; mutually beneficial

Nitrogen fixation refers to the conversion of atmospheric nitrogen gas (N_2) into a form usable by plants and other organisms. Nitrogen fixation is conducted by a variety of bacteria, both as free-living organisms and in **symbiotic** association with plants. Because it is the principal source of the nitrogen in the soil, nitrogen that plants need to grow, nitrogen fixation is one of the most important biochemical processes on Earth. Even modern agricultural systems depend on nitrogen fixation by alfalfa, clover, and other legumes to supplement chemical nitrogen fertilizers.

amino acid a building block of protein

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

Living organisms need nitrogen because it is a part of the **amino acids** that make up **proteins**, and the nucleic acids that make up DNA (deoxyribonucleic acid) and RNA (ribonucleic acid). Nitrogen within living organisms is eventually decomposed and converted to atmospheric nitrogen (N_2). This form, however, is highly stable and unreactive chemically, and is therefore not available for use by most organisms. Some species of bacteria, though, can convert N_2 into NH_3 (ammonia) or other usable forms of nitrogen. These nitrogen-fixing bacteria include species of the genera *Rhizobium*, *Anabaena*, *Azotobacter*, and *Clostridium*, as well as others.

enzyme protein that controls a reaction in a cell

Each of the nitrogen-fixing bacteria employs the same **enzyme**, nitrogenase. The nitrogenase enzyme is shaped something like a butterfly, and contains an atom of molybdenum at its core that is crucial for the reaction. Soils deficient in molybdenum cannot sustain effective nitrogen fixation, and monitoring soil for this element is important to ensure maximum fixation in managed fields or pastures.

Nitrogenase requires a large amount of energy to convert N_2 to NH_3. Free-living bacteria must obtain the nutrients for supplying this energy themselves. Other bacteria have developed symbiotic associations with plants to provide them with sugars, supplying both a source of energy and a source of carbon for the bacterium's own synthetic reactions. The bacteria, in turn, supply the plant with some of the fixed nitrogen. For instance, the nitrogen-fixing *Anabaena* lives symbiotically with a water fern, *Azolla*. *Azolla* is grown in rice paddies early in the season. As the rice grows above the water surface, it shades out the fern, which dies, releasing the stored nitrogen. In this way, the paddy is fertilized without application of chemical fertilizers.

The bacterial genera *Rhizobium* and *Bradyrhizobium* have developed a large number of symbioses with members of the Fabaceae (legume) family. Fabaceae includes alfalfa, clover, beans and peas of all kinds, mesquites, acacias, and dozens of other species both domesticated and wild. The roots of the host plant become infected with the bacteria as seedlings, and respond by surrounding the bacteria with root hairs. The relationship between a particular host species and a particular bacterium is highly specific,

Nitrogen-fixing bacteria *Rhizobium* on the roots of the broad bean plant *Vicia faba.*

and is regulated by a series of recognition events that prevent the wrong species of bacterium from taking up residence in the wrong plant.

The plant eventually develops a specialized structure known as a nodule, while the bacteria inside grow into enlarged forms known as bacteroids. The oxygen concentration inside the nodule must be closely regulated, since oxygen inhibits nitrogenase. This regulation is aided by the presence of leghemoglobin, an oxygen-binding protein similar to **hemoglobin**. The heme (oxygen-binding) portion is produced by the bacterium, while the globin (protein) portion is produced by the host plant, again illustrating the closeness of the symbiotic relationship.

Richard Robinson

hemoglobin oxygen-carrying protein complex in red blood cells

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Nonspecific Defense

In animals, there are two types of defenses against foreign invaders: specific and nonspecific. Specific immune responses can distinguish among different invaders. The response is different for each invader. With nonspecific defenses, the protection is always the same, no matter what the invader may be. Whereas only vertebrates have specific immune responses, all animals have some type of nonspecific defense. Examples of nonspecific defenses include physical barriers, **protein** defenses, cellular defenses, inflammation, and fever.

Barriers

One way for an organism to defend itself against invasion is through barriers that separate the organism from its environment. Physical barriers such as the skin and **mucous membranes** mechanically regulate what enters the body. **Secretions** provide protection at the barrier as well. Mucus, for example, can trap potential invaders. Also, skin secretions are slightly **acidic**, inhibiting bacterial growth. Many body secretions (such as mucus, tears, and saliva) contain an **enzyme** called lysozyme that destroys bacteria.

Proteins

There are proteins that protect the body nonspecifically. Complement proteins are found in the blood. When they bind to an invader, they stimulate inflammation, **phagocytosis**, and destruction of the invader's membrane. Although complement proteins may bind to an invader directly, they are most effective when they bind to antibodies that are attached to an invader. Antibodies are part of the body's specific immune response.

Some immune cells and cells that are infected with viruses produce another set of proteins called **interferons**. Interferons send a warning to nearby cells. They help prevent infection by stimulating the production of antiviral proteins. Interferons also stimulate natural killer cells and macrophages.

Cellular Defenses

Natural killer cells and macrophages are examples of nonspecific cellular defenses. Natural killer cells are a class of lymphocytes that recognize abnormal cells (such as cancerous cells or virus-infected cells), attach to them, and release chemicals that destroy them.

Macrophages, neutrophils, and eosinophils are examples of phagocytes. In their attempt to defend the body, some phagocytes stay within a tissue and others travel freely throughout the body. However, all phagocytes are attracted to sites of tissue damage. In a process called phagocytosis, these cells surround debris or a foreign invader, bringing it inside the cell. The phagocyte then uses special enzymes to digest the material.

All animals have phagocytes that recognize and eliminate foreign invaders. For example, if a piece of one sponge is transplanted to a sponge from another colony, phagocytes in the sponges will attack and destroy each other. The same response can be observed in earthworms, **arthropods**, starfish, and all vertebrates. Scientist Elie Metchnikoff observed this process in starfish.

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

mucous membrane outer covering designed to secrete mucus, often found lining cavities and internal surfaces

secretion material released from the cell

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

enzyme protein that controls a reaction in a cell

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

interferons signaling molecules of the immune system

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

In 1882 a scientist named Elie Metchnikoff stuck a thorn into a starfish larva. He observed starfish cells trying to destroy the thorn. His discovery was an important step in understanding nonspecific defenses in animals.

A colored scanning electron micrograph of a macrophage engulfing a parasite of the *Leishmania* genus. To defend the body, macrophages will surround a foreign invader, bring it inside the cell, then use enzymes to digest the material.
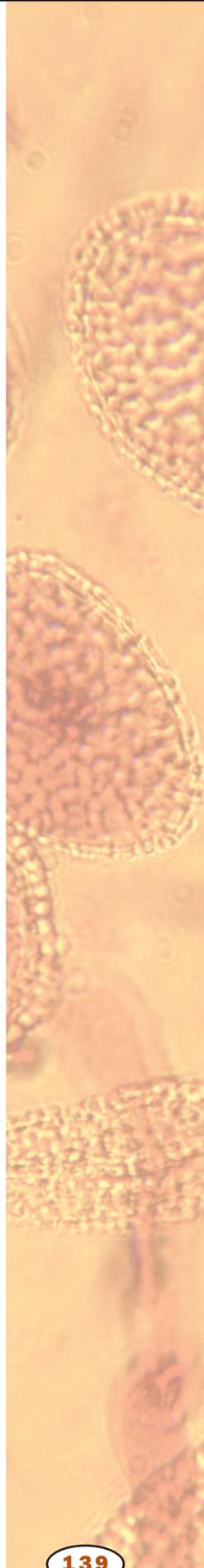
In vertebrates, some phagocytes are also important in stimulating specific immune responses. Additionally, phagocytosis is stimulated when the invaders are coated with antibodies. Consequently, phagocytes (like complement proteins) represent an important link between nonspecific and specific immunity.

Inflammation

Infection, mechanical force, chemicals, and extreme heat or cold can damage tissues, causing the nonspecific process of inflammation. The goal of inflammation is to clean up the damage and start the repair process. Inflammation begins when damaged tissues release chemical messengers such as histamine, **prostaglandins**, and leukotrienes. These chemicals cause nearby blood vessels to expand and become more leaky, allowing more blood flow to the damaged area. These chemicals also attract white blood cells (such as phagocytes) to the site to remove debris and foreign invaders. The results of these activities are easily observed when the skin is inflamed: swelling, redness, heat, and pain.

prostaglandins hormonelike molecules released by one cell that affect nearby cells, including smooth muscle

Fever

Another nonspecific protection against infection is the development of a fever. Either the invader or the response to an invader causes a part of the

brain called the hypothalamus to increase the body temperature. Fevers may increase body **metabolism**, speeding up the repair process. Fevers may also slow down the reproduction of some bacteria and viruses.

metabolism chemical reactions within a cell

Whether the mechanism is as complex as fever and inflammation or as simple as physical barriers and phagocytosis, all nonspecific defenses provide the body with general protection against foreign invaders. SEE ALSO ANTIBODY; BLOOD; ENDOCYTOSIS; IMMUNE RESPONSE

John M. Ripper

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Nuclear Transport

The distinguishing feature of **eukaryotic cells** is the segregation of ribonucleic acid (RNA) synthesis and deoxyribonucleic acid (DNA) replication in the **nucleus**, keeping it separate from the **cytoplasmic** machinery for **protein** synthesis. As a consequence, messenger RNAs, ribosomal RNAs, transfer RNAs, and all cytoplasmic RNAs of nuclear origin must be transported from their site of synthesis in the nucleus to their final cytoplasmic destinations. Conversely, all nuclear proteins must be imported from the cytoplasm into the nucleus.

eukaryotic cell a cell with a nucleus

nucleus membrane-bound portion of cell containing the chromosomes

cytoplasm material in a cell, excluding the nucleus

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

macromolecules large molecules such as proteins, carbohydrates, and nucleic acids
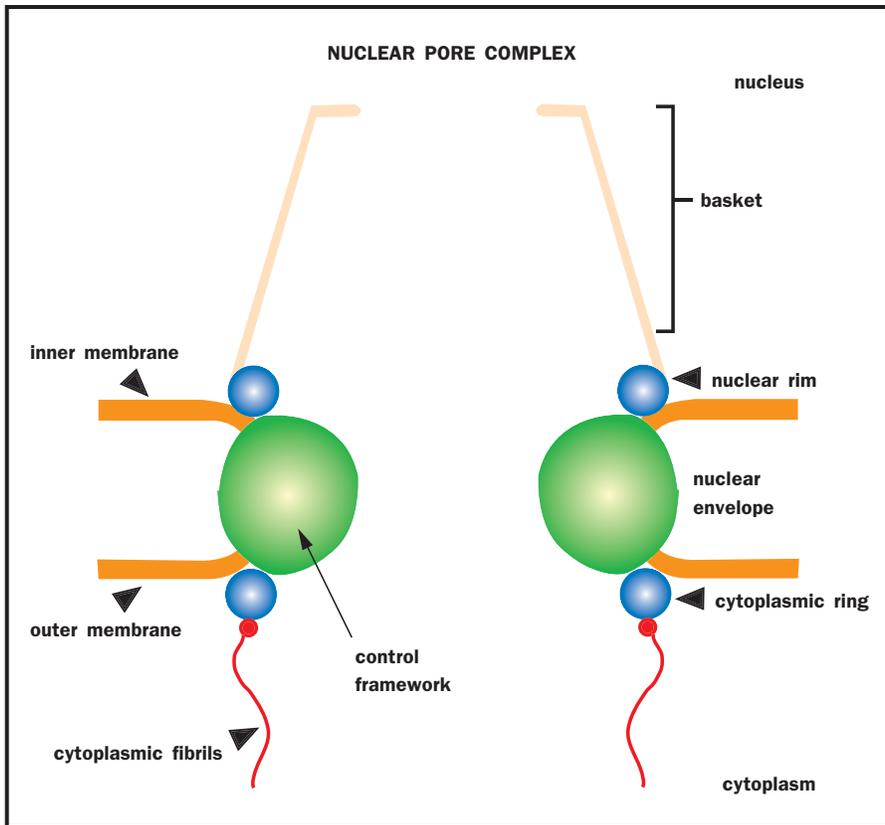
aqueous watery or water-based

nuclear envelope double membrane surrounding the cell nucleus

amino acid a building block of protein

Traffic of **macromolecules** between the nucleus and cytoplasm occurs through nuclear pore complexes (NPCs). NPCs are large proteinaceous structures that form **aqueous** channels across the **nuclear envelope** or membrane. NPCs are composed of multiple copies of up to about fifty proteins termed nucleoporins and consist of three structural units. A ringlike central framework surrounding the central channel of the pore is sandwiched between two peripheral structures: the cytoplasmic ring from which eight cytoplasmic fibrils emanate, and the nuclear rim that anchors the nuclear basket.

Nuclear transport depends on signals for import or export that form part of the transported molecules. These signals are referred to as nuclear localization signals (NLSs) or nuclear export signals (NES), respectively. In proteins, they are specific **amino acid** sequences. NLSs or NESs are recognized and bound by soluble import or export receptors that shuttle between nucleus and cytoplasm. The interaction of the receptors with their cargoes (or substrates) can be direct or mediated by an additional adapter protein. Upon binding, the transport receptors dock their cargoes to the NPC and facilitate their translocation across the central channel of the pore. After delivering their cargoes, the receptors are recycled to initiate addi-

NUCLEAR PORE COMPLEX

nucleus

basket

inner membrane

nuclear rim

nuclear envelope

outer membrane

cytoplasmic ring

control framework

cytoplasmic fibrils

cytoplasm

The structure of the nuclear pore complex.

tional rounds of transport. According to this model, an export receptor (R) binds its substrate (S) in the nucleus and carries it through the NPC into the cytoplasm. On the cytoplasmic side, the exported cargo is released and the receptor returns to the nucleus without the cargo. Conversely, an import receptor binds its import cargo in the cytoplasm and releases it in the nucleus.

The vast majority of nuclear transport receptors are members of a large family of proteins that exhibit a high **affinity** for a small GTPase, called Ran, in the GTP bound form. GTP (guanosine triphosphate) is an energy-carrying molecule used in cell signaling. A GTPase like Ran can cause GTP to become GDP (guanosine diphosphate), which will change the properties of the GTPase. The GTPase Ran regulates the interaction of the receptors with their cargoes.

affinity attraction

The GTPase acts in concert with several cofactors. The striking property of Ran cofactors is that they are asymmetrically localized in the cell, with some predominantly cytoplasmic while others are predominantly found in the nucleus. This asymmetry helps to control the two-way transport between nucleus and cytoplasm. SEE ALSO MEMBRANE TRANSPORT; NU-CLEOTIDES; NUCLEUS; PROTEIN TARGETING; RNA

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Nucleolus

nucleus membrane-bound portion of cell containing the chromosomes

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

transcribe creation of an RNA copy of a DNA gene

cytoplasm material in a cell, excluding the nucleus

translation synthesis of protein using mRNA code

mitosis separation of replicated chromosomes

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

transcription messenger RNA formation from a DNA sequence

The nucleolus is by far the most easily recognized substructure in the eukaryotic **nucleus**, and can be seen by using a variety of dyes as well as by phase contrast microscopy. Indeed, in budding yeast, the single nucleolus takes up nearly half of the nucleus. Cells from other species often have multiple nucleoli. The nucleolus is a **ribosome** factory, composed of deoxyribonucleic acid (DNA), ribonucleic acid (RNA), and **protein**. At the nucleolus, a long ribosomal RNA (rRNA) precursor molecule is **transcribed** from DNA, processed into three mature RNAs, and packaged together with specific proteins to make the large and small ribosomal subunits. Once the subunits have been assembled, they are transported out of the nucleolus to the **cytoplasm** for use in **translation** (protein synthesis).

Nucleoli are not static structures. They disassemble during **mitosis** and reform in early G1 phase. Nucleolar formation does not *cause* expression of rRNA **genes**. Rather, nucleoli are the *result* of rRNA **transcription** and processing.
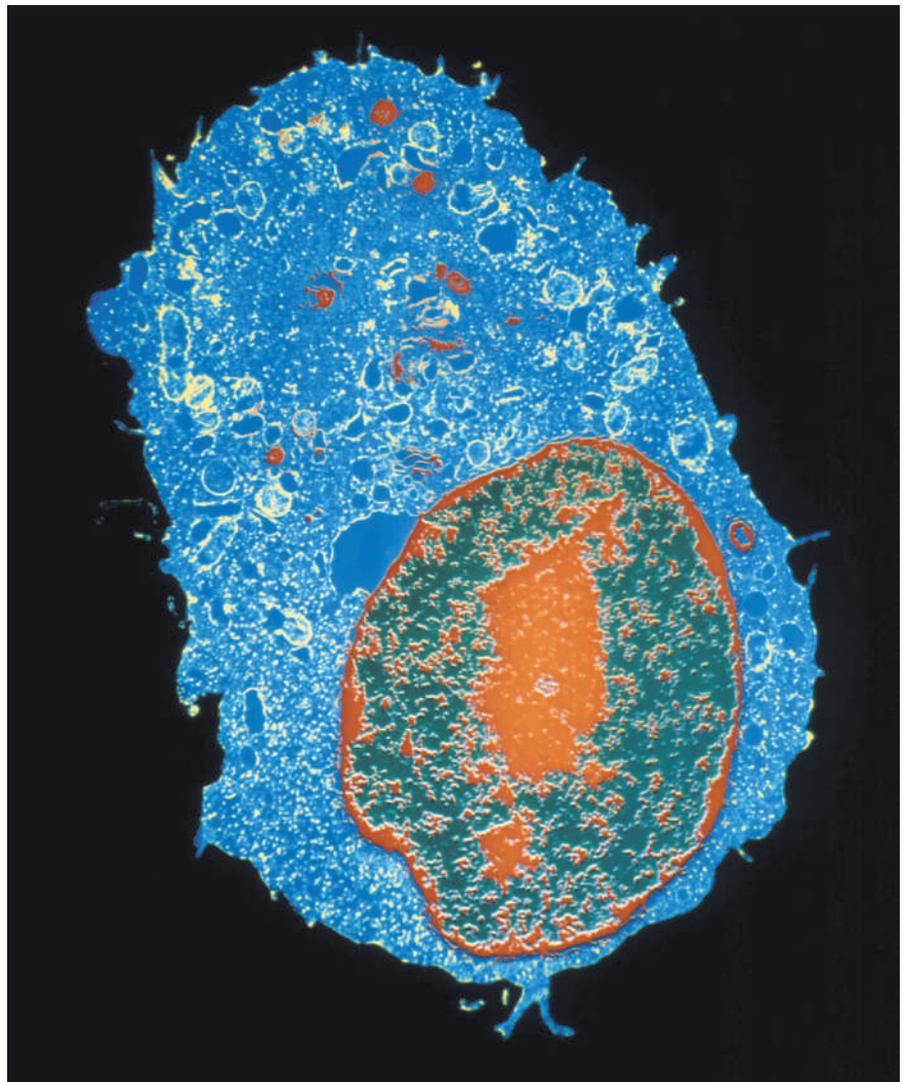
A colored transmission electron micrograph of a mammalian tissue culture cell, showing the nucleus (red), nucleolus (orange), and cytoplasm (blue),

Viewed in the electron microscope, a nucleolus has two distinct parts: the fibrillar component and the granular component. The fibrillar component can be subdivided into two compartments: the dense fibrillar component and the fibrillar center. Fibrillar centers contain large amounts of RNA polymerase I, which transcribes rRNA. Transcription of rRNA genes is thought to occur at the interface between the dense fibrillar component and the fibrillar center. Later stages of ribosome assembly take place in the granular component.

Human **chromosomes** contain five nucleolar organizer regions (called NORs), located on the short arms of the chromosomes 13, 14, 15, 21, and 22. In humans, each NOR contains approximately one hundred tandemly repeated rRNA gene copies. The NORs of different chromosomes typically come together in interphase. Thus, a single nucleolus is often made up of rRNA genes from two or more different NORs. Some species have only a single NOR-bearing chromosome and thus a single nucleolus.

In addition to the well-established function of nucleoli in ribosome assembly, recent evidence suggests that nucleoli are also involved in several other cellular processes, including assembly and modification of various small **ribonucleoproteins** (RNPs), sequestration of important cell-cycle regulatory proteins, export of other nonribosomal RNAs, and control of cellular senescence or aging. SEE ALSO CHROMOSOME, EUKARYOTIC; NUCLEAR TRANSPORT; NUCLEUS; RIBOSOME; RNA; TRANSCRIPTION

A. Gregory Matera

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

ribonucleoprotein combination of RNA and protein

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Nucleotides

Nucleotides are the subunits that are linked to form the nucleic acids ribonucleic acid (RNA) and deoxyribonucleic acid (DNA), which serve as the cell's storehouse of genetic information. Free nucleotides play important roles in cell signaling and **metabolism**, serving as convenient and universal carriers of metabolic energy and high-energy electrons.

metabolism chemical reactions within a cell

All nucleotides are composed of three parts: a five-carbon sugar, a phosphate, and a nitrogen-rich structure called a nitrogenous base. The sugar can be ribose, which is found in ribonucleotides and RNA, or deoxyribose, which is found in deoxyribonucleotides and DNA. The only difference between these two sugars is that deoxyribose has one fewer oxygen atom than ribose. The five carbon atoms in the sugar are numbered sequentially. To distinguish these carbon atoms from those of the nitrogenous base, which are also numbered, they are designated as 1′ (prime), 2′, and so on.

There are five nitrogenous bases. The so-called pyrimidines (cytosine, thymine, and uracil) are smaller, having only one ring structure. The larger purines (adenine and guanine) have two rings. Adenine, guanine, and cytosine are found in both ribonucleotides and deoxyribonucleotides, while

The molecular structures of the five nitrogenous bases.

thymine occurs only in deoxyribonucleotides and uracil only in ribonucleotides.

The phosphate group is bonded to the 5′ carbon of the sugar (see Figure 2), and when nucleotides are joined to form RNA or DNA, the phosphate of one nucleotide is joined to the sugar of the next nucleotide at its 3′ carbon, to form the sugar-phosphate backbone of the nucleic acid. In a free nucleotide, there may be one, two, or three phosphate groups attached to the sugar, as a chain of phosphates attached to the 5′ carbon.

Three nucleotides merit special consideration because of their specialized roles in cellular function. These are adenosine triphosphate (ATP), flavin adenine dinucleotide (FAD), and nicotinamide adenine dinucleotide (NAD$^+$). Most **biosynthetic** reactions require energy, which is usually supplied by ATP. When ATP is **hydrolyzed** to ADP (adenosine diphosphate) or **AMP** (adenosine monophosphate), energy is released. By coupling this energy release to a reaction requiring energy, that reaction can be made to occur. Since ATP is so frequently used this way, it is commonly called the "energy currency of the cell."

Adenine-containing molecules are also important coenzymes, serving to carry chemical functional groups that are needed for **enzyme** activity. Three important adenosine-containing coenzymes are coenzyme A (CoA), FAD, and NAD$^+$. CoA carries acetyl groups into the Krebs cycle (the central metabolic pathway in **mitochondria**), and FAD and NAD$^+$ carry high-energy electrons from the Krebs cycle to the **electron transport system**, where their energy is used to synthesize ATP from ADP and **inorganic** phosphate.

Another adenine-based molecule is important in cellular signaling. When a **hormone** binds at a cell-surface receptor, it often promotes the production of cyclic AMP (cAMP) inside the cell. In cAMP, the phosphate group is joined to the 3′ and 5′ carbons of the ribose, forming a small ring struc-

BASES
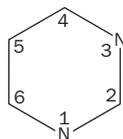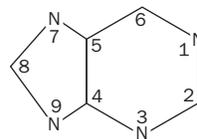
The bases are nitrogen-containing ring compounds, either purines or pyrimidines.
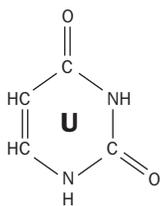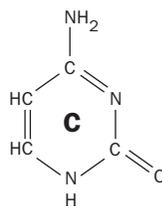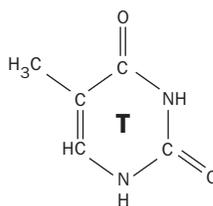
uracil   cytosine   thymine   adenine   guanine
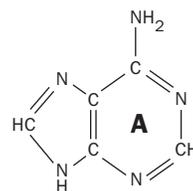
NUCLEOTIDES

PHOSPHATE

BASE

$$\text{}^-O-\overset{\overset{\displaystyle O}{\|}}{\underset{\underset{\displaystyle O^-}{|}}{P}}-O-CH_2$$

SUGAR

OH |OH|
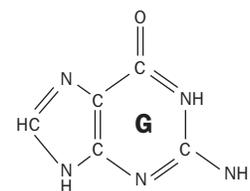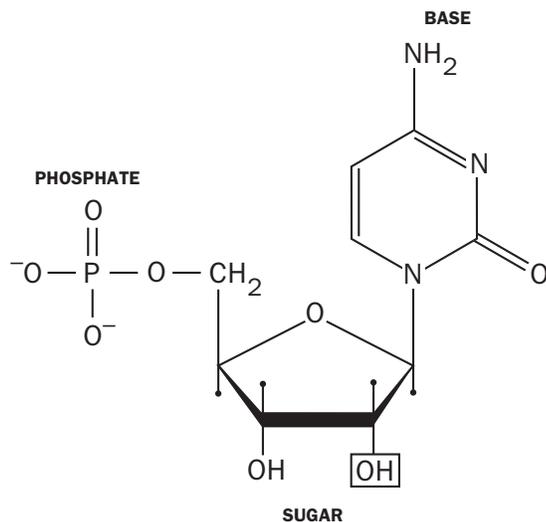
A nucleotide consists of a nitrogen-containing base, a 5-carbon sugar, and one or more phosphate groups. The sugar dipicted is ribose. Deoxyribose has an H instead of an OH in the boxed position.

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ture. cAMP can activate or suppress various cell processes, thereby serving as an **intracellular** signal and messenger that responds to hormone binding. SEE ALSO DNA; METABOLISM, CELLULAR; RNA; VITAMINS AND COENZYMES

David W. Tapley

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Nucleus

In eukaryotic cells, **chromosomes** are found in a special compartment called the nucleus. The nucleus is a defining feature of eukaryotic cells, which range from single-celled yeasts to plants and humans. In contrast, bacteria and other prokaryotes are more ancient in evolution and lack a nucleus. The development of the nucleus contributed to the evolution of complex life forms by separating **transcription** (reading of **genes**, occurring inside the nucleus) from **translation** (protein synthesis, occurring in the **cytoplasm**) and by providing a structural framework for organizing and regulating larger **genomes**. In multicellular organisms, individual cells can express different subsets of genes and thereby form specialized tissues such as muscle or skin.

The Nuclear Envelope

The nuclear envelope surrounds the nucleus and creates and maintains a special environment inside it. The envelope consists of two nuclear mem-

intracellular within a cell

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

transcription messenger RNA formation from a DNA sequence

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

translation synthesis of protein using mRNA code

cytoplasm material in a cell, excluding the nucleus

genome total genetic material in a cell or organism
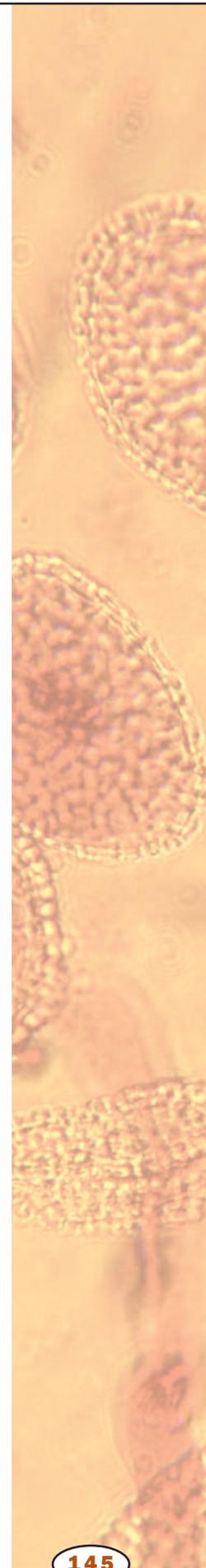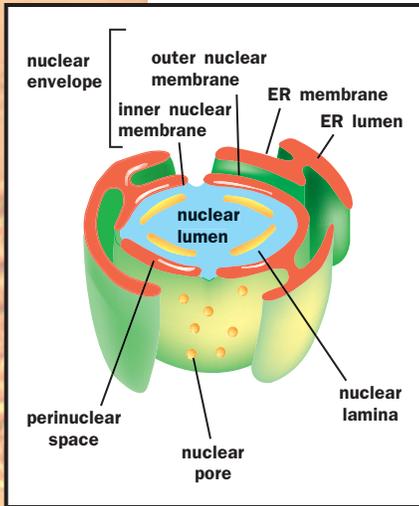
Illustration of the nuclear envelope.

endoplasmic reticulum network of membranes within the cell

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

intermediate filament protein one type of cytoskeleton protein

neuron nerve cell

enzyme protein that controls a reaction in a cell

gene expression use of a gene to create the corresponding protein

chromatin complex of DNA, histones, and other proteins making up chromosomes

aqueous watery or water-based

ribosome protein-RNA complex in cells that synthesizes protein

branes (inner and outer), nuclear pore complexes, and the lamina, a fibrous network. The nuclear membranes form an impermeable barrier. The outer membrane faces the cytoplasm and is part of the **endoplasmic reticulum** (ER). The inner membrane faces the chromosomes. Movement into and out of the nucleus occurs through pores (holes) where the inner and outer membranes are fused together. However, the pores are not empty; nuclear transport is controlled by nuclear pore complexes, each consisting of about a thousand **proteins** ("nucleoporins"). Each pore complex is large enough to accommodate the passage of ribosomal subunits, large protein-RNA (ribonucleic acid) complexes, which exit the nucleus after being assembled in the nucleolus.

The third major component of the envelope, the nuclear lamina, is found in multicellular eukaryotes (including humans), but not in single-celled eukaryotes or plants. (The plant nucleus evolved independently; less is known about its structure.) The lamina is a meshwork of fibers, formed by the head-to-tail polymerization of proteins named lamins. These fibers are concentrated near the inner membrane and also extend throughout the nuclear interior. Lamins are a type of **intermediate filament protein** and are strong yet flexible. Humans have three lamin genes, which through alternative messenger RNA (mRNA) splicing can produce seven "flavors" of A- and B-type lamin proteins. Different cell types, such as muscles and **neurons**, express different combinations of lamins.

Lamin filaments are key architectural elements in the nucleus. Beside providing structural stability, lamins also provide attachment sites for other proteins inside the nucleus. Biologists are discovering a growing number of proteins that bind to lamins. Lamin-binding proteins such as LAP2, emerin, and LBR are anchored at the inner nuclear membrane and also bind to chromosomes. This results in two-way and three-way attachments between the inner membrane, lamina, and chromosomes.

Three-Dimensional Organization inside the Nucleus

When purified nuclei are treated with salts and **enzymes** to remove most proteins and DNA, what remains is a three-dimensional filamentous structure named the nuclear matrix. The composition of the matrix, and whether it includes lamins, has been controversial. However, deoxyribonucleic acid (DNA) replication machinery is stably attached to the matrix. Thus, the matrix may provide a scaffold that allows the orderly replication of chromosomal DNA, and possibly other activities inside the nucleus.

Chromosomes fill much of the nuclear interior, with each chromosome occupying its own neighborhood. In differentiated human cells, sectors of each chromosome are structurally compressed to prevent **gene expression**. This repressed **chromatin**, termed heterochromatin, is often located near the nuclear envelope. Other sections of chromosomes are loosely extended ("euchromatin"), making these genes available for transcription and mRNA processing at the surface of compact chromatin. Proteins responsible for transcription and mRNA processing are highly mobile and move rapidly within the **aqueous** spaces between and surrounding the chromatin fibers. There are also two specialized structures inside the nucleus, which are factories for making multiprotein "machines." The nucleolus is the factory where **ribosomes** (the translational machines) are assembled. Nucleoli form

around the genes that encode ribosomal structural RNAs. Cajal bodies (coiled bodies) are smaller round structures that are proposed to be factories for assembling "transcription machines" responsible for transcribing genes into mRNA.

In Multicellular Eukaryotes, the Nucleus Disassembles During Mitosis

In mammalian cells, the nucleus organizes about 0.7 meters (2.3 feet) of DNA inside a sphere approximately 5 **microns** in diameter. Remarkably, this structure is completely disassembled when mammalian cells undergo **mitosis**. Nuclear disassembly is triggered by mitotic **phosphorylation** of key structural proteins, including lamins, lamin-binding proteins, and nucleoporins. Phosphorylation causes these proteins to change **conformation** and release each other. Released nuclear membranes merge into the ER network, whereas released lamins and nucleoporins disperse throughout the cytoplasm. These components are then recycled to form two nuclear envelopes, soon after the two sets of daughter chromosomes are segregated.

During nuclear assembly, membranes reattach to chromosomes and fuse to enclose the chromosomes within one unified envelope. Pore complexes assemble and begin importing nuclear proteins that were released during mitosis, including lamins. The lamins reassemble into filaments, and the condensed chromosomes expand as the envelope expands to its full size. Few of these steps are understood at the molecular level.

Defects in Nuclear Envelope Proteins Cause Human Disease

In the **nematode** worm, *C. elegans*, which has only one lamin gene, lamins are essential for life. Lamins are also important, either directly or indirectly, for nuclear shape, nuclear stability, chromatin attachment to the envelope, spacing of nuclear pore complexes, chromosome segregation, completion of mitosis, nuclear assembly, and the elongation phase of DNA replication.

In organisms with multiple lamin genes, the "extra" lamins appear to have specialized functions. For example, the lamin A/C gene is expressed mostly in differentiated cells. People who inherit one mutated copy of the lamin A/C gene develop one of three different diseases: the **autosomal dominant** form of Emery-Dreifuss muscular dystrophy; dilated **cardiomyopathy** with conduction system disease; or Dunnigan-type familial partial lipodystrophy (loss of fat tissue). Cardiomyopathy and lipodystrophy are correlated with **missense mutations** that change one **amino acid** in different regions of lamin A. Missense mutations might prevent lamin A/C from assembling properly, or might prevent its recognition by one or more binding partners. The loss of emerin, a membrane protein that binds lamins A/C, causes the X-linked recessive form of Emery-Dreifuss muscular dystrophy.

These diseases are not yet well understood. However, lamins and lamin-binding proteins may provide attachment sites needed by other nuclear proteins. For example, retinoblastoma, a transcriptional repressor critical for cell growth control, associates with the nuclear lamina. Insight into the functions of the nucleus may help to alleviate some diseases. SEE ALSO

micron one-millionth of a meter; also called a micrometer

mitosis separation of replicated chromosomes

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

conformation three-dimensional shape

nematode worm of the Nematoda phylum, many of which are parasitic

autosomal dominant pattern of inheritance in which inheritance of a single allele from either parent results in expression of the trait

cardiomyopathy heart muscle disease

missense mutation nucleotide change that causes a change in the amino acid normally added to the protein

amino acid a building block of protein

Chromosome, Eukaryotic; DNA; Nuclear Transport; Nucleolus; Replication

Katherine L. Wilson

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Nurse

Nurses are health care professionals with direct responsibility for patient care. Nurses work in hospitals, clinics, long-term care facilities, schools, corporations, and many other settings. In hospitals, nurses provide care under a treatment plan prescribed by doctors, but often have considerable responsibility for managing the details of the patient's daily care. In other settings, nurses may be the first health care professional seen by a patient, and may be responsible for recommending treatment in conjunction with the doctor. Nurses combine medical expertise with strong interpersonal skills and a desire to help people.

To become a nurse, high school courses in math and science are required. Nurse training programs are offered at hospitals, junior colleges, community colleges, and four-year colleges. The degree of training offered by each differs, as does the advancement possible as a result. Following graduation from the training program, the student must pass a state licensure exam to become a registered nurse (RN), and is then able to work as a nurse. Further education allows the RN to obtain a master's degree in nursing. This is required to become a nurse practitioner (a nurse who performs many of the same functions as a family-practice doctor), a nurse-midwife (provides care to maternity patients), or several other nursing specialties. SEE ALSO DOCTOR, FAMILY PRACTICE; MEDICAL ASSISTANT; NURSE PRACTITIONER

Richard Robinson

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National Student Nurses' Association. <http://www.nsna.org/>.

Nurse Practitioners

Nurse practitioners are registered professional nurses who have completed a graduate education program in advanced practice nursing. They provide many of the same services as physicians. A major focus for the nurse practitioner is the promotion of healthy lifestyles to prevent illness. Nurse practitioners can also diagnose and treat common minor health problems as well as chronic conditions, such as high blood pressure or diabetes. They order laboratory tests, prescribe medications, and prescribe various treatments. Studies have

NIGHTINGALE, FLORENCE (1820–1910)

English nurse, founder of the profession of nursing and one of the first scientists to use statistical analysis. Nightingale used sophisticated data analysis, presented in diagrams, to persuade English authorities to make reforms necessary to save the lives of wounded soldiers in military hospitals in Turkey.

shown that they provide cost-effective and high quality care. Although some nurse practitioners practice in hospitals, most work in clinics. Many provide health care to those who may not otherwise have access to care, such as in rural areas, community clinics, shelters, schools, and other settings.

Nurse practitioners must complete a four-year bachelor's degree in nursing and must have experience working as a registered nurse. The graduate nurse practitioner education program takes approximately two years to complete. Graduate study includes nursing coursework as well as advanced study in performing physical examinations, diagnosis, and treatment. The student also has hands-on education with a nurse practitioner and/or a physician preceptor in a clinic or other health care facility.

Students can choose from several specialty areas of study. Some of these specialties include family nurse practitioner (FNP), adult nurse practitioner (ANP), geriatric nurse practitioner (GNP), pediatric nurse practitioner (PNP), and women's health care nurse practitioner (WHCNP).

Students interested in becoming a nurse practitioner would benefit by taking high school sciences and the required college level prerequisites for nursing school. Spending time with a nurse practitioner and working or volunteering in any type of health care service organization is also suggested.

In 1990 nurse practitioners numbered 28,600. In 2000 nearly 70,000 existed, and it was predicted that there would be 116,000 by 2005. SEE ALSO DOCTOR, FAMILY PRACTICE; NURSE; PHYSICIAN ASSISTANT

Kevin Smith

A registered nurse listens with a stethoscope to a patient's heart.

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American Academy of Nurse Practitioners. <http://www.aanp.org/>.

Nutritionist

Nutrition is the study of food, essential nutrients, and other substances in food and their effects on the body in relation to health and disease. It concerns how we eat, digest, absorb, use, and **excrete** the many components of food. The study of nutrition encompasses psychological and social perspectives as well as biochemical and physiological approaches.

excrete deposit outside of

Nutritionists work in many different settings. Public health nutritionists may focus on developing programs to improve the nutritional status of specific populations, such as expectant mothers or the elderly. Community nutritionists may counsel individuals how to improve their diets, or develop educational materials on nutrition. These types of nutritionists often work for governmental agencies. They usually have obtained a bachelor's degree in nutrition, and often have advanced degrees, such as a master's degree in public health or science. There are also many opportunities in nutrition research, usually in a university or research institute. Nutritional epidemiologists, for example, study associations between nutrient intake and disease incidence in populations. Nutritional biochemists investigate how too little or too much of specific nutrients, both essential and nonessential, affect metabolic pathways and the development of various diseases. These positions require a B.S. in a biological science, with a doctoral degree (Ph.D.) in nutrition or closely related field.

Dietitians have completed a B.S. in nutrition from an accredited program and completed an approved internship, as certified by the American Dietetics Association. Dietitians often work in hospitals or clinics providing nutritional services to patients. They also manage food service operations in hospitals, long-term care facilities, and universities.

Since nutrition is a biological science, high school courses in math and the sciences are necessary. Strong communication and computer skills are also extremely important. In college, nutrition degrees include courses in chemistry, physiology, and biochemistry, similar to other biological majors.

Daniel D. Gallaher

Ocean Ecosystems: Hard Bottoms

The term "hard bottom" refers to the ocean region close to shore, where wave action prevents the accumulation of muddy sediment that will create a soft bottom. Plants and animals living on or in the seafloor are called benthos. Benthic epifauna reside on or attach to a rocky substrate (surface). Benthic infauna bury themselves in soft sediments or bore into the rocky bottom or shells of other animals.

Seaweeds, a kind of algae, anchor to the bottom with holdfasts. Unlike the roots of higher plants, holdfasts do not extract nutrients. Many seaweeds have pneumatocysts, gas-filled bladders that keep the photosynthetic parts of the seaweed in the photic zone, the near-surface layer of the ocean that light penetrates. All benthic animals are invertebrates. Although they inhabit all water depths, most are in the photic zone where light and nutrients are more abundant. Many benthic animals are **sessile**. Some are suspension feeders; they strain the fresh seawater brought in by waves, tides, or currents for **plankton** and other nutrients. Others wait for food to arrive.

When a small fish swims against a sea anemone's tentacles, it is stunned by poisonous nematocysts and then dragged into the anemone's central mouth. Some benthic animals can move to pursue their prey, scavenge over the bottom, or graze on seaweed-covered rocks. Starfish crawl on tube feet over a shellfish or sea urchin; they pry apart the shell with their arms, extrude their stomach into the prey's shell, and begin digestion. Many benthic animals exist for part of their life cycle as tiny planktonic larvae, drifting with the water to colonize new areas.

Benthic epifauna have enormous species diversity, reflecting the diversity in the benthic environment. In the intertidal—between the highest high and the lowest low tides—small distances bring large variations in substrate, temperature, salinity, moisture, **pH** level, wave action, dissolved oxygen, and food supply. Organisms at the top must contend with weather, predators from land, crashing waves, and an occasional influx of fresh water from storms. Organisms at the bottom face ocean predators and sometimes land predators, waves, weather, and drying out. For protection against predators and **desiccation**, the animals of the intertidal have shells (clams and barnacles) or **exoskeletons** (crabs and lobsters), or they appear as crusts on rocks (lichens and algae). Sea anemones huddle together to conserve moisture, and segmented worms and crabs retreat into mussel beds or rocks.

sessile attached and remaining in one place

plankton microscopic floating organisms

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

desiccation drying out

exoskeleton external skeleton

150

The anemone, tunicate, oyster, and sponge are examples of benthic fauna at the bottom of a lagoon in the Truk Islands.

For protection against waves and tides, intertidal organisms attach to rocks with holdfasts (seaweed), cement (barnacles), threads (mussels), or arms (starfish). Snails squeeze a muscular foot tightly into a rock and retreat into their shells.

The rocky intertidal has been the site of important ecological studies. In the rocky intertidal of Washington state, the top carnivore is the starfish *Pisaster ochraceus.* Removal of the starfish caused a decline in the number of species from fifteen to eight, including an enormous increase in the population of the mussel *Mytelus edulis*, the starfish's favorite prey. *Pisaster ochraceus* is therefore a keystone predator in its community; by limiting the size of mussel's population, it clears out space for other species. Keystone predators are often at a high risk for extinction since they are often high in the food chain and sparsely distributed. SEE ALSO ALGAE; COMMUNITY; ECHINODERM; ECOSYSTEM; MOLLUSK; OCEAN ECOSYSTEMS: OPEN OCEAN; OCEAN ECOSYSTEMS: SOFT BOTTOMS

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Ocean Ecosystems: Open Ocean

The realm of open water, called the pelagic zone, has the greatest volume and vertical range of any life zone. It includes the region above the **continental shelf**, called the **neritic** province, and the region beyond, called the oceanic province. Gradations in light, temperature, water chemistry, nutrient content, and pressure result in a diversity of environments that are filled by a large number of species.

continental shelf submerged offshore area demarcated by land on one side and deep sea on the other

neritic zone near the shore

photosynthesis the process by which plants use the energy of light to produce carbohydrates and molecular oxygen from carbon dioxide and water

plankton microscopic floating organisms

phytoplankton microscopic floating creatures that photosynthesize

Life is found throughout the water column (that is, top to bottom), but mostly in the photic zone, the region where sunlight makes **photosynthesis** possible. Organisms are also more abundant where there are more nutrients: in the neritic, where nutrients wash off the land, and in upwelling zones, where relatively cold nutrient-rich waters from the deep ocean rise to the surface. Pelagic life is dominated by **plankton**, mostly tiny organisms that move with water currents. Photosynthesis by **phytoplankton** is directly or indirectly the primary food source for all marine life. The animals, or zooplankton, that eat them may also be tiny, like krill, or they may be larger, like jellyfish, and able to make small, directed motions.

The active swimmers that inhabit the open ocean are called nekton. While the vast majority of nekton are fish and mammals, they include invertebrates, such as mollusks and crustaceans. The most productive waters in the world are upwelling zones, such as those of the west coast of South America. Here, the abundance of nutrients supports a large population of phytoplankton, which in turn is the foundation of rich fishing grounds. If upwelling stops, as happens off Peru during an El Niño event, the fish population declines; if the fishery has already been weakened by overfishing, it may collapse, as did the Peruvian anchovy fishery in the early 1970s.

The ocean has a moderating effect on world climate because water has a high ability to absorb and store heat. When prevailing winds come off an ocean the climate is milder than in locations with no oceanic influence. This is why annual temperature fluctuations are much smaller in western than in eastern coastal North America. The surface layer of the ocean is a heat reservoir that may maintain temperature anomalies for years, and alter rainfall patterns. For example, increased sea surface temperature results in increased evaporation. This increases rainfall and therefore condensation, which provides the energy to drive an El Niño event.

The enormous productivity of phytoplankton has a large effect on the atmosphere, since these organisms use carbon dioxide (CO_2) and release oxygen. Also, CO_2 is highly soluble in seawater and the ocean is a carbon

A bottlenosed dolphin in the Bahamas. Gradations in light, temperature, water chemistry, nutrient content, and pressure result in a diversity of open ocean environments that are filled by a large number of species.

dioxide sink. Manipulations of oceanic chemistry have been proposed to control atmospheric levels of CO_2, and possibly reduce greenhouse warming. In large regions of the ocean, phytoplankton growth is limited by lack of the trace element iron. In two experiments, small patches of the sea surface were fertilized with minute amounts of dissolved iron. This triggered a massive phytoplankton bloom: the phytoplankton growth rate doubled, its biomass increased by nearly thirty times, and its nitrate uptake increased by fourteen times. If phytoplankton populations were increased on a wide scale, phytoplankton might use more CO_2. When these organisms died, some would fall to the seafloor, taking with them the carbon they had harvested from atmospheric CO_2. SEE ALSO BIOGEOCHEMICAL CYCLES; BONY FISH; CARTILAGINOUS FISH; CRUSTACEAN; GLOBAL CLIMATE CHANGE; MOLLUSK; OCEAN ECOSYSTEMS: HARD BOTTOMS; OCEAN ECOSYSTEMS: SOFT BOTTOMS; PLANKTON

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Ocean Ecosystems: Soft Bottoms

Where water movements are not strong enough to wash them away, sediments coat much of the benthic environment. Soft bottoms are common along coasts, along continental margins, and in the deep sea. Plants and animals that attach to sandy or rocky surfaces are called benthic epifauna; those that bury themselves in soft sediments or bore into the rocky bottom or shells of other animals are called benthic infauna. Few benthic organisms can live in shifting sediments, as on a beach exposed to wave action, and many more are found in sediments in protected bays or estuaries.

The plants of soft bottoms are marine angiosperms, seed-bearing vascular plants with true roots. So that they can photosynthesize, benthic plants live only in the photic zone. Grasses are the only marine plants that live on soft bottoms. They catch sediments and **organic** matter in their roots, protecting the shoreline from erosion and providing shelter, substrate, and food for a diverse group of animals. Much organic material from these wetland **ecosystems** is carried offshore, where it provides nutrients for organisms living beneath the photic zone.

The animals found on the shore or in near-shore sediments live primarily on **plankton** and organic debris from land. Suspension feeders attach themselves to hard or sandy bottoms and strain water for food. Filter feeders are similarly attached but actively pump large amounts of water through their bodies to get food. Many benthic infauna are deposit feeders who eat sediments, extracting the organic matter trapped between the grains. Predators and scavengers on soft bottoms include starfish, snails, cephalopods, and crustaceans. Bacteria are an important **protein** source and play a major role in decomposition.

organic composed of carbon, or derived from living organisms

ecosystem an ecological community and its environment

plankton microscopic floating organisms

protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions
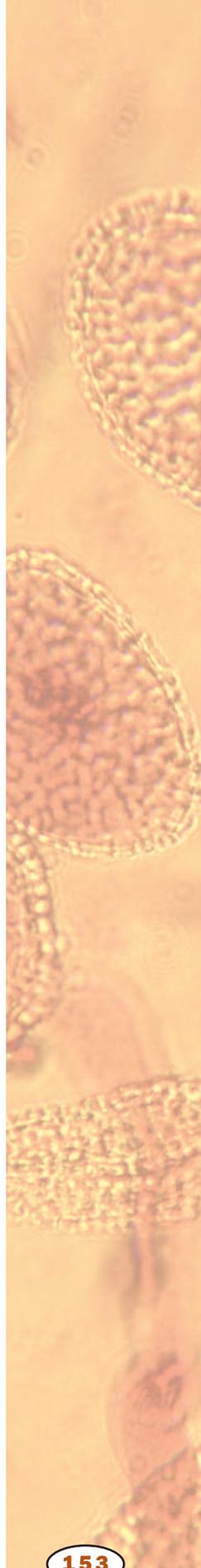
aerobic with oxygen, or requiring it

anaerobic without oxygen, or not requiring oxygen

The benthic environment is extremely diverse in water depth, temperature, salinity, substrate type, and predation and competition. The most important factor determining the distribution of near-shore benthic infauna is grain size. Large-grained particles, such as sands, are fairly porous. They gain and lose water, gases, and organic material quickly. Filter feeders attach to sands, since smaller sediments are easily swept up by water and can clog the animals' mucus-lined filtration systems. Deposit feeders prefer to live in the top 1 to 2 centimeters of organic-rich, fine-grained mud. This is the **aerobic** zone, where dissolved oxygen permeates. Below the oxygenated layer is the black, oxygen-depleted, or **anaerobic**, zone, where only anaerobic bacteria can live fully. Anaerobic bacteria produce hydrogen sulfide, the rotten egg smell of black mud. Some animals, like clams, live in the anaerobic zone to avoid predators but extend siphons into the aerobic zone to obtain food and oxygen.

The deep sea is uniformly cold and dense, and sediment particles are small and relatively uniform in size. The number of benthic species increases from the near shore to the deep ocean but the number of individuals and total biomass decreases. All major groups of shallow water benthos have deep ocean counterparts. But shortage of food causes the deep-sea organisms to be smaller, live longer, and reproduce less frequently. Most deep-sea organisms are deposit feeders with a few conspicuous filter feeders and predators. SEE ALSO CRUSTACEAN; CORAL REEF; ESTUARIES; OCEAN ECOSYSTEMS: HARD BOTTOMS; OCEAN ECOSYSTEMS: OPEN OCEAN

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Oncogenes and Cancer Cells

cell cycle sequence of growth, replication, and division that produces new cells

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

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

somatic nonreproductive; not an egg or sperm

Cancers are a collection of diseases that result from loss of control over cell division (mitosis). Because the **cell cycle** is controlled by **proteins**, and proteins are encoded by **genes**, cancers are genetic diseases.

Despite being genetic in origin, cancer is not usually inherited in as predictable a way as a Mendelian (single-gene) disorder, such as color blindness. Instead, cancer arises as a consequence of accumulated mutations in **somatic** (body) cells of a individual. This can happen in two ways. In the first method, a person inherits a cancer susceptibility allele (gene variant) from a parent, and therefore has that mutation present in one copy in each cell of the body. If a mutation then occurs in the second copy of the susceptibility gene in one somatic cell, that cell begins to divide uncontrollably. As the cell divides, the offspring cells inherit these mutations and perpetuate the cancerous characteristics. Alternatively, two somatic mutations may occur spontaneously in the same cell. For example, exposure to ultraviolet wavelengths in sunlight, or to cancer-causing chemicals, can cause somatic mutations. The somatic nature of the mutations that underlie cancer is the
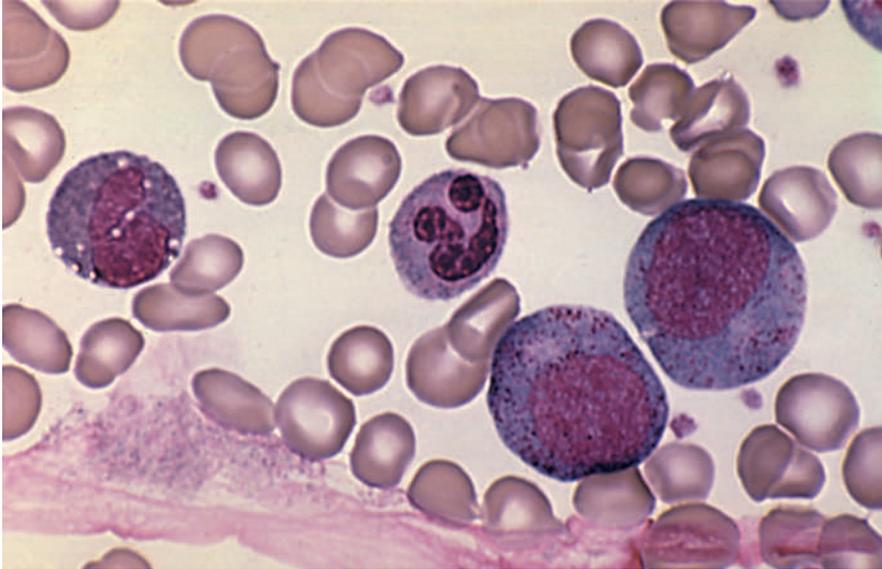
mechanism by which environmental factors can contribute to the disease. The nature and location of the cell type determines the type of cancer.

Types of Cancer Genes

Mutations of two major types of genes cause cancer. An oncogene increases cell division rate in an inappropriate place in the body or at an inappropriate time in development. The oncogene is a mutated form of a so-called proto-oncogene, which is a gene that normally causes high cell division rates where it is needed, such as in the fetus or in a wound where cells must be replaced. The abnormal activation of such a gene in time or place causes cancer. Some oncogenes encode **transcription factors**, whose overexpression then activates other genes that cause the specific characteristics of cancer cells. An oncogene mutation is usually a single deoxyribonucleic acid (DNA) base substitution.

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

The second type of cancer-causing gene is a tumor suppressor, whose normal function is to halt cell division. Just as a proto-oncogene has a normal function, so too does the unaltered version of a tumor suppressor gene and its encoded protein; it shuts down cell division when it is no longer necessary. Tumor suppressors are critical to development and to the maintenance of organs because they keep cells from dividing uncontrollably. A tumor suppressor mutation is often a deletion. This makes sense, for removal of the gene lifts its normal control of cell division, and a cancer forms.

Many cancers are the culmination of several genetic steps, which may include the actions of both oncogenes and mutant tumor suppressor genes. For example, a type of colon cancer called familial adenomatous polyposis includes deletions of tumor suppressor genes on **chromosomes** 17 and 18, and activation of an oncogene called ras on chromosome 12.

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

Activating Oncogenes

Oncogenes arise when proto-oncogenes mutate or are moved to a part of the **genome** where their expression is greatly heightened. For example, a virus might insert its DNA into a human chromosome next to a proto-oncogene,
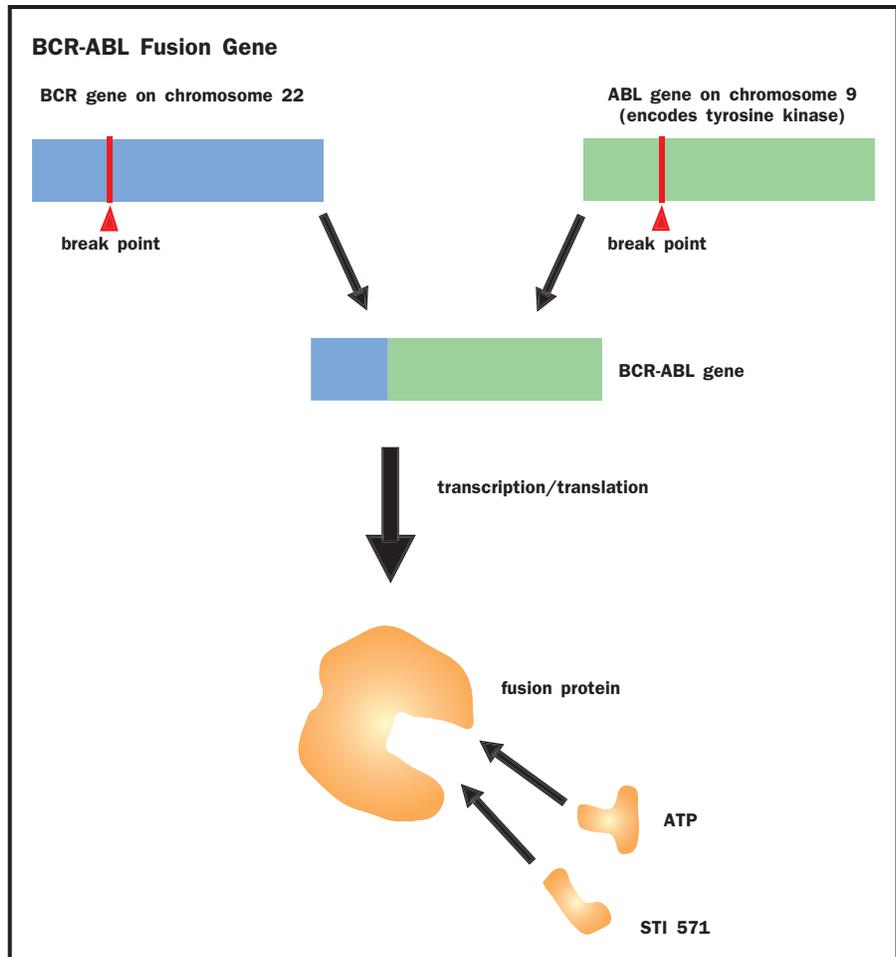
genome total genetic material in a cell or organism

The BCR-ABL fusion gene causes chronic myelogenous leukemia. The experimental drug STI 571 competes with ATP to block the action of the fusion protein, thus stopping the cancer.

BCR-ABL Fusion Gene

BCR gene on chromosome 22

ABL gene on chromosome 9 (encodes tyrosine kinase)

break point

break point

BCR-ABL gene

transcription/translation

fusion protein

ATP

STI 571

transcribe creation of an RNA copy of a DNA gene

and as the viral genes are **transcribed** at their characteristically high rate, the adjacent proto-oncogene sequence is rapidly transcribed too. The result is a loss of control over cell division. Another way that a proto-oncogene can be overactivated and thereby turned into an oncogene is if a chromosome is inverted or translocated (two different chromosomes exchange parts or combine). Either action may relocate a proto-oncogene next to a highly expressed gene. This happens, for example, in a cancer of the parathyroid glands in the neck. An inversion of chromosome 11 places a proto-oncogene next to the gene that encodes parathyroid **hormone**. When the gland synthesizes the hormone, it also synthesizes too much of the encoded protein (called an oncoprotein) and cancer begins.

hormone molecule released by one cell to influence another

Oncogenic cancers can also start when proto-oncogenes are placed near **antibody** genes, which are highly expressed during infection. In Burkitt's lymphoma, which causes a large tumor to form in the lymph glands near the jaw, infection with Epstein-Barr virus in B cells places a proto-oncogene on chromosome 8 next to an antibody gene on chromosome 14. The cancer cells of these patients have the telltale chromosomal exchange.

antibody immune system protein that binds to foreign molecules

Chronic Myeloid Leukemia and the BCR-ABL Fusion Gene

Sometimes a proto-oncogene that has been moved next to a highly expressed gene is transcribed and translated with the second gene. The result is called

a fusion protein, which then causes cancer. Discovery of the first cancer-causing fusion protein was a milestone in medical history, and has recently received renewed attention because of development of a highly effective drug treatment. This fusion protein forms in people with a tiny, unusual chromosome, named the Philadelphia chromosome, who also have chronic myeloid leukemia (CML). The errant chromosome forms from a translocation of the tip of chromosome 9 to the minuscule chromosome 22, and transfer of a bit of chromosome 22 material to chromosome 9.

Researchers discovered the Philadelphia chromosome in 1958, when two men were hospitalized in that city complaining of chronic fatigue. Each man's blood had far too many white blood cells, which led to the diagnosis of leukemia. Their blood samples were sent to two young investigators at the University of Pennsylvania, assistant professor Peter Nowell and graduate student David Hungerford, who detected the small, unusual chromosome. At that time, cancer was not considered to be a genetic disorder, and so the apparent association of leukemia with a chromosomal abnormality was a surprise. With time, cases accumulated, and the link strengthened.

By 1972, chromosome banding technology made it possible to describe the nature of the material that makes up the Philadelphia chromosome, and to infer its origin. Janet Rowley at the University of Chicago identified the translocation between chromosomes 9 and 22 that produces the tiny Philadelphia chromosome. By 1984, other researchers discovered the genes that are juxtaposed in the translocation. One gene from chromosome 9 is called the Abelson oncogene (ABL), and the other gene, from chromosome 22, is called the breakpoint cluster region (BCR).

Because the translocation is reciprocal, swapping parts of two chromosomes, two different fusion genes form called BCR-ABL and ABL-BCR. The BCR-ABL fusion gene is part of the Philadelphia chromosome, and this is the one that causes CML. The encoded fusion protein, called the BCR-ABL oncoprotein, is a form of the **enzyme** tyrosine **kinase**, which is the normal product of the ABL gene. The cancer-causing form of tyrosine kinase is active for too long, which somehow turns on a cascade of signals that ultimately results in deregulated cell division and cancer. Further evidence that implicates the BCR-ABL oncoprotein in causing CML is that mice genetically modified to harbor the fusion gene develop leukemia. (The other translocated chromosome, which is mostly chromosome 9 material, includes the ABL-BCR fusion gene, which is not known by itself to affect health.)

The discovery that a fusion oncoprotein sets into motion the cellular changes that cause CML has led directly to a new and very promising treatment. The new drug is called signal **transduction** inhibitor 571, or STI571. (Existing treatment is the immune system biochemical interferon alfa, but it does not help most patients.) In 1990, Brian J. Druker, now at the Oregon Health Sciences University in Portland, proposed to a major pharmaceutical company that he design a small molecule that would lock onto the aberrant tyrosine kinase and squelch its overactivity. He knew that the tyrosine kinase must bind **ATP** to begin the signal cascade that causes cancer. So he synthesized the small molecule in a shape that enabled it to nestle into the pocket where ATP binds. This, he hoped, would block the signal cascade and stop the cancer.

enzyme protein that controls a reaction in a cell

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

transduction conversion of a signal of one type into another type

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

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Following the usual drug discovery trajectory, Druker and his coworkers demonstrated that the molecule indeed halts the cancer in cell culture, and in mice. By 1998, STI571 was ready for phase I clinical trials, which are set up to determine safety at different dosages. In the study, 83 patients for whom interferon had not worked received doses ranging from 25 to 1000 milligrams per day (each participant received the same dose each day). Of the 54 participants who received 300 milligrams or more daily, 53 had their blood counts return to normal, and 29 of them had significantly fewer cells that had the telltale Philadelphia chromosome. In 7 participants, the unusual chromosome disappeared completely.

The new drug appears to have many benefits. Side effects are minimal; the drug is taken by mouth, unlike interferon, which must be injected; response is evident by four weeks; and perhaps most important, it helps people who did not respond to the conventional treatment.

Chronic myeloid leukemia is in many ways a landmark in cancer biology. It was the first type of leukemia to be recognized, in the 1840s, and was the subject of the first chromosome-cancer link. CML was also the type of cancer that led to identification of the first oncogene fusion protein. Finally, a highly effective new treatment is in development, based on understanding the molecular events that underlie the disease. SEE ALSO CANCER; CELL CYCLE; CHROMOSOME ABERRATIONS; CHROMOSOME, EUKARYOTIC; CLINICAL TRIALS; GENETIC DISEASES; MITOSIS; MUTATION

Ricki Lewis

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Organ

An organ is a structure composed of two to four types of tissues working to perform functions that are beyond the scope of an individual tissue type. A set of related organs working cooperatively toward the performance of even more complex functions constitutes an organ system.

Organs come in many different forms. The stomach, with its composition of **epithelium**, **connective tissue**, nervous tissue, and smooth muscle tissue, is a familiar example. Bones are organs; although they consist primarily of **osseous** tissue, bones have a vast supply of nervous tissue in their nerves, fibrous tissue lining their cavities, and muscle and epithelial tissue in their blood vessels. The skin (integument) is an organ consisting of an epithelium (epidermis) overlying a thick layer of connective tissue (dermis) rich with blood vessels and accessory structures such as secretory glands.

Even the glands within the integument can be considered organs; any gland is primarily secretory epithelium surrounded by connective tissue for

As of early 2001, clinical trials of STI571 had reached more than 2,800 patients in some 30 countries.

epithelium one of four tissue types found in the body, characterized by thin sheets and usually serving a protective or secretory function

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

osseous related to bone

support and protection. Likewise, the blood vessels and nerves in these organs are organs unto themselves.

This "organ within an organ" motif is also exhibited in the sense organs. For example, within the eyeball is an organ called the retina, an association of **neural** and epithelial tissue that detects light entering the eyeball. SEE ALSO BONE; CONNECTIVE TISSUE; DIGESTIVE SYSTEM; EPITHELIUM; KIDNEY; LIVER; MUSCLE; NEURON; PANCREAS; SKIN; TISSUE

James A. Crowder

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neural related to nerve cells or the nervous system

Organelle

An organelle is a specialized cellular structure in **eukaryotic cells** analogous to an organ in the body. Organelles are discrete structures within the cell that perform a specialized function. Most are surrounded by internal membranes and can be seen in the light or the electron microscope. Organelles increase the efficiency of cellular processes by concentrating the factors necessary to carry out specific biochemical reactions separate from the rest of the cell. Bacterial cells do not contain organelles or **intracellular** membrane-bound structures. Examples of organelles are lysosomes, **nucleus**, **mitochondria**, and the **endoplasmic reticulum**. SEE ALSO CELL; CHLOROPLAST; ENDOPLASMIC RETICULUM; GOLGI; LYSOSOMES; MITOCHONDRION; NUCLEUS; RIBOSOME; VACUOLE

Stephen A. Adam

eukaryotic cell a cell with a nucleus

intracellular within a cell

nucleus membrane-bound portion of cell containing the chromosomes

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

endoplasmic reticulum network of membranes within the cell

Organic Agriculture

Organic agriculture uses the principles of diversity and nutrient cycling found in nature to raise crops and livestock. All kinds of food are grown using organic practices, from fruits and vegetables to grains and dairy products. Organic agriculture is popularly understood to mean farming without the chemical herbicides and pesticides used in conventional agriculture. Just as important are the techniques used by organic growers that make chemical use unnecessary. These include intelligently managing the **agroecosystem** by using crop rotation, cover crops, and tillage.

agroecosystem agricultural ecosystem

Principles of Organic Agriculture

Crop rotation means growing a different crop in a field each year. When the same crop is grown year after year in an artificial **monoculture**, a habitat is created for weeds, pests, and diseases that attack that crop. Organic growers imitate the complexity found in nature by changing the crops grown in a field from year to year. Rotation continually disrupts pest habitat and reduces weeds and diseases.

Crop yields also increase because of the "rotation effect." A basic two-year rotation involves alternating a grass family crop such as wheat or corn

monoculture cultivation of a single type of crop in a large area

Worm composting (vermi-composting) turns food scraps into a rich mixure of decayed organic matter used as fertilizer. Organic growers strive to make chemical use unnecessary.

with a broadleaf crop such as tomatoes or soybeans. Any pests that become established in the wheat will no longer have a habitat the following year when tomatoes are planted. Similarly, most corn pests do not find what they need to survive in a soybean field.

Many organic growers use more sophisticated four- to eight-year rotations carefully designed to optimize yield and the ecological function of each crop. Often, the complexity of such an organic system is similar to the complexity found in nature, and weeds, insects, and diseases are almost eliminated from the system.

Using cultural control of pests rather than chemical control makes organic farming better for the environment and for wildlife.

Organic farmers will often plant a cover crop in the fall that protects the soil from wind and rain erosion during the winter. Usually the cover crop will provide other benefits as well. If the cover crop is a member of the bean plant family (a legume), it will bring nitrogen into the soil that will be available for the next crop to use. If the cover crop has allelopathic, or toxic, properties, as does rye, it can help control weeds.

From handheld hoes to tractor-pulled cultivators, organic farmers use a wide range of cultivation equipment to control weeds during the growing season. All of these implements operate on the same principle: drag weeds out of the soil onto the surface to dry out and die.

Commercial Organic Farming

A national law provides a set of standards that farmers in the United States must follow in order to sell what they grow as "organic." Organic growers must be certified, or have their farming practices verified by an application and inspection process, every year in order to sell into the organic market.

Increasing awareness of the pesticides used in conventional farming has made many people decide to buy organic food. Because of increased labor costs in organic farming, organic produce may be priced higher than conventional produce. Farmers' markets and roadside stands are places where consumers can purchase organic produce directly from the growers and eliminate retail mark-up costs.

Since the mid-1990s, sales of organic products have increased by at least 20 percent every year. Between 1995 and 1997, certified organic acres in the United States increased by 47 percent, making organic agriculture the largest growing segment of U.S. agriculture. SEE ALSO AGRICULTURE; AGRONOMIST; HISTORY OF AGRICULTURE; NITROGEN FIXATION.

Jane Sooby

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Origin of Life

How did life begin on Earth? The fact is that no one knows the answer yet, and it remains one of the primary unsolved questions of biology. We may never know with certainty because life began on Earth nearly four billion years ago. The events that initiated life no longer occur, and even the conditions of that the early Earth are not known with any certainty.

We do know one thing with reasonable certainty: Even bacteria, the simplest forms of life today, are so complex that they could not have appeared spontaneously on the early earth. More likely there were even simpler forms of life that required several hundred million years to evolve into bacterial life, complete with deoxyribonucleic acid (DNA) **genes**, metabolic pathways, ribonucleic acid (RNA) machinery, and **protein catalysts**.

The first life probably appeared several hundred million years after Earth was formed as a planet in the early solar system 4.5 billion years ago. There are many lines of evidence that support this statement, but the simplest to understand is the fossil record. Even bacteria leave fossils, and such microfossils were discovered in Australian rocks that are about 3.5 billion years old.

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

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

catalyst substance that aids in a reaction without being used up
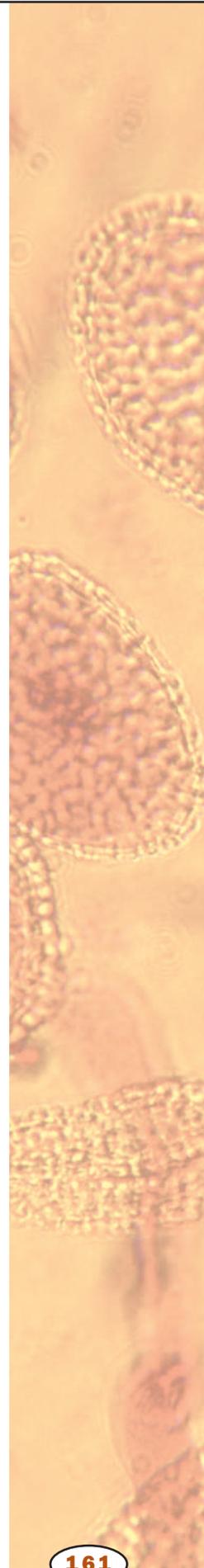
Something else scientists know with certainty is that Earth was very different when life first began. For example, the large number of craters on the moon's surface were produced by giant impacts of comets and asteroid-sized objects that were part of the accretion process by which the moon formed. The collisions continued until about 3.9 billion years ago. During that time Earth was also being hit by objects many kilometers in diameter, and the first life could not have begun until the violent bombardment ceased. Therefore, scientists estimate that the simplest form of life probably was present about 3.8 billion years ago, and over a few hundred million years evolved into the bacteria that left the Australian microfossils.

What sorts of chemical and physical processes might have produced the first forms of life? A brief summary of the properties of life today can tell scientists a lot about how life began. All life is cellular, from single-celled bacteria to multicellular human beings. Cells have anywhere from a thousand or so genes (bacteria) to thirty thousand genes (human beings) and each gene carries the information to synthesize a specific protein. The synthesis of proteins requires energy and occurs on **ribosomes**. RNA carries genetic information **transcribed** from DNA to the ribosomes where it is used to direct the synthesis of proteins.

Properties of Life

The most basic activity of life is a process called polymerization. During this process organized systems of molecules use energy and nutrients to grow by linking smaller molecules into larger molecules. The chemical reactions involving energy and nutrients are collectively called **metabolism**, and the individual reactions of metabolism are catalyzed, meaning their rates are increased in a controlled way by specific molecules (proteins, in the case of all living organisms). Second, a living organism has the potential to reproduce itself at some point in its life cycle. Third, because mutations can lead to variations among individuals, populations of living organisms can evolve over time from generation to generation, responding to changes in their environment through natural selection. When one talks about the origin of life, one therefore must think about how organized systems of **organic** molecules could have appeared on the early Earth, and how they could take on the basic properties of the living state defined above.

Early Proposals

Louis Pasteur was the first scientist to think about how life can begin. In 1865, Pasteur showed that bacteria do not occur spontaneously in sterile culture media, and concluded that life can only appear from preexisting microorganisms. This view was accepted by the scientific community for more than fifty years, until a young Russian scientist named Alexander Oparin realized that preexisting organisms could not have been present on the early earth, which must have been sterilized by the heat of its formation. And yet, somehow life began. Oparin suggested that organic molecules could spontaneously **aggregate** into larger structures he called coacervates, one of which could have happened to have the basic properties of life. In general, Oparin's proposal about aggregation remains a viable hypothesis for the origin of life, but his coacervates are no longer considered to be plausible models of the first forms of life.
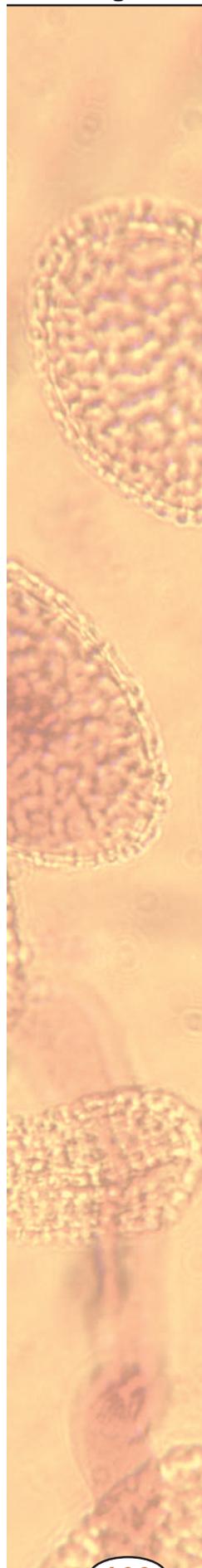
ribosome protein-RNA complex in cells that synthesizes protein

transcribe creation of an RNA copy of a DNA gene

metabolism chemical reactions within a cell

organic composed of carbon, or derived from living organisms

aggregate clump together

The next advance came with a better understanding of chemistry and biochemistry. Life as it is known in the twenty-first century requires organic compounds containing carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur, and these are present in four kinds of biochemical compounds and their polymers: **amino acids** and proteins, **nucleotides** and nucleic acids, simple sugars and **polysaccharides** like starch and **cellulose**, and **lipids**, which self-assemble into cell membranes. Were such compounds available for the origin of life? The answer seems to be yes. Even today, certain meteorites fall to Earth that contain thousands of different organic compounds, including amino acids, synthesized by nonbiological processes. Scientists also know from the early experiments of Stanley Miller and Harold Urey that organic compounds can be synthesized under simulated **prebiotic** conditions, so it seems reasonable to assume that simple organic compounds were present on the early Earth.

Self-Assembly

Now one can think about the actual process by which a living organism could appear on the early Earth. An important point to understand is that some organic molecules have properties that allow them to spontaneously organize into larger structures. A common example is the self-assembly of soap molecules into soap bubbles. A living cell resembles a microscopic bubble, and the same forces that produce a soap bubble also stabilize the membrane that surrounds all living cells like a skin and separates the **cytoplasm** from the outside world. It is easy to imagine that such microscopic bubbles were present on the early Earth, and it has been shown that some of the organic compounds in meteorites can in fact produce bubblelike structures.

Although the assembly of microscopic membranes from soaplike molecules is interesting, two other self-assembly processes are equally important. The first is that the long strings of polymerized amino acids called proteins can fold up into tightly packed balls that represent the functional proteins, such as **enzymes**. This folding process occurs in all cells as proteins are synthesized from amino acids on ribosomes. If proteinlike molecules were somehow produced on the early Earth, they would also have the capacity to fold into a variety of structures, some of which might act as catalysts.

The second self-assembly process is that long strings of polymerized nucleotides called nucleic acids can wind together into double stranded structures. The famous DNA double helix is an example, and this is the only way that scientists know that a molecule can reproduce itself. That is, one strand of DNA acts as a **template**, and a second strand is produced on the template when nucleotides bind to it and are then linked together. All life today depends on this process, which is called replication, and the earliest forms of life must have had a primitive version incorporated into their system of molecules.

Defining How Life Began

Given all this, scientists can hypothesize how life began on Earth. There is little doubt that mixtures of organic compounds became organized into complex systems by self-assembly processes, because the same thing happens in the organic compounds of meteorites, which are as old as the

amino acid a building block of protein

nucleotide the building block of RNA or DNA

polysaccharide carbohydrate composed of many individual units of sugar

cellulose carbohydrate made by plants and some other organisms; part of the cell wall
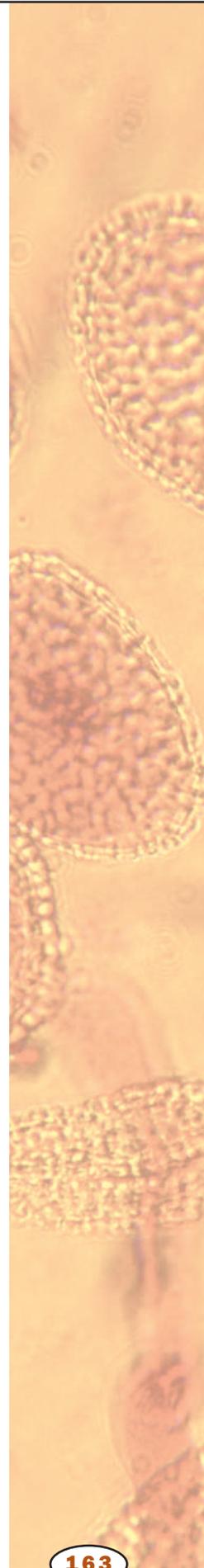
lipid fat or waxlike molecule, insoluble in water

prebiotic before the origin of life

cytoplasm material in a cell, excluding the nucleus

enzyme protein that controls a reaction in a cell

template master copy

A meteorite from Mars, thought to be about 4.5 billion years old. There is a possibility that life similar to bacteria, the simplest form on Earth today, could be present on Mars.

solar system. These self-assembled systems can be thought of as countless natural experiments that occurred all over Earth for hundreds of millions of years.

The next step occurred when a few of the microscopic systems had the particular set of molecules and properties that allowed them to capture energy and nutrients from the environment, and use them to produce larger polymeric molecules. In the next step toward life, one of the growing systems contained molecules that could be used as templates to direct further growth, so that a second polymeric molecule was in a sense a replica of the first molecule. DNA synthesis in cells is a primary example of molecular growth by polymerization, and also demonstrates how the information in one molecule can be reproduced in a second molecule. Because these processes can be reproduced under laboratory conditions, one can be reasonably certain that they are plausible reactions on the early Earth, even though scientists don't know yet how the first long polymers were produced.

The last step in the origin of life is that one or more of the growing, replicating systems happened to find a way to use the sequence of **monomers** in one molecule, such as a nucleic acid, to direct the sequence of monomers in another kind of molecule such as a protein. This was the origin of the **genetic code** and the beginning of life. It also marked the beginning of evolution, because molecular systems composed of two different interacting molecules like nucleic acids and proteins have the potential to undergo mutational change followed by selection.

It is amazing to think that this complex set of events occurred spontaneously on the early Earth, and that life was up and running only a few hundred million years after Earth had cooled sufficiently for liquid water to exist. And yet, this seems to be what happened, and if it happened on Earth it could also happen elsewhere, since the laws of chemistry and physics are believed to be universal. This larger understanding of life has led to a new scientific discipline called astrobiology, which is defined as the study of life in the universe.

monomer "single part"; monomers are joined to form a polymer

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

Could Life Have Begun Elsewhere?

Could life have begun elsewhere? The simplest place to look is in the solar system and compare other planets with Earth. Scientists now have a better understanding of where life exists on Earth, and it is much more widely distributed than we might have guessed. Bacterial life exists over a remarkable temperature range, from near 0°C (32°F) on melting snow to over 115°C (239°F) in submarine hydrothermal vents. It exists in **acidic** environments as strong as battery acid or as **alkaline** as household ammonia. Bacterial life exists in the dark, in the absence of oxygen, and has even been found growing in the radioactive water of nuclear reactors. In fact, the only constant is that microbial life requires liquid water, and if liquid water exists elsewhere we might expect that life could have started as it did on Earth, and may even still be flourishing.

Where in the solar system might one find liquid water? There are only two places that scientists know of: Mars and Europa. Mars certainly has water, but in the form of ice. Liquid water cannot exist for long on the surface of Mars, due to the cold temperature and low atmospheric pressure, but it could be locked up in ice beneath the surface, just as water is present in the permafrost of Arctic tundras. Recent images from the Mars Global Surveyor clearly show that liquid water occasionally breaks through the ice and pours down steep slopes on the edges of craters. Europa, a moon of Jupiter about the size of Earth's moon, also has water in the form of a thick sheet of ice, and beneath the ice is a global ocean of liquid water. On both Mars and Europa there is a distinct possibility that life similar to bacteria could be present, and future space missions may finally answer the age-old question: Does life exist elsewhere? SEE ALSO CELL EVOLUTION; EVOLUTION; EVOLUTION, EVIDENCE FOR; LIFE, WHAT IS

David W. Deamer

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

alkaline chemically basic, with an excess of OH- ions

Europa was discovered by Galileo Galilei in 1610. This moon of Jupiter is the sixth largest moon in our solar system.

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Osmoregulation

Osmoregulation means the physiological processes that an organism uses to maintain water balance; that is, to compensate for water loss, avoid excess water gain, and maintain the proper osmotic concentration (osmolarity) of the body fluids. Most humans are about 55 to 60 percent water by weight (45 percent in elderly and obese people and up to 75 percent in newborn infants). Many jellyfish are 95 percent or more water.

Osmoconformers and Osmoregulators

Not all organisms osmoregulate. Some marine animals such as the sea stars are osmoconformers; their body fluids are similar to seawater in osmolarity, so they gain and lose water at equal rates and have no need to expend

organelle membrane-bound cell compartment

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

ion an electrically charged particle

gradient difference in concentration between two places

osmosis passage of water through a membrane in response to concentration differences

excrete deposit outside of

hormone molecule released by one cell to influence another

cytoplasm material in a cell, excluding the nucleus

superficial on the surface; not deep

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

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

amino acid a building block of protein

energy expelling water or salt from the body. However, if they are placed in water more or less concentrated than seawater, their tissues shrink or swell, their **organelles** and cell membranes are damaged, and they die. This is why echinoderms are not found in estuaries, or river mouths where fresh and salt water meet and the salinity fluctuates greatly. Osmoconformers are stenohaline (*steno* means "narrow range," and *hal* means "salt"), unable to tolerate much variation in environmental salinity.

Osmoregulators, on the other hand, maintain a more or less stable internal osmolarity by physiological means. Terrestrial animals must osmoregulate because they unavoidably lose water by evaporation and excretion, and replacement water is not always immediately available. Marine osmoregulators maintain an internal salinity lower than that of seawater, and freshwater osmoregulators maintain an internal salinity higher than that of fresh water. Euryhaline (*eury* means "broad") animals, those able to tolerate a broad range of environmental salinity, must be good osmoregulators. The blue crab, *Callinectes sapidus*, for example, thrives in estuaries and requires efficient osmoregulation to survive there.

Osmoregulatory Mechanisms

Water cannot be actively transported across cell membranes because there are no carrier **proteins** capable of binding and transporting it. Water can, however, pass directly through membranes in response to changes in **ion** concentration. Water movement is therefore controlled indirectly, by pumping ions such as sodium and potassium across cell membranes, creating a concentration **gradient** that causes water to follow by **osmosis**. If sodium is **excreted** from the body, for example, water tends to follow it. The rate of water loss can thus be regulated by **hormones** that control the rate of sodium excretion or the water permeability of the excretory ducts.

Osmoregulation is usually achieved by excretory organs that serve also for the disposal of metabolic wastes. Thus, urination is a mechanism of both waste excretion and osmoregulation. Organelles and organs that carry out osmoregulation include contractile vacuoles, nephridia, antennal glands, and malpighian tubules of invertebrates, and salt glands and kidneys of vertebrates.

Contractile vacuoles are organelles in the cells of sponges and freshwater protozoans. In the freshwater *Amoeba proteus*, for example, the bubble-like contractile vacuole swells with excess fluid from the **cytoplasm**. Its membrane then pumps valuable ions back into the cytoplasm, leaving mainly water in the vacuole. Contractile proteins surrounding the vacuole then abruptly compress it, squirting the water out of the cell through a pore in the cell membrane. The vacuole then slowly begins to refill, repeating the process with a rhythm **superficially** resembling a heartbeat.

Nephridia are tubular structures that filter body fluids other than blood, found in flatworms, annelids, and many other invertebrates. Beating **cilia** or flagella draw fluid into the tubular system, leaving cells and proteins behind in the tissues. The tubules then reabsorb useful substances such as **glucose** and **amino acids** from the fluid and return them to the tissues, while secreting excess ions into the fluid. Finally, the excess water, ions, and meta-

bolic wastes are expelled from the body by way of nephridiopores in the body wall. Nephridia are called protonephridia if the inner end of the tubule is closed, like a porous bulb, and extracts liquid from the tissue fluid. These occur in flatworms such as planarians and tapeworms. Metanephridia have a funnellike opening at the internal end, through which they draw in fluid from the body cavity. Earthworms have metanephridia.

Antennal glands occur in crustaceans such as crayfish. They receive a blood **filtrate**, modify it by the reabsorption of some substances and **secretion** of others into the fluid, and then expel the modified fluid (urine) from a pore at the base of the antenna.

Malpighian tubules are found in spiders and insects. Numbering from two to several hundred, they are attached in clusters to the digestive tract between the midgut and hindgut and hang freely in the abdominal cavity. They absorb water and ions from the coelomic fluid and pass the fluid to the gut. The hindgut reabsorbs most of the water, leaving excess ions and metabolic wastes to be excreted with the feces, which are often dry.

Salt glands are associated with the eyes, nostrils, or tongue of marine reptiles (sea snakes, sea turtles, marine iguanas, saltwater crocodiles) and birds (gulls, albatrosses). These animals ingest excess salt with their food and water and excrete it by way of these glands.

Kidneys are vertebrate osmoregulatory organs in which blood pressure forces fluid to filter through the walls of blood capillaries into tubules that process the filtrate into urine. Each human kidney has about 1.2 million tiny balls of capillaries called glomeruli, where the blood pressure is very high. A filtrate of the blood plasma, free of cells and protein, seeps from these capillaries into a hollow ball called a glomerular (Bowman) capsule. From there, it flows into a series of tubules that remove most of the salt and water along with useful material such as glucose and vitamins, while secreting hydrogen and potassium ions, urea, and drugs (for example, penicillin and aspirin) into the tubular fluid. A final tube in the pathway, called the collecting duct, adjusts the salinity of the urine by reabsorbing variable amounts of water, before the urine leaves the kidney for storage in the urinary bladder and eventual elimination from the body.

Two hormones, aldosterone and antidiuretic hormone, regulate the amounts of salt and water reabsorbed, enabling the human kidney to adjust water loss or retention to the body's state of hydration. Human blood plasma and tissue fluid normally has an osmolarity of 300 milliosmoles per liter (mOsm/L); that is, 0.3 mole of dissolved particles per liter of solution. Human urine can be as dilute (hypoosmotic) as 50 mOsm/L when the body is voiding excess water, or as concentrated (hyperosmotic) as 1,200 mOsm/L when conserving water.

Freshwater fish, by contrast, cannot produce hyperosmotic urine, but they have no need to. Surrounded by water, they can afford to produce abundant, dilute urine to flush away their metabolic wastes. Among mammals, the ability to concentrate the urine is also little developed in aquatic forms such as beavers and muskrats. Kangaroo rats, by contrast, are desert rodents that need never drink water (they obtain it from food), and can concentrate their urine to as much as fourteen times the osmolarity of their blood plasma (compared to four times for humans). SEE ALSO ARACHNID; BLOOD; CRUS-

filtrate material passing through a filter

secretion material released from the cell

Human kidneys are about the size of a fist. They are located in the back, just below the rib cage. Every day, the kidneys filter about 200 quarts of fluid. Approximately 2 quarts leave the body in the form of urine, while the rest is retained in the body.

glycolysis initial stages of sugar breakdown in a cell

Krebs cycle central metabolic pathway in mitochondria

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

substrate the molecule acted on by an enzyme

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

aerobic with oxygen, or requiring it

electron transport system membrane-bound system of proteins that extracts energy from high-energy electrons, found in mitochondria and chloroplasts

inorganic not bonded to carbon

chemiosmosis use of proton gradients to make ATP

eukaryotic cell a cell with a nucleus

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

prokaryotic without a nucleus

ion an electrically charged particle

matrix a network, usually of threadlike fibers

gradient difference in concentration between two places

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

TACEAN; ECHINODERM; ESTUARIES; EXCRETORY SYSTEMS; HOMEOSTASIS; INSECT; KIDNEY; PHYSIOLOGICAL ECOLOGY; PASTEUR, LOUIS; PROTISTA

Kenneth S. Saladin

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Oxidative Phosphorylation

Glycolysis and the **Krebs cycle** both generate the high-energy compound adenosine triphosphate (**ATP**) directly, by **substrate**-level phosphorylation, but this represents only a small fraction of the energy in each **glucose** that passes through these pathways. Much more of the energy in glucose is conserved in the form of high-energy electrons carried in pairs by the electron "shuttles" NADH and $FADH_2$, which are generated in glycolysis and the Krebs cycle. In **aerobic** cells, these high-energy electrons are used to produce more ATP by oxidative phosphorylation, a process during which the electrons are passed to molecular oxygen via an **electron transport system** (ETS), giving up their energy along the way. This energy is used to phosphorylate adenosine diphosphate (ADP) and **inorganic** phosphate to ATP in a process called **chemiosmosis**. In **eukaryotic cells**, oxidative phosphorylation takes place on the inner **mitochondrial** membrane; in **prokaryotic** cells, it is associated with the plasma membrane. The remainder of this discussion will refer only to mitochondrial oxidative phosphorylation, but the process is similar in prokaryotes.

The ETS consists of a chain of electron carriers, associated with the inner mitochondrial membrane, that bind electrons at successively lower energy levels. The energy released as the electrons are passed from carrier to carrier moves hydrogen **ions** (protons) across the membrane, from the mitochondrial **matrix** to the intermembrane space, creating a concentration **gradient** of protons. Since the protons carry a charge, an electrical potential (voltage) also develops across the membrane, so the gradient is often called an electrochemical gradient. This electrochemical gradient is a form of stored energy, some of which is used to phosphorylate ADP to ATP, a process carried out by a complex of **proteins** called ATP synthase. As protons move down their concentration gradient, from the intermembrane space back to the matrix, the energy they release is used by the ATP synthase complex to phosphorylate ADP.

The electron transport chain consists of a series of carriers, including integral membrane proteins, peripheral proteins, and smaller, nonprotein carriers. Most of these carriers are arranged into four distinct aggregations embedded in the inner mitochondrial membrane, called electron-carrier complexes I through IV. Complex I receives electrons from NADH, whereas complex II receives them from $FADH_2$. Complexes III and IV are further down the chain, and ultimately transfer the electrons to molecular oxygen to form water. In addition to these integral complexes, two smaller carriers play critical roles. Ubiquinone, a low-molecular-weight compound within the membrane, receives electrons from complexes I and II, and transfers
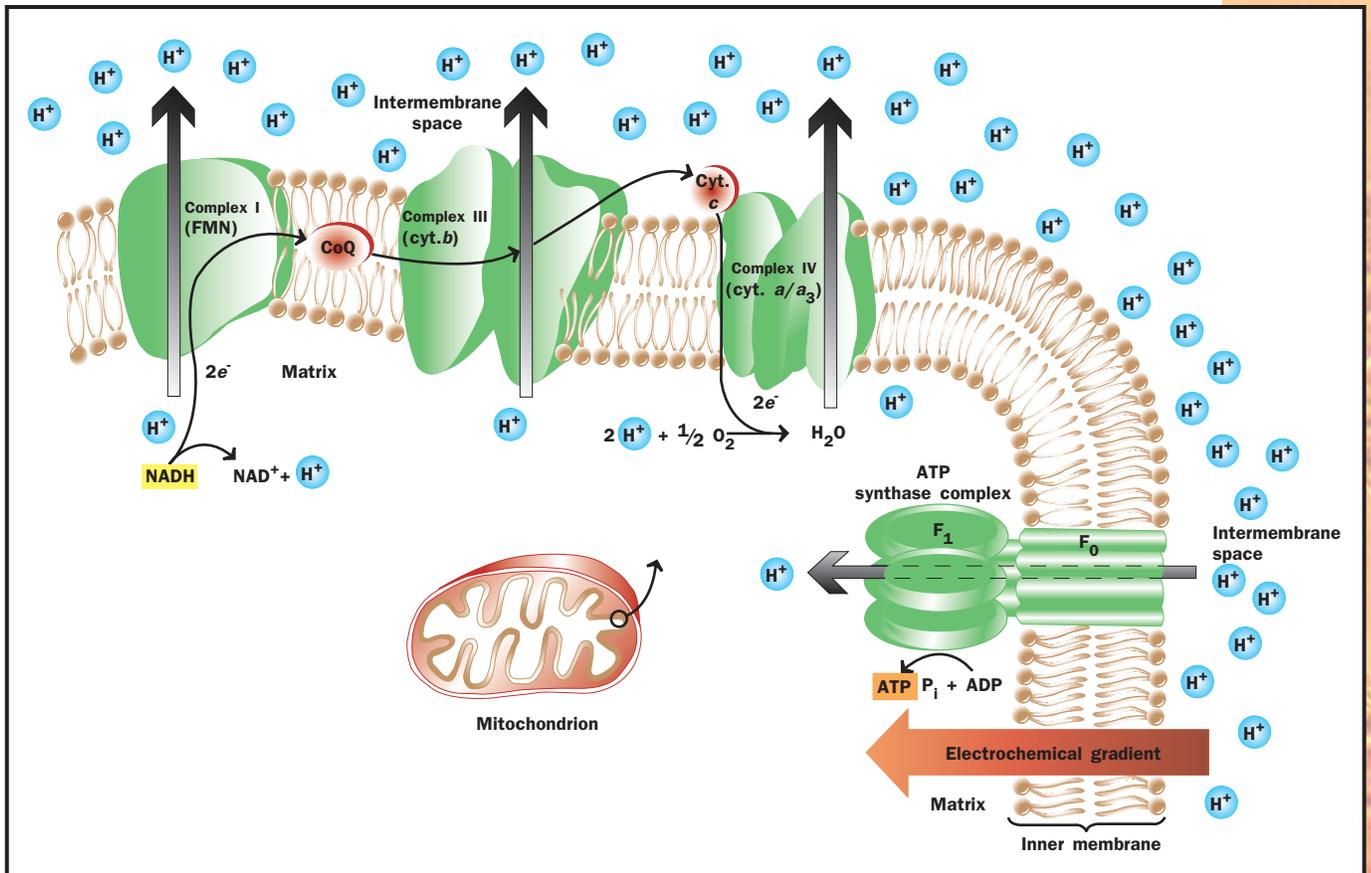
them to complex III. Cytochrome c, a small peripheral protein, receives electrons from complex III and transfers them to complex IV. Several other cytochromes are included as members of the four electron-carrier complexes. Cytochromes are a class of small proteins containing **heme** that are important in transferring electrons in cellular processes.

There are three sites along the ETS where protons are pumped across the membrane: complexes I, III, and IV. At each site, one proton is pumped across the membrane for each pair of electrons that passes through. Since each proton that returns through ATP synthase phosphorylates one ADP to ATP, each pair of electrons passing through the ETS can produce at most three ATP molecules. Electron shuttles such as NADH or $FADH_2$ carry pairs of electrons at specific energy levels, as do the carriers in the ETS. Electrons cannot be passed to a carrier at a higher energy level, so these shuttles pass electrons to different points in the ETS. NADH donates electrons to the highest energy carrier, complex I, whereas $FADH_2$ donates electrons to complex II, which can accept the lower-energy electrons it carries. Because one of the three sites that pump protons across the membrane, complex I, is bypassed by the electrons from $FADH_2$, these electrons can ultimately produce only two molecules of ATP whereas those donated by NADH can produce three. This is consistent with the idea that $FADH_2$ carries electrons possessing less energy than those carried by NADH.

ATP synthase is a large complex of proteins that is imbedded in the inner mitochondrial membrane. It consists of two parts: an integral protein

Illustration of the chemiosmotic synthesis of ATP in the mitochondrion.

heme the deep-red iron containing, nonprotein portion of hemoglobin and myoglobin

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

amino acid a building block of protein

ubiquitous found everywhere

anaerobic without oxygen, or not requiring oxygen

complex that serves as a channel through which the protons cross the membrane, and a peripheral complex that phosphorylates the ADP to ATP. As the protons pass through the integral complex, they cause the peripheral complex to rotate. In a manner that is not completely understood, this mechanical action provides the energy needed to phosphorylate ADP. However, it seems that the rotation of the peripheral complex is necessary. This complex is made of six subunits, arranged in three identical pairs, each of which can bind ADP or ATP. At any given time, one of the pairs will be empty, one will bind ADP and phosphate, and one will bind ATP. As the complex rotates, the site binding ADP and phosphate passes a stationary extension of the integral complex, which causes that pair of subunits to change shape. The result is that the ADP is phosphorylated to ATP. At the same time, the ATP that was bound by the other pair of subunits is released, and the empty pair of subunits picks up ADP and phosphate, rendering ATP synthase ready for the next step. Altogether, for each complete rotation of the peripheral complex, three ATPs are generated.

The pathways for oxidizing all food molecules—**carbohydrates**, fats, and **amino acids**—unite at oxidative phosphorylation. All these pathways produce NADH, which donates electrons to the ETS. The ETS and oxidative phosphorylation are thus versatile and **ubiquitous** pathways in all aerobic cells, and even in some **anaerobic** bacteria. Many such microbes use a similar mechanism to generate ATP, but in the absence of free oxygen they pass electrons to other acceptor molecules, such as sulfate or a variety of metal ions, thereby generating significant ATP in the absence of oxygen. SEE ALSO GLYCOLYSIS AND FERMENTATION; KREBS CYCLE; MEMBRANE PROTEINS; MEMBRANE TRANSPORT; METABOLISM, CELLULAR; METABOLISM, HUMAN; NUCLEOTIDES

David W. Tapley

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Pain

Pain is experienced by humans and animals in response to excessive pressure, heat, or chemicals. Although humans often view pain as undesirable, pain helps protect them from injury by alerting them to its presence. The need for pain is revealed by diseases in which pain is absent or suppressed, as in leprosy. People with such disorders, unaware of injuries or infections, often die prematurely or require limb amputations because unfelt injuries may be neglected until they lead to massive infection and tissue death.

Although skin and other tissues contain cells that are activated by heat and pressure, pain arises from specialized cells that only respond to excessive stimuli that have the potential to cause damage. Light pressure or warming has no effect on these cells. Once activated, these cells transmit pain signals to the spinal cord and brain where pain sensations occur.

Unlike other senses such as sight, pain is highly variable. For example, pain sensitivity decreases in animals pursued or caught by predators, in

women giving birth, and in patients taking pain-killing drugs like morphine. Although the ability of morphine to decrease pain sensation has been known for thousands of years, it was not until the 1970s that specific receptors were found in the brain that mediate the effect of the drug. Shortly thereafter, it was discovered that the human body manufactures its own morphinelike chemicals, known as endorphins, that provide the body with its own built-in pain-regulatory system. This internal pain-suppression system is activated during stress such as fleeing lions or delivering babies.

Injury to skin or nerves can also cause a long-lasting increase in pain sensitivity, known as hyperalgesia, that can persist for days or even years. Sunburn is a common example; the skin burn causes normally nonpainful touch to become painful for days. Changes in both the skin and the **central nervous system** appear responsible for hyperalgesia. In the skin, chemicals released by inflammation, the process that also causes redness and swelling, sensitize the pain nerve endings to touch. In the central nervous system, **neural** circuits are permanently altered in much the same way that memories are stored.

central nervous system brain and spinal cord

neural related to nerve cells or the nervous system

Pain arises not only from skin and muscle, but also from internal organs such as the heart and kidney. Interestingly, pain from internal organs is often not perceived as arising from the internal organ, but instead from nearby areas of skin or muscle. This is known as referred pain. For example, heart attacks commonly produce pain perceived to arise from the left shoulder and not the heart.

Neurological injury following trauma or caused by diseases such as diabetes sometimes leads to severe, unrelenting pain. Following amputation, the cut nerve in the limb continues to send pain signals to the brain even though the limb has been severed. Consequently, the brain perceives the pain as arising from the amputated limb. This is known as phantom pain.

Given how commonly humans experience pain, it is not surprising that many medical treatments have been developed to suppress it. For example, aspirin blocks the inflammation in skin that leads to hyperalgesia. Acupuncture, an ancient treatment in which the skin is punctured by a pattern of fine needles, activates the internal morphine system and reduces pain in much the same way as taking morphine. SEE ALSO Hormones; Immune Response; Neuron; Pituitary Gland

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Paleontology

Paleontology is a broad field of study that focuses on the history of life on Earth. Fossils, which are the material remains (bones, teeth, shells) or traces (physical or chemical) of ancient organisms, are what paleontologists study.

CUVIER, BARON GEORGES (1769–1832)

A gifted French paleontologist and anatomist who, in 1812, proposed the theory of "catastrophism" to explain the appearance and disappearance of dinosaurs and other species in the layers of the fossil record. Cuvier said that Noah's flood was just one of dozens of catastrophes in Earth's history, each one succeeded by a new Judeo-Christian creation.

Peter Larson, president of the Black Hills Institute of Geological Research, studies the skeleton of a *Tyrannosaurus rex*.

isotopes forms of an atom that differ by the number of neutrons in the nucleus

prokaryote single-celled organism without a nucleus

eukaryote a cell with a nucleus

Fossils of single-celled organisms are known from rocks approximately 3.5 billion years old, and chemical traces of life (carbon **isotopes** of presumed biological origin) may extend even further back in time. It is an undeniable fact that the fossil record is an incomplete archive of the history of life, and this is especially true for organisms with poor preservation potential, such as soft-bodied worms and jellyfish. However, the quality of the fossil record is surprisingly good for those animals with durable skeletons, such as brachiopods, trilobites, mollusks, and vertebrates.

Many subfields fall under the broad heading of paleontology. The majority of modern paleontologists focus their efforts on describing fossils and deciphering evolutionary history, or phylogeny. These "paleobiologists" tend to specialize on particular groups of fossil organisms, such as single-celled **prokaryotes** or **eukaryotes**, plants, invertebrates, or vertebrates. Through their efforts scientists gain a deeper understanding of life's evolution and diversification through time. Scientists also gain a better appreciation of the evolutionary process, because the fossil record provides the long-term record of evolution in action. Indeed, proposed modes of evolu-

tionary change, such as **phyletic gradualism** and **punctuated equilibrium**, are based on patterns derived directly from the fossil record.

Another active branch of paleontological research is paleoecology, which is the study of the relationships and interactions between fossil organisms and their paleoenvironments. Paleontologists engaged in paleoecological research might focus their efforts on a single **taxon**. For example, a paleontologist may choose to study the predatory activities of a particular fossil snail by tracking distinctive traces of its predation (borings) in associated fossil bivalve shells. Another paleontologist may examine the fossilized leaves and woody tissues of ancient trees in order to identify diagnostic traces of a fossil insect that made its living within the tissues of the extinct plant. Still another may study the contents of fossilized feces (called coprolites) in order to decipher the dietary preferences and digestive capabilities of an extinct species of dinosaur. On a larger scale, paleontologists may choose to track ecological changes in entire communities through time. A prime example of this type of paleoecological research would be the analysis of ancient plant communities in response to long-term climate change.

Yet another contemporary field within the realm of paleontological research is taphonomy, which is the study of how **organic** remains are incorporated into the rock record. Taphonomic analyses focus on the post-mortem history of biological remains, such as decay, disarticulation (separation of body parts), transport (perhaps out of life habitat), and burial. Taphonomic studies can reveal important trends and biases in the fossil record, which must be recognized in order to produce accurate paleoecological and evolutionary reconstructions. At the most basic level, taphonomy points out that the scarcity of soft-bodied creatures in the fossil record is not due to scarcity of the original organisms, but to the poor preservation of soft body parts.

Finally, many paleontologists today are engaged in research directly related to the phenomenon of mass extinction, which unfortunately is also a contemporary environmental issue. By tracking the record of extinction through time, paleontologists can provide unique insights into the potential agents that cause the decimation of entire **ecosystems** on a global scale, such as extraterrestrial impacts. They can also gain an appreciation for the timing and nature of **biotic** recovery after major extinction events. SEE ALSO CAMBRIAN EXPLOSION; EVOLUTION, EVIDENCE FOR; EXTINCTION; HISTORY OF EVOLUTIONARY THOUGHT; MOLLUSK

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Pancreas

The pancreas is a soft oblong organ located in the upper central region of the abdominal cavity, just behind the lower surface of the stomach. It has three portions: an expanded medial portion called the head, a central portion called the body, and a tapering **lateral** portion called the tail. The head is partially encircled by the C-shaped duodenum, the first portion of

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phyletic gradualism the belief that evolutionary change is slow and steady

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

taxon a level of classification, such as kingdom or phylum

organic composed of carbon, or derived from living organisms

ecosystem an ecological community and its environment

biotic living

ANNING, MARY (1799–1847)

English paleontologist who supported her family by finding and selling fossils. For example, she dug up the first complete skeletons of swimming dinosaurs, the ichthyosaur and plesiosaur. Although a woman of low birth, Anning was recognized as the most knowledgeable paleontologist in Great Britain in the early nineteenth century. In her old age, the British Association for the Advancement of Science helped support her.

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lateral side-to-side

exocrine gland gland that secretes substances to an external or internal surface rather than into the bloodstream

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

electrolytes ions in body fluids

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

lipid fat or waxlike molecule, insoluble in water

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

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

metabolism chemical reactions within a cell

hyposecretion lack of secretion

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

the small intestine. The pancreas is both an **exocrine gland** and an **endocrine** gland.

The exocrine portion of the pancreas consists of acinar cells (which account for about 99 percent of all secretory cells in the pancreas) that are organized into numerous small clusters called acini. The acinar cells secrete a clear fluid called pancreatic juice, which plays a critically important role in the digestion of food within the small intestine. The pancreatic juice is usually delivered to the duodenum by way of two ducts, the main pancreatic duct and the accessory pancreatic duct. (In some people, the accessory duct disappears during development.) Pancreatic juice consists of water, **electrolytes**, sodium bicarbonate, and several digestive **enzymes** capable of digesting virtually all the nutrient molecules in food.

Among these enzymes are several **protein**-digesting enzymes (trypsin, chymotrypsin, carboxypeptidase, and elastase), a carbohydrate-digesting enzyme (pancreatic amylase), and a **lipid**-digesting enzyme (pancreatic lipase). These enzymes do not digest the pancreas itself because they are not activated or provided with optimal ionic conditions until pancreatic juice enters the duodenum. The sodium bicarbonate establishes the optimal **pH** for the actions of pancreatic and intestinal enzymes within the small intestine.

The remaining 1 percent of the secretory cells form the endocrine portion of the pancreas. These cells are organized into clusters called pancreatic islets (islets of Langerhans) that are scattered among the acini. These cells secrete several **hormones**, including glucagon (secreted by alpha cells) and insulin (secreted by beta cells), which play important roles in blood **glucose** regulation and carbohydrate **metabolism**. Diabetes mellitus is an endocrine disorder that arises from **hyposecretion** of insulin or a decreased sensitivity of body cells to insulin. SEE ALSO BLOOD SUGAR REGULATION; DIGESTIVE SYSTEM; ENDOCRINE SYSTEM; ENZYMES; HORMONES

Izak Paul

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Parasitic Diseases

A parasite is typically an organism that lives in or on the body of another living organism, the host, and harms it by feeding on its tissues or stealing nutrients. In the broad sense, parasites include certain bacteria, fungi, protozoans, worms, **arthropods**, and a few vertebrates. Bacterial, fungal, and protozoan diseases are discussed elsewhere in this encyclopedia. This article focuses on a few human diseases caused by parasitic worms and arthropods.

The worms that infect humans include trematodes (flukes), cestodes (tapeworms), and nematodes (roundworms). One of the most serious trematode diseases is schistosomiasis, caused by three species in the genus Schistosoma. Schistosomes, or blood flukes, live in blood vessels of the urinary bladder and intestines. They lay eggs that digest their way through the blood
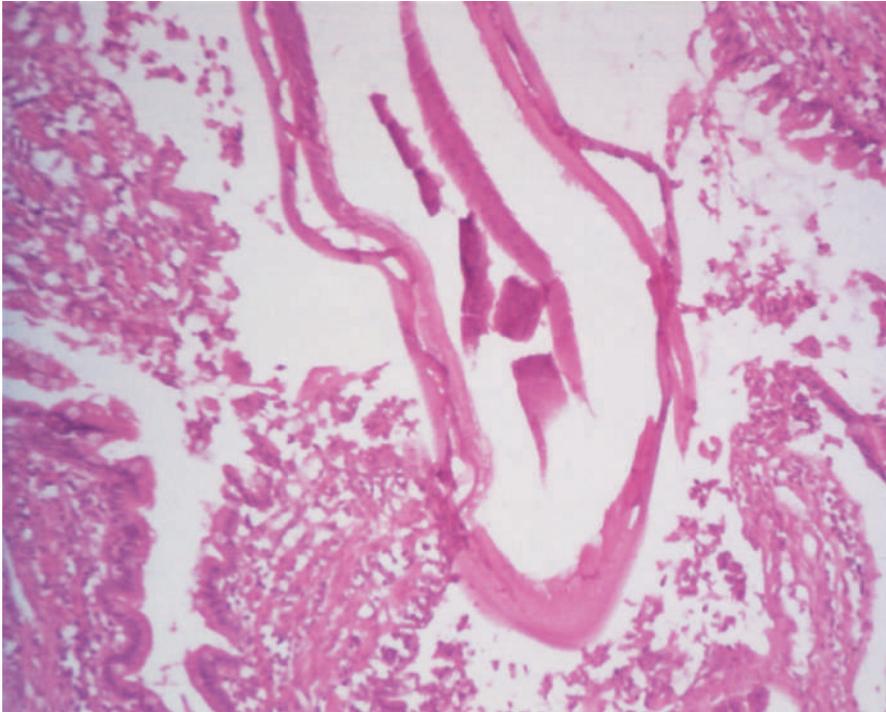
Hookworms (fuschia stain) in a dog's small intestine. Thousands of hookworks may attach to the wall of the small intestine, sucking so much blood that they make the victim severely anemic.
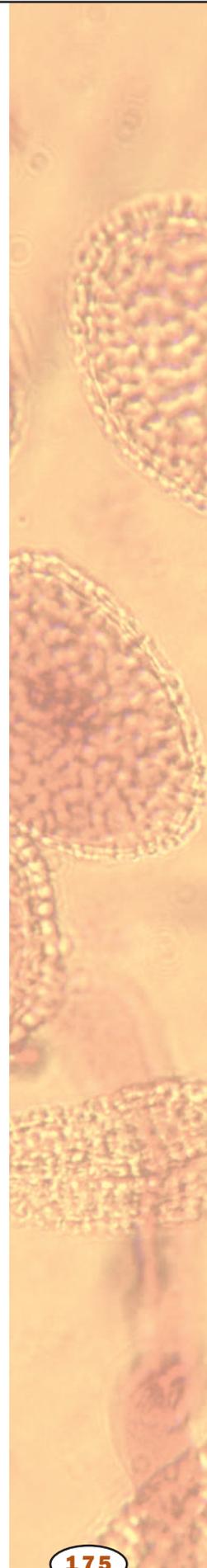
vessel and the bladder or intestinal wall, and thus find their way into the urine or feces.

When discharged into fresh water, they hatch and produce a swimming larva, the miracidium, which infects a snail. Later, another larva called the cercaria emerges from the snail and penetrates the skin of people who come in contact with the water. Eggs lodged in the human intestine or bladder, or washed by the bloodstream into the liver, cause an intense allergic reaction that leads to degeneration of these organs and often death of the victim.

Cestodes in general are less **pathogenic** (disease-producing) than trematodes. However, the fish tapeworm, *Diphyllobothrium latum*, can cause severe **anemia** by robbing the human host of vitamin B_{12}. The pork tapeworm, *Taenia solium*, can cause intestinal obstruction and produces eggs that sometimes hatch in the human body, leading to larval invasion of the muscles, brain, lungs, heart, and other organs. *Echinococcus granulosus*, a tapeworm of dogs and wolves, sometimes infects humans when a dog licks a person in the face. It does not mature in humans, but its larvae can produce hydatid cysts, ranging from grape-sized to grapefruit-sized, in the liver, brain, and lungs, with fatal results.

Among the most widespread nematode infections of humans is hookworm disease, caused by *Necator americanus* and *Ancylostoma duodenale*. Hookworms are only 1 centimeter (0.4 inch) long, but thousands of them may attach to the wall of the small intestine, collectively sucking so much blood that they make a person severely anemic and stunt the victim's growth and mental development.

Onchocerca volvulus, a nematode transmitted by the bites of blackflies, produces larvae that migrate through the cornea of the human eye. In parts

pathogen disease-causing organism

anemia lack of oxygen-carrying capacity in the blood

of Latin America and Africa, it blinds many people before middle age. Blackflies breed in flowing waters, and this disease is therefore called river blindness.

The major parasitic arthropods of humans are mites, ticks, fleas, lice, mosquitoes, and blood-sucking flies. In themselves, these parasites usually cause little more than irritation, although it can be intense. More seriously, however, they act as **vectors**—agents that transmit pathogenic viruses, bacteria, and protozoans. Millions of people have died in great **epidemics** of plague, transmitted by fleas, and typhus, transmitted by body lice. Malaria, transmitted by mosquitoes, remains one of the world's greatest killers and most stubborn public health problems today.

Any **parasitology** textbook can provide further details on these and related parasites, how they infect humans, mechanisms of disease, and how to control or avoid them. Parasitic arthropods are also covered by books on medical entomology. SEE ALSO ARTHROPOD; NEMATODE; PROTOZOAN DISEASES; SYMBIOSIS

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Pasteur, Louis

French microbiologist
1822–1895

Louis Pasteur was a French microbiologist who made major discoveries about the biology of bacteria; invented techniques to prevent the spoilage of milk, wine, and beer by microorganisms; and pioneered the prevention of infectious disease through vaccination.

Pasteur was born in 1822 in Dôle, France. He studied physical sciences at a prominent teachers' college in Paris and, at the age of twenty-six, presented his first significant research results to the Paris Academy of Sciences. Pasteur had discovered that a certain chemical could form two different crystals, whose shapes were mirror images of each other. Pasteur proposed, correctly, that this difference reflected a molecular difference, and that the two forms of the molecule had the same relationship as the left and right hands, being similar in form but opposite in orientation of parts. Pasteur showed that many molecules display this property, and that often only one form can be used by living organisms for food. This mirror-image property (called chirality) was later shown to be possessed by virtually every molecule of biological importance, including the **amino acids** that make up **proteins**.

In 1854, Pasteur was appointed dean of the Science Faculty at the University of Lille, where he offered evening classes to local workmen and introduced his day students to the foreign world of the industrial factories of

vector carrier

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

parasitology study of parasites

amino acid a building block of protein

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

Lille, demonstrating to both groups the connection between scholarship and industry he believed would profit them both. Pasteur became deeply involved in the study of fermentation, the process by which grape juice becomes wine, grain mash becomes beer, and milk sours. Back in Paris several years later, Pasteur showed that microorganisms (yeasts and bacteria) were responsible for the fermentation process, and that fermentation could be accelerated or retarded by changing the conditions of the liquid in which it occurred. He invented the process of preserving milk and other drinks by heating, which killed the microorganisms within, a process called pasteurization in his honor. In the following years, he discovered a bacterium threatening the French silk industry and devised procedures to identify and destroy infected silkworms.

Pasteur also played a critical role in a theoretical debate of the time, that of spontaneous generation. Proponents argued that the rank growth produced in standing water was due to creation of new organisms from inanimate matter. By first boiling the water and then excluding any airborne sources of contamination, Pasteur showed the water remained clear. Thus the most likely source of growth was preexisting microorganisms, not the spontaneous generations of new ones.

At age fifty-two, Pasteur was given financial security by the French parliament, allowing him to continue his researches without worry about income. At age fifty-nine, he devoted himself to vaccination, the process of disease prevention invented by Englishman Edward Jenner in 1796. Jenner had prevented smallpox infection by inoculation with cowpox, a related but less harmful organism. Not all virulent organisms have such relatives, though, and so the problem faced by Pasteur was how to weaken the infectious organism so it could be used as the vaccine. Pasteur discovered that storing cultures under various conditions for weeks to months accomplished this, and he used this technique to develop vaccines for anthrax in sheep and rabies in humans. He first used the rabies vaccine on July 6, 1885, to cure a young boy bitten by a rabid dog. Pasteur saved the boy's life, and earned international fame in the process. Pasteur became the head of the Pasteur Institute in 1888, where he remained until his death in 1895. SEE ALSO GLYCOLYSIS AND FERMENTATION; HISTORY OF BIOLOGY: BIOCHEMISTRY; MICROBIOLOGIST; VACCINES

Richard Robinson

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The Pasteur Institute has led the fight against infectious diseases for more than a century. The worldwide biomedical research organization was the first to isolate the AIDS virus in 1983.

Patterns of Inheritance

Whether an organism is a worm or a human, virtually all its characteristics are influenced by its genetic makeup. Since Gregor Mendel's pioneering studies of inheritance in the mid-nineteenth century, enormous strides have been made in understanding the molecular basis of inheritance. With the blossoming of the biotechnology industry in the 1980s and the birth of the field of genomics in the 1990s, which seeks to sequence and study the entire genetic content of organisms, countless genes have been identified and their contributions to specific characteristics elucidated. Such understand-

ing will amplify in the decades to come, undoubtedly leading to advances in many fields, but particularly in agriculture and medicine. With the draft of the human genome DNA sequence completed in 2001, scientists can anticipate a vast increase in their understanding of the molecular genetics of human disease.

Phenotype and Genotype

The **phenotype** includes all observable characteristics of an individual. Although Mendel's studies were restricted to the outward traits of pea plants, such as flower color and plant height, phenotype can include characteristics observable only under certain circumstances or with specialized tools and technology. For example, a human phenotype certainly includes eye and skin color, but it also includes characteristics such as blood type and bone density.

A genotype is the complete genetic makeup of an individual. Nonetheless, as it has been impractical to consider the entire genetic makeup of an individual, the reference to genotype is usually restricted to those genes influencing the aspect of phenotype being studied at the time. In other words, if scientists are interested in studying the coat color trait in Labrador retrievers, they focus their attention on the gene(s) identified with influencing coat color.

Proteins Dictate Phenotype

Genotype controls phenotype because genes direct the production of **proteins**. Proteins, in turn, dictate virtually every reaction in the cell and thus are directly responsible for observable characteristics.

How do the proteins work to direct phenotype? Some proteins serve structural functions (for example, in the maintenance of cell and/or tissue shape and rigidity) while others are involved in the transport of molecules and communication between cells. A substantial proportion of proteins are **enzymes**, catalyzing chemical reactions for the synthesis and transformation of virtually all biological molecules. The varying types and quantities of all biological molecules in the cells and tissues of an individual is what ultimately leads to phenotypic variation. For example, slight variation in the activity of an enzyme for pigment synthesis in a plant may result in white flowers rather than red. Likewise, a slight difference in a protein responsible for cell communication during the development of leaf tissue might result in variation of leaf shape. Understanding the path from genotype to phenotype is a major concern of modern molecular biology and one of the ultimate goals of the human **genome** project.

Mutation and Genetic Variation

If a particular gene is mutated (the deoxyribonucleic acid [DNA] sequence is somehow altered), the result can be a change in the **amino acid** sequence of a protein or the quantity of a protein produced. Such a change may affect phenotype for the organism in a detrimental manner (for example, a mutation that causes muscle deterioration in humans), a seemingly neutral manner (a change from purple to green stems in cultivated tomato plants), or sometimes even a beneficial manner (a mutation that allows a soil bacterium to survive freezing).

A young native of the Solomon Islands. A slight variation in the activity of an enzyme for pigment synthesis may result in phenotypic variation.

phenotype observable characteristics of an organism

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

genome total genetic material in a cell or organism

amino acid a building block of protein

Mutation is an essential and ongoing component of evolution. All living organisms are "mutants" in some sense, having arisen by virtue of genetic change from an ancestor. Within a population, there may be many versions of a given gene, called **alleles**. The term "mutant" allele is used somewhat arbitrarily to describe a version of a gene that is found very rarely in the population, whereas any version of a gene is considered "wild-type" or "normal" if it is relatively common. Each human being contains a handful of mutated alleles because of errors in replication early in development, as well as a number of rare, harmful alleles each has inherited from his or her parents.

allele a particular form of a gene

Mutation Affects Protein Function

In order to understand how mutations cause changes in phenotype, it is essential to study how mutations affect protein function. If one amino acid in the protein sequence is changed to another with very similar properties, the **conformation** of the folded protein may not be functionally altered. However, if the amino acid change is substantial (for instance, from small to large or from nonpolar to **polar**), the protein architecture may be altered in such a way as to cause a decline or abolition of function. It is likely that such a loss of function will ensue from mutation, since protein function has been fine-tuned during evolution and depends on the precise architecture of the protein. (If a person whacks a computer with a sledgehammer, it is unlikely that the computer's performance will actually increase.) In some rare situations, however, instead of causing an ineffective protein, a mutation may result in a hyperactive protein. An enzyme may work at its job overtime, for example, by synthesizing excessive quantities of a product. Although a hard-working protein may sound like a benefit to the organism, this is rarely the case. Such gain-of-function mutations are usually toxic, disrupting the delicate balance of biomolecules needed for life.

conformation three-dimensional shape

polar partially charged, and usually soluble in water

Dominance Between Alleles

The path from allele to phenotype is complex in most organisms, since more than one allele of a given gene is usually present. In **diploid** organisms such as humans, an individual carries two alleles of each gene. If the individual carries two identical alleles (a homozygote), then the phenotype necessarily will reflect the only version present. However, if an individual carries two different alleles (a heterozygote), each encoding a slightly different characteristic, what will the phenotype show? For example, if a diploid plant carries one allele encoding red flowers and one allele encoding white flowers, will the flowers be red or white? The answer depends on the molecular behavior of the encoded proteins.

diploid having pairs of chromosomes in the nucleus

Imagine that the red flower allele encodes a functional enzyme essential for the synthesis of the chemical compound leading to red pigmentation. If the white flower allele is a loss-of-function mutation, the enzyme encoded by this allele will not be functional and consequently will not contribute toward the synthesis of red pigment; the absence of red pigment leads to white flowers. In the heterozygote, however, enough functional enzyme may be produced by one allele to result in pigmented flowers.
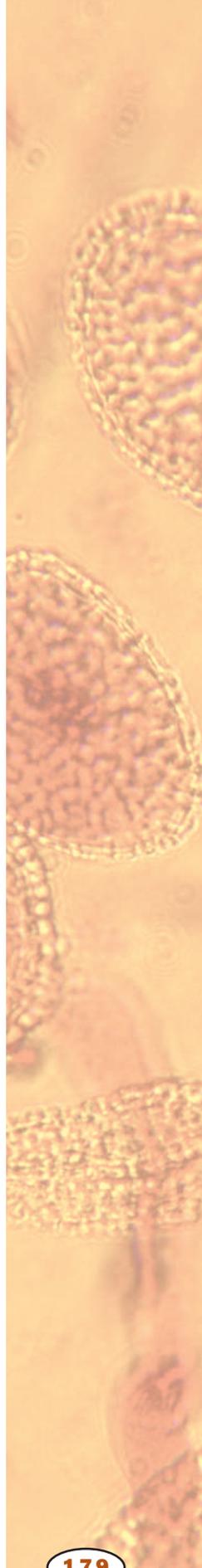
In this case, geneticists would describe the red allele as dominant and the white allele as recessive. If the allele encoding red flowers is dominant,

then this allele will phenotypically mask expression of the recessive allele (in this case encoding white flowers), resulting in the expression of red flowers. Thus, in order for a recessive allele to be expressed in the phenotype, only the recessive alleles can be present.

Alternatives to Dominance

Two dissimilar alleles in a pair need not have a completely dominant/recessive relationship. In fact, it is often the case that neither allele is fully dominant, causing the heterozygote to appear different from either homozygote. In one type of allelic relationship, termed incomplete or partial dominance, the heterozygote produces a phenotype that is intermediate between both homozygotes. Snapdragons provide a good example of partial dominance. In this organism, the two homozygotes produce either red or white flowers, but the heterozygote produces pink flowers. In this case, the single functional allele in the heterozygote does not produce enough enzyme to synthesize large quantities of red pigment; the result is just enough pigment to make the flowers appear pink.

In another type of allelic relationship, termed codominance, the heterozygote produces a phenotype that incorporates both phenotypes of the homozygotes. A codominant relationship between alleles is often more apparent at the cellular or molecular level. A good example of codominance is seen in human blood type. People who are **homozygous** for the A blood type allele produce an enzyme that adds a particular type of sugar onto the exterior of red blood cells, thereby producing the "A **antigen**." Similarly, homozygotes for the B blood type allele produce a different type of sugar on red blood cells, leading to the presence of "B antigen." Heterozygotes with one A and one B allele produce enzymes that deposit both different types of sugars, resulting in red blood cells displaying both the A and B antigens.

When Does Mutation Affect Phenotype in Diploids?

If a mutant allele is dominant, a **heterozygous** individual will display the mutant phenotype; if the mutant allele is recessive, heterozygotes will have a normal phenotype (although they will be "carriers" of the mutant allele). What determines whether a mutant allele is recessive or dominant?

Loss-of-function mutations are usually recessive because the single functional allele can often create adequate levels of protein. Such is the case with the recessive cystic fibrosis disease in humans. Most homozygous children with this lethal disorder do not live to adulthood, although advances in treatment have prolonged life significantly. The normal allele of the cystic fibrosis gene encodes a cell membrane protein that provides an essential function of transporting chloride **ions** across the cell membrane. Mutant alleles of the gene encode a defective protein, and consequently chloride transport is blocked in people who are homozygous for the defective allele. There are many downstream consequences to this defect that ultimately lead to the cystic fibrosis disease. The most serious effects are in the lungs and the pancreas. In heterozygous carriers of mutant alleles, however, the single normal allele produces enough functional protein to transport chloride effectively and these individuals lead healthy lives.

homozygous containing two identical copies of a particular gene

antigen foreign substance that provokes an immune response

heterozygous characterized by possession of two different forms (alleles) of a particular gene

ion an electrically charged particle

The most common mechanism by which a mutant allele is dominant is through a gain-of-function mutation. In one type of gain-of-function mutation, termed hypermorphic, the protein is produced in excessive quantities or is somehow hyperactive. The presence of a single normal allele can do nothing to tone down the activity resulting from the mutant allele. This situation is observed, for example, in an extreme type of dwarfism called achondroplasia and in many human cancers. In these cases, specific molecular switch proteins are continually in the "on" mode, causing a number of processes to occur when they otherwise would not.

In a second type of gain-of-function mutation, termed neomorphic, the mutant protein takes on a new, inappropriate role. Although the normal protein may function adequately in its usual role, it cannot stop the mutant protein from wreaking havoc in the cell. Such is the case with Huntington's disease and some other human neurodegenerative disorders in which **neurons** in the brain slowly die off. The normal function of the protein responsible for Huntington's disease has yet to be determined, but it is known that the mutant protein forms abnormal aggregates in neurons. Whether this, or some other less visible, function is the toxic event is not yet clear.

neuron nerve cell

Living with a Single Allele

It is often the case that a loss-of-function mutation is fully recessive, allowing heterozygous human carriers of mutant alleles to lead completely healthy lives. But suppose a person has only a single allele of a gene. This is the normal situation for all human males, who carry only a single X **chromosome** along with a single Y chromosome (the sex determination chromosomes). The X is a large chromosome with many essential genes having functions outside of sex determination. Women have two X chromosomes and therefore have two alleles for all the genes that lie on the X.
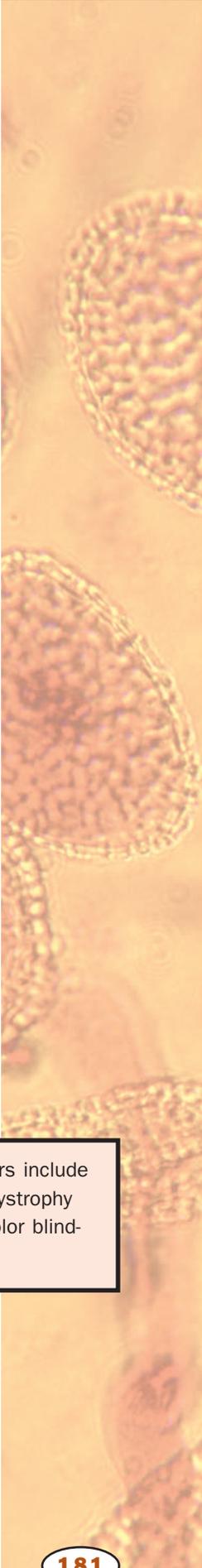
chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and nongene regions

Traits carried on the X or Y chromosome are known as "sex-linked traits." Those on any of the other chromosomes are called "autosomal traits."

While women can carry recessive alleles of X-linked genes without disease manifestation, males with a single recessive allele are forced to express it, as they lack the possibility to mask the effect with a dominant, normal allele. Affected males necessarily pass the mutant allele onto their daughters and cannot pass it onto their sons (because they give their sons a Y, not an X, chromosome).

Hemophilia is an example of a human disorder caused by a mutation of a gene on the X chromosome. Hemophilia is caused by a loss-of-function mutation in a gene encoding a blood-clotting protein. Before treatment was available, males often bled to death in childhood from a small cut.

Other X-linked disorders include Duchenne muscular dystrophy and some forms of color blindness.

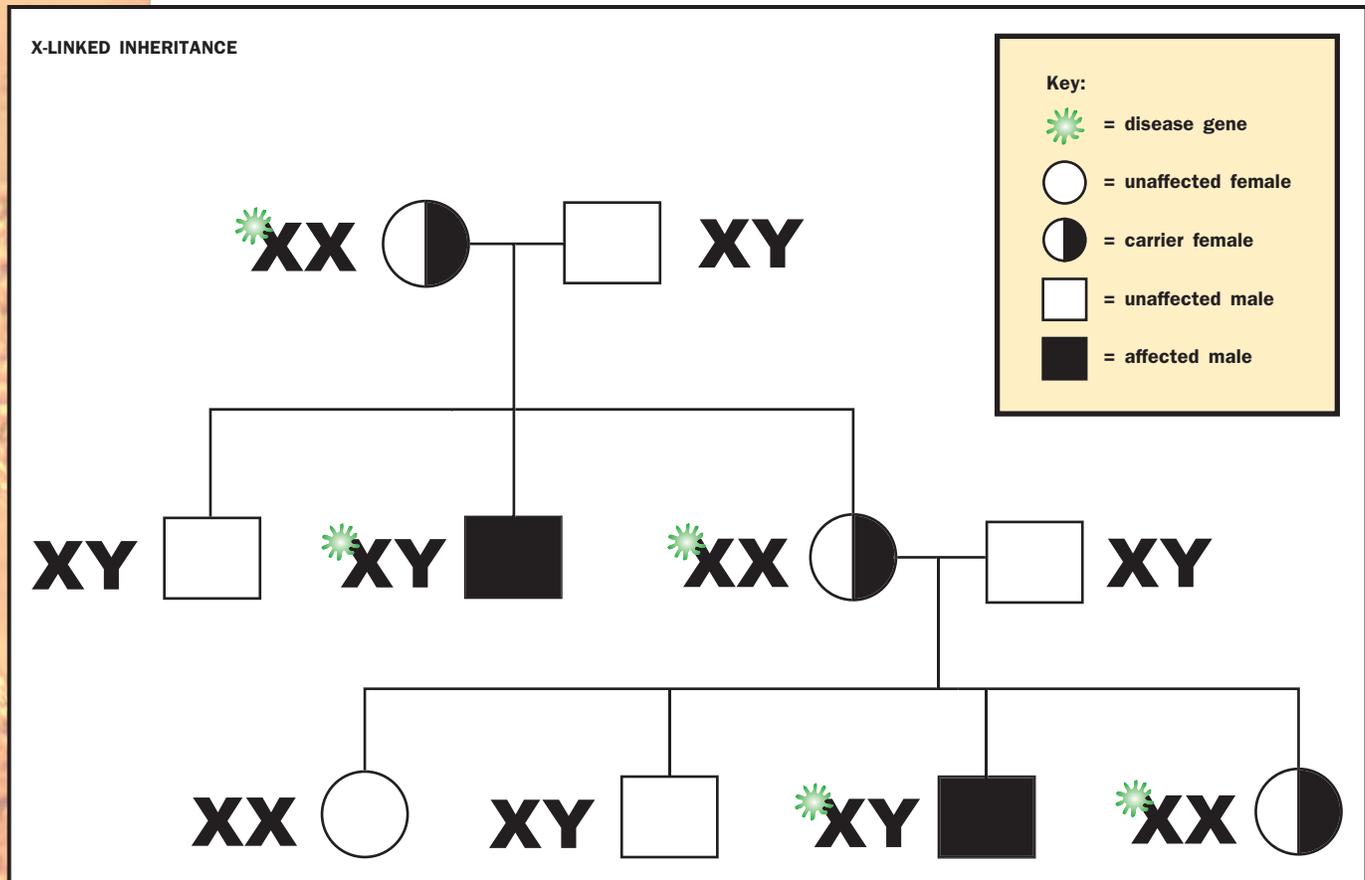## Many Factors Influence Phenotype

Genetic studies clearly are facilitated by phenotypes readily identified as resulting from a single gene, inherited in a simple so-called Mendelian fashion (a one gene–one phenotype relationship). It is important to keep in mind, however, that genes do not work in isolation. The expression of a single gene is dependent on many other genes in the genome (the genetic background) and many external, or environmental, factors such as nutrition, climate, or exposure to infectious agents. Although the complete DNA

X-LINKED INHERITANCE

Key:

✳ = disease gene

◯ = unaffected female

◖ = carrier female

☐ = unaffected male

■ = affected male

sequence analysis of a genome will hasten one's understanding of the many genes responsible for a trait, the identification of environmental factors will undoubtedly be slower because understanding these factors requires careful and controlled experimentation and observation. Such conditions are difficult to study, particularly in humans.

The effect of environment is evident in many experimental organisms, such as fungi, where "conditional" mutants are artificially constructed and utilized in genetic studies. For instance, temperature-sensitive mutants grow well at certain temperatures but die at a slightly elevated temperature that normal cells can easily tolerate. Even in humans, some environmental contributions to the manifestation of disease have been identified. Until the molecular mechanism for the phenylketonuria disease (PKU) was elucidated, it was not known that the mental retardation normally associated with this disease could be prevented by diet. Homozygotes with this recessive condition are unable to metabolize the amino acid phenylalanine (also found in some artificial sweeteners). The resulting excessive buildup of phenylalanine leads to impairment of mental abilities. By placing homozygous-recessive babies on a diet restrictive of phenylalanine, normal brain function occurs during development.

Epistasis: Many Genes, One Effect

The contributions of more than one gene on phenotypic expression have been well documented in genetic studies. In many instances, one gene has

been found to mask the expression of a second gene; the former gene is said to be epistatic to the latter. Epistasis relationships are often observed in biochemical pathways, which employ numerous proteins in an assembly-line fashion. If enzyme A normally converts compound X into compound Y, and then enzyme B converts compound Y into red flower pigment, B can only affect the phenotype if a functional allele for enzyme A is first expressed. If enzyme A loses function and is unable to produce compound Y, the red pigment will not be produced irrespective of whichever gene B alleles might be present. This situation differs from dominance, as it involves two separate genes (and two separate proteins).

Nonpenetrance

The influence of other, unidentified factors can be seen when some individuals in a study do not display the phenotype normally associated with their defined genotype, a situation termed nonpenetrance. For example, polydactyly is a dominant human disorder resulting in the development of more than five digits on hands and feet. Since the mutant allele is dominant, all individuals carrying the allele should display the phenotype. Nonetheless, some individuals have normal numbers of fingers and toes in spite of the presence of the dominant allele. Thus, there must be other factors that influence the penetrance of the mutant allele; these factors might be other genes in the individual's genome, or certain unknown factors in the individual's environment.

Pleiotropy: One Gene, Many Effects

Sickle cell disease is a very common genetically inherited disorder that is often fatal in childhood; although some treatment is available, there is no cure to date. The disease is characterized by **anemia**, extreme pain and fatigue, heart failure, spleen enlargement, severe microbial infection, and impaired mental abilities. Early genetic studies demonstrated that the disease is inherited in an autosomal (not linked to the sex chromosomes), recessive manner.

The responsible allele of sickle cell disease expresses a mutated version of a protein subunit of **hemoglobin**. Normal hemoglobin is found in red blood cells and is essential for the transport of oxygen to all tissues of the body. In sickle cell disease, the conformation of the mutant hemoglobin subunit is altered, by virtue of a single amino acid change from the wild-type subunit, causing the proteins to associate with each other into abnormal fibers. This association inhibits the binding of oxygen and causes the red blood cells to appear stretched out in a characteristic "sickle" shape. The sickle cells clog capillaries, seriously compounding the effect by reducing all blood flow to various tissues.

Sickle cell disease provides a useful example of how a highly complex phenotype can result from a single, well-defined genotype (in this case a single **nucleotide** mutation). Such a situation, termed pleiotropy, arises due to a cascade of consequences from the single mutated protein. In this case, the abnormal hemoglobin causes poor oxygen transport and sickling of red blood cells, which in turn causes anemia, poor blood circulation, and accumulation of sickle cells in the spleen. The poor blood circulation in turn causes heart failure, lung damage (often followed by pneumonia), and brain dam-

A scanning electron micrograph showing healthy, round red blood cells and a diseased sickle-shaped cell.

anemia lack of oxygen-carrying capacity in the blood

hemoglobin oxygen-carrying protein complex in red blood cells

nucleotide the building block of RNA or DNA

age. Overloading the spleen with sickle cells causes extreme pain and an increased frequency of infectious disease. SEE ALSO BLOOD CLOTTING; DISEASE; GENE; GENETIC ANALYSIS; HUMAN GENOME PROJECT; MENDEL, GREGOR

Karen E. Kirk

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Pauling, Linus

American chemist
1901–1994

Linus Carl Pauling, American chemist, is the only person to have won two undivided Nobel prizes (in chemistry in 1954 and the Nobel Peace Prize in 1962). He is best known for his work on molecular structure, the nature of the chemical bond, and the effects of various chemical agents on the human body.

Pauling was born on February 28, 1901, in Portland, Oregon, the son of a pharmacist. In 1922, he received his bachelor's degree from Oregon State College. He then became a doctoral student at California Institute of Technology (CIT), from which he received his doctoral degree in 1925. For the next two years, Pauling received fellowships that allowed him to study abroad with Niels Bohr in Denmark, Erwin Schrodinger in Switzerland, and Arnold Sommerfield in Germany.

In 1927, Pauling was appointed assistant professor at CIT, and four years thereafter became chairman of the Department of Chemistry and Chemical Engineering, a position he held until 1964. Meanwhile, between 1963 and 1967, he was a professor at the Center for the Study of Democratic Institutions at Santa Barbara. From 1969 until his death he was affiliated with Stanford University.

Pauling made significant contributions to molecular biology and **organic** chemistry. His work focused on the spatial architecture of molecules, and the relationship between molecular structure and molecular behavior. The theory of resonance, which Pauling first formulated, has since explained certain properties of the carbon compounds, particularly the subgroup known as the **aromatics**.

Pauling successfully applied the theories of physics to biological problems. He helped make strides in the field of immunology, for example, by looking at the basic molecular structure of **antitoxins**. His substantial research on the structure of **amino acids** helped determine the **conformation** of **proteins**. For this work, Pauling was awarded the 1954 Nobel Prize in chemistry.

During World War II, Pauling worked as a part of the National Defense Research Committee and the Research Board for National Security, helping design substitutes for human serum and blood plasma, rocket propellants, and an oxygen efficiency indicator.

As a result of the dropping of the atomic bomb at the end of the war, Pauling became concerned about the negative effects that nuclear fallout has on the molecules of the human body. After the war, Pauling became a member of Albert Einstein's Emergency Committee of Atomic Scientists, as well as of many other pro-peace organizations that formed in the 1950s. Among other things, he protested the development of the hydrogen bomb and vigorously promoted the adoption of a nuclear test ban treaty.

Finally, in the 1960s and 1970s, Pauling became an outspoken advocate of the value of vitamin C to human nutrition. He proposed the theory that colds could be prevented by improving nutrition, and particularly by increasing intake of ascorbic acid (vitamin C).

In 1962, Pauling won the Nobel Peace Prize for his work toward the nuclear test ban treaty. In addition, he was one of seven individuals awarded the International Lenin Peace Prize in 1968–1969. The U.S. government gave him the National Medal of Science in 1975.

Among his most significant publications are *The Nature of the Chemical Bond and the Structure of Molecules and Crystals* (1939); *No More War* (1951), a cry for world peace; and *Vitamin C and the Common Cold* (1970). SEE ALSO HISTORY OF BIOLOGY: BIOCHEMISTRY

Hanna Rose Shell

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PCR   *See Polymerase Chain Reaction*

organic composed of carbon, or derived from living organisms

aromatic compound including a double-bonded carbon ring

antitoxin molecule used to inactivate a toxin

amino acid a building block of protein

conformation three-dimensional shape

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

Linus Pauling took 18,000 milligrams of vitamin C each day, which is 300 times the recommended daily allowance.

Pedigrees and Modes of Inheritance

A pedigree is a diagram that depicts the blood relationships of family members, as well as which individuals express the trait or disorder under study. Construction of a pedigree is often the first step in the identification of a **gene** variant that causes a particular disease or trait. Several terms are encountered in pedigree analyses.

Phenotype, Genotype, and Alleles

A **phenotype** is an observable trait that is the expression of a gene combination, or genotype. Eye color, blood group, and the symptoms of inherited diseases are examples of phenotypes. **Chromosomes**, and therefore genes, occur in pairs in a **diploid** organism, such as a human. An individual inherits one copy of each gene from his or her mother and another copy from the father. A gene can exist in alternate forms, called **alleles**. A gene may have many alleles, but a person can only have two copies of the same allele, or two different alleles, for a particular gene. An individual who inherits two copies of the same allele is **homozygous**; inheriting two different alleles is termed **heterozygous**.

Pedigree Symbols

The figures in this article show symbols commonly used in pedigrees. Squares represent males, circles represent females, and diamonds depict individuals of unknown or, for reasons of confidentiality, disguised gender. A double line between parents indicates consanguineous marriages (between blood relatives) (see Figure 3). Filled symbols represent individuals who display a certain trait, such as an inherited disease. Bars next to the symbols represent genetic loci, and different alleles are color-coded. Disease-causing mutations are shown as stars or crosses. Symbols that are half filled indicate heterozygous individuals, but often this information isn't known.

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

phenotype observable characteristics of an organism

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

diploid having pairs of chromosomes in the nucleus

allele a particular form of a gene

homozygous containing two identical copies of a particular gene

heterozygous characterized by possession of two different forms (alleles) of a particular gene

Figure 1. In autosomal dominant inheritance, one copy of the disease gene (shown as a star on one homologous chromosome) is enough to cause the disease. Affected individuals are shown in black.

AUTOSOMAL DOMINANT INHERITANCE

PENETRANCE (ALL OR NONE)
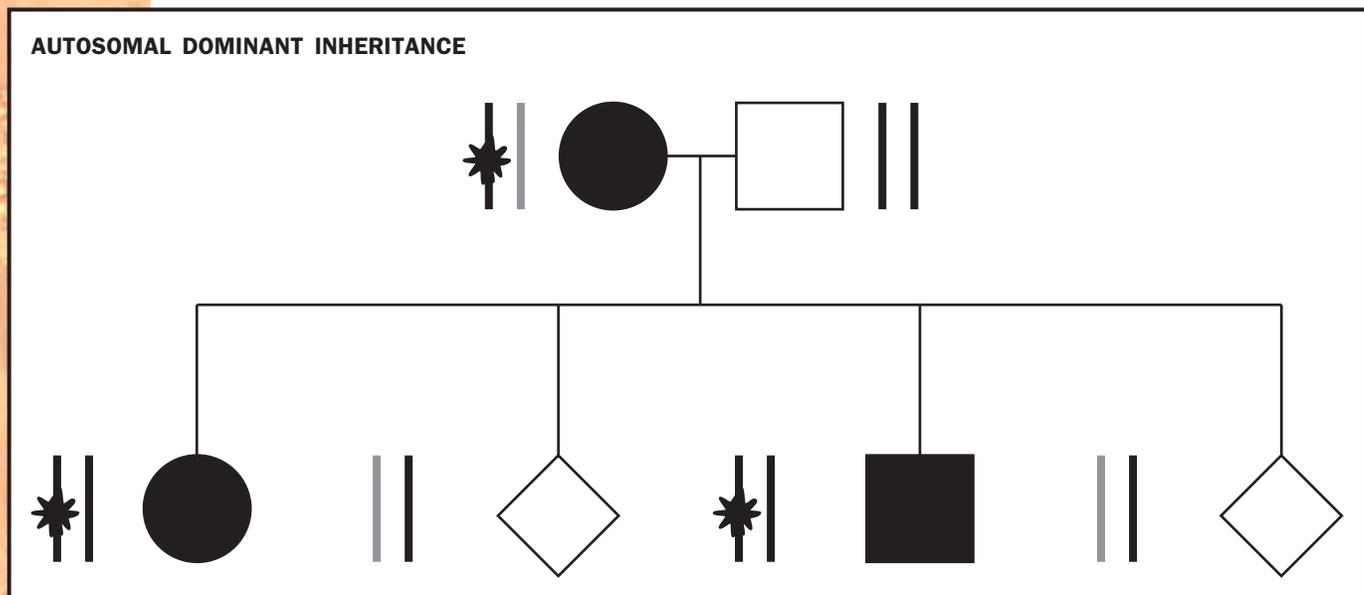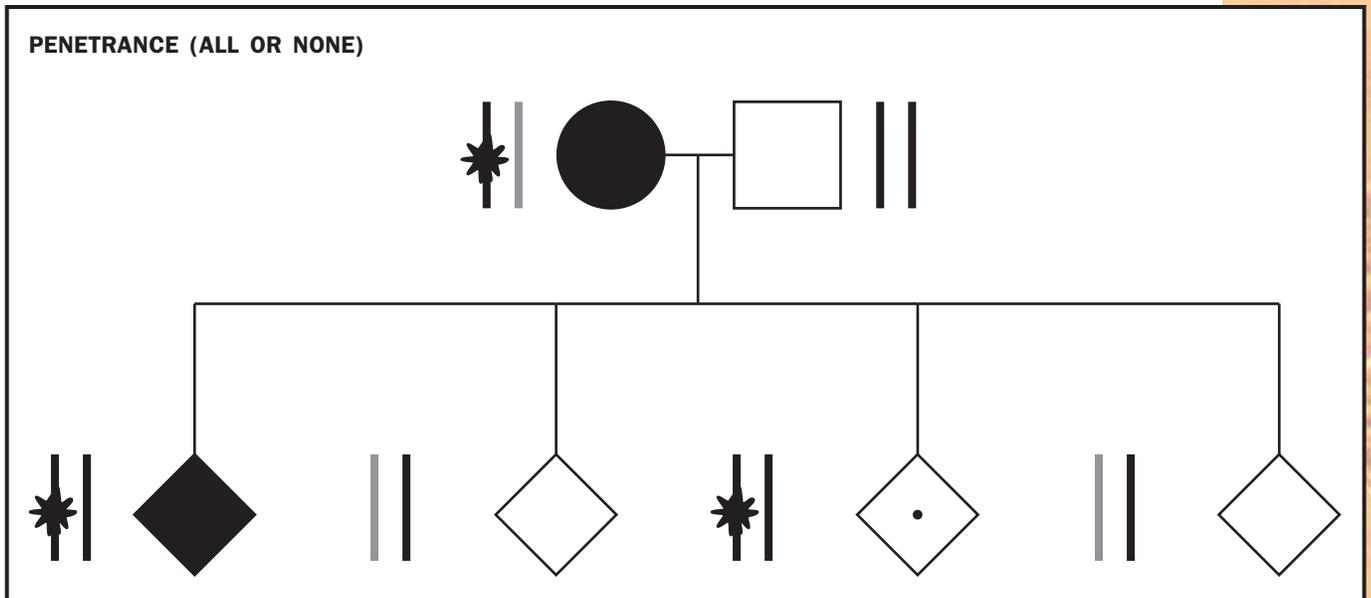
Modes of Inheritance

A pair of alleles can show one of three modes of inheritance. Augustinian monk and botanist Gregor Mendel (1822–1884) demonstrated these patterns of inheritance using pea plant crosses. The modes of inheritance are **autosomal dominant**, autosomal recessive, and X-linked. To simplify the discussion of these different forms, the trait used in the following text will be a hereditary disease.

Autosomal Dominant

In individuals with an autosomal dominantly inherited condition (Figure 1), one mutation is sufficient to cause disease. Statistically, an affected individual is therefore expected to have 50 percent affected and 50 percent unaffected offspring. However, each child has the same chance (50 percent) of inheriting the mutated gene. That is, if the first two children are affected, the next two are not necessarily going to be unaffected. "Autosomal" indicates genes on the chromosomes that do not carry genes that determine sex, and so both males and females are affected in successive generations. Usually, the disease does not occur in the offspring of unaffected individuals. Rarely, an autosomal-dominant mutation does not cause disease, perhaps because of the effects from other genes. Such a mutation is said to be incompletely penetrant (Figure 2). Penetrance is an all-or-none phenomenon: the disease is either present or absent. In contrast, expressivity refers to the degree of phenotypic expression. For example, the trait of extra fingers or toes, called polydactyly, is incompletely penetrant, because some individuals with affected parents and children have the normal numbers of fingers or toes. Polydactyly is also variably expressive, because affected individuals vary in the numbers of extra digits.

Autosomal Recessive

In individuals with an autosomal recessively inherited disease (see Figure 3), both alleles are mutant. Usually, the parents of the affected individual are

Figure 2. Penetrance refers to "all or none" inheritance; the disease is either present or absent. The first is affected (darkened diamond), but the third child is not (diamond with dot).

autosomal dominant pattern of inheritance in which inheritance of a single allele from either parent results in expression of the trait
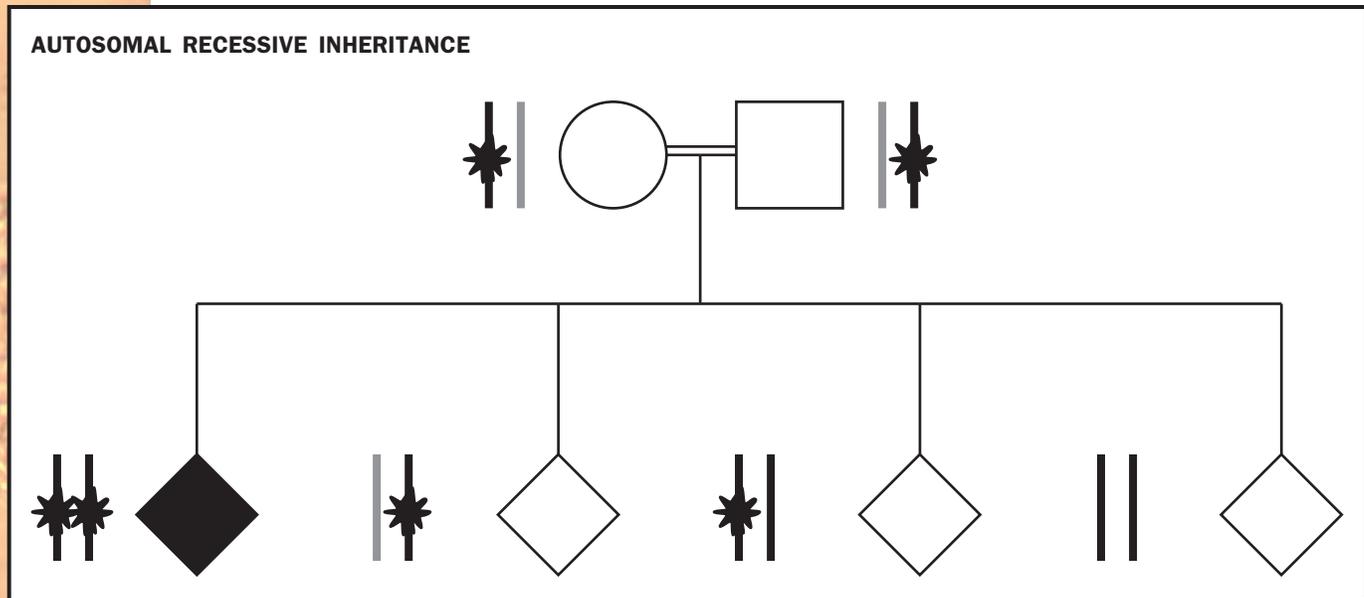
AUTOSOMAL RECESSIVE INHERITANCE

Figure 3. In autosomal recessive inheritance, both alleles are mutant. Parents of affected individuals are unaffected carriers.

consanguineous descended from the same ancestor

heterozygous for this mutation and thus unaffected carriers. Each of the parent's offspring has a 25 percent chance of inheriting the illness and a 75 percent chance of being unaffected. However, of the latter, two-thirds will be heterozygous like their parents, and one-third will be homozygous for the normal gene and thus cannot pass on the trait. An autosomal recessive trait or disease may occur in individuals of both sexes. People with homozygous mutations are frequently the product of a **consanguineous** marriage (Figure 3). A recessive disease can, however, also be caused by two *different* mutations in the same gene (more frequent in nonconsanguineous marriages), which are then called *compound heterozygous* mutations.

X-linked

An X-linked trait is carried on the X chromosome. In pedigrees depicting X-linked inheritance, usually only males are affected and, although affected males may occur in consecutive generations, transmission is always through females. This is based on the fact that males have a single X chromosome (in addition to their Y chromosome), which they always inherit from their mother and will always pass on to their daughters but never to their sons. Females, on the other hand, have two X chromosomes. Therefore, they can be carriers of an X-linked mutation, but in most cases are phenotypically unaffected because they have a second (nonmutated) X chromosome, compensating for whatever loss of function is caused by the mutated gene.

Mitochondrial

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

oocyte unfertilized egg

fertilization union of sperm and egg

Some additional genetic material in humans is contained in the **mitochondrial** genome, and some diseases result from mutations in mitochondrial genes. Only females can transmit mitochondrial diseases because sperm cells rarely contribute mitochondria to the **oocyte** at **fertilization**. Therefore, a mitochondrial disease is typically passed from an affected mother to all her children, but not from an affected man to any of his children. Many mitochondrial disorders cause muscle fatigue, because muscle cells contain thou-

sands of mitochondria that provide energy for contraction. SEE ALSO GENETIC ANALYSIS; GENETIC DISEASES; MENDEL, GREGOR; PATTERNS OF INHERITANCE

Christine Klein

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Peripheral Nervous System

The peripheral nervous system (PNS) refers to all the **neurons** (and their supporting cells, or glia) of the body outside the brain and spinal cord (central nervous system [CNS]). The brain is the organ that decides how a person responds to what happens in the surrounding world. While this is an extremely important function, the brain relies upon the peripheral nervous system, and its information gathering capabilities, to receive information about the world and to send appropriate responses to various body parts, such as muscles and glands. The neurons of the peripheral nervous system do not make complex decisions about the information they carry. The appropriate decisions are made instead in the brain and spinal cord. However, without the peripheral nervous system's ability to bring in sensory information and send out motor information, it would be impossible for a person to walk, talk, ride a bike, or even watch television. Without the ability to take in information and send out responses, the brain would be useless.

neuron nerve cell

Peripheral neurons are of two types, sensory and motor. Sensory (afferent) neurons bring information about the world within and around the body from sense organs to the brain and spinal cord, while **motor** (efferent) **neurons** carry messages from the brain and spinal cord out to the muscles and glands. For example, if a mosquito lands on a person's arm, sensory neurons in the skin send a message to the spinal cord and then the brain, where the message is understood, and a reaction formulated. The brain's response may be to use motor neurons to cause muscle contractions resulting in a slap on the skin where the mosquito landed.

motor neuron nerve cell that controls a muscle or gland

Sensory Division

The sensory division of the PNS carries all types of sensory information to the CNS, including that from the "special senses" of touch, smell, taste, hearing, and sight, as well pain, body position (proprioception), and a variety of **visceral** sensory information. The information from the viscera (internal organs) includes some of which the body is aware (bladder fullness and stomach aches, for example), as well as much of which the body is not aware, including blood pressure, concentration of substances in the blood, and many other bits of sensory information used to regulate the internal environment.

visceral related to the viscera, or internal organs

Central and peripheral nervous systems

CNS (brain and spinal cord)

PNS (motor and sensory nerves)

Autonomic nervous system

- Parasympathetic nerves
- Sympathetic nerves
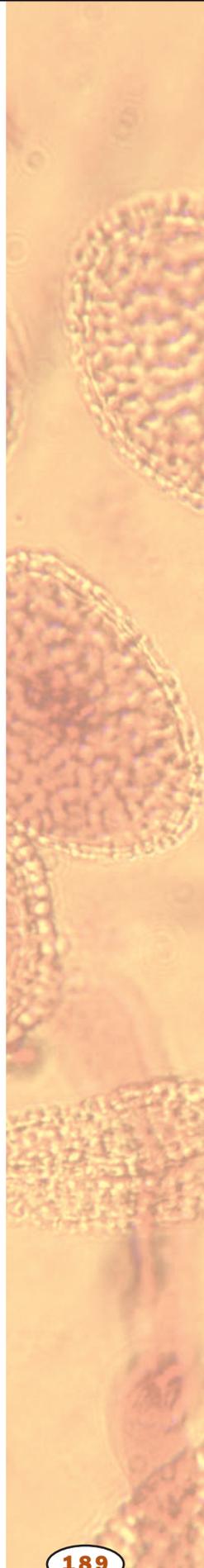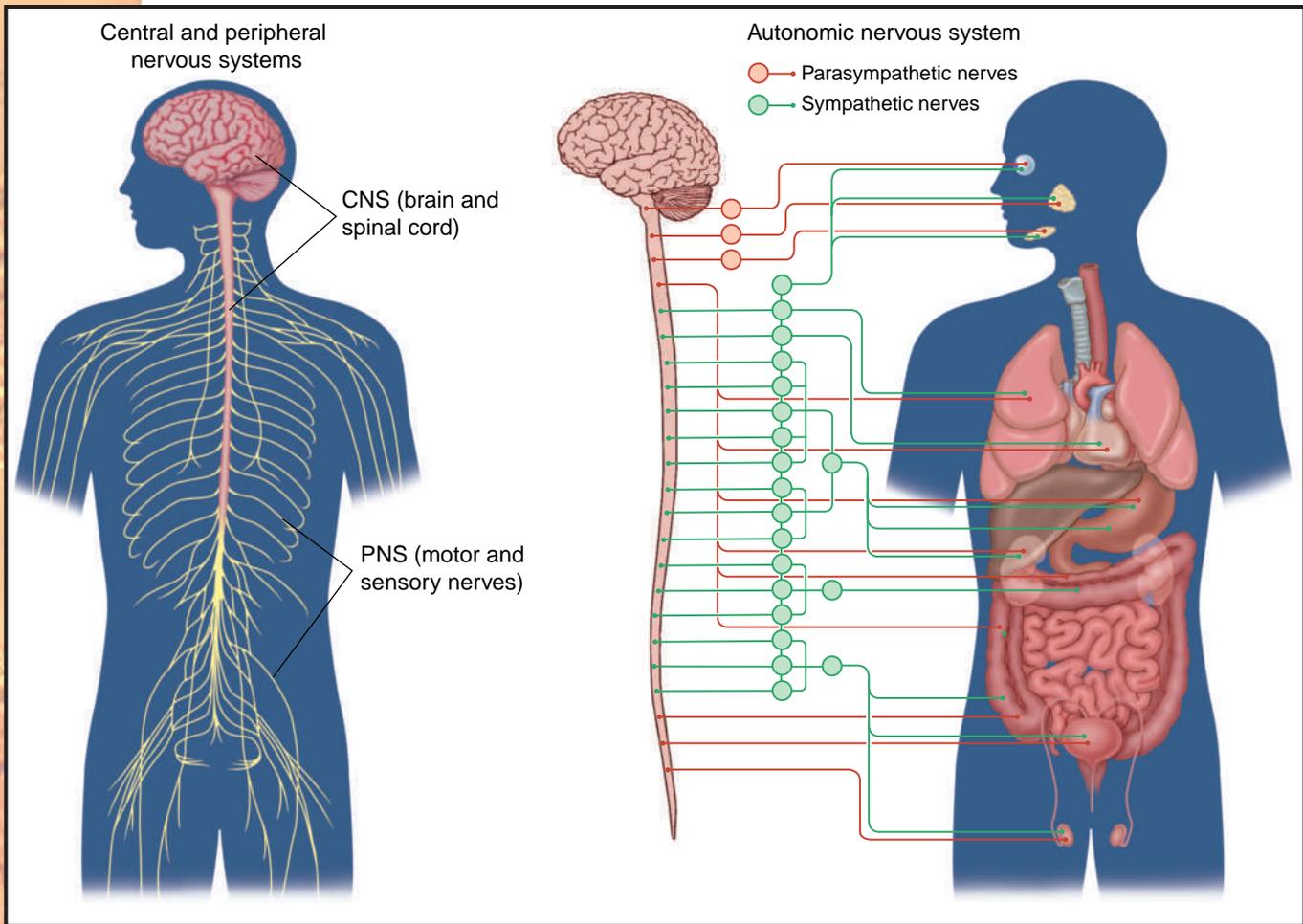
The central and peripheral nervous systems (left) and the autonomic nervous system (right).

hormone molecule released by one cell to influence another

Motor Division

The motor division of the PNS is subdivided into several branches. The somatic motor branch carries voluntary (willed) commands to the skeletal muscles, allowing a person to perform such action as swatting a mosquito or sticking out the tongue. The autonomic motor branch carries autonomic (automatic, or unwilled) commands to a variety of muscles and glands throughout the body, allowing the brain to control heart rate, blood pressure, breathing rate, sweat production, and **hormone** release, among other functions.

Much like a car, which has both a gas pedal and a brake to give the driver very precise speed control, the autonomic nervous system can be subdivided into two parts, the sympathetic and the parasympathetic. The sympathetic part of the autonomic nervous system generally acts in opposition to the parasympathetic part. So while the sympathetic motor neurons speed up the heart, the parasympathetic motor neurons will slow it down, and while the sympathetic motor neurons slow down digestion, parasympathetic motor neurons speed digestion.

When a person is frightened, for example, sympathetic motor neurons trigger adrenaline release, increase the heartbeat and blood pressure, close off blood vessels to the gut and open them to the skeletal muscles, dilate

the pupils, and open the airways. Combined, these are known as the "fight or flight" response, since they prepare the body for rapid action. Afterward, parasympathetic neurons reverse these actions, bringing the body back to a more peaceful resting state.

Anatomical Considerations

Some of the somatic sensory neurons are very long, stretching from the sensory receptors all over the body all the way into the spinal cord, or even directly into the brain. Likewise, a single somatic motor neuron spans the distance from the spinal cord or brain to whichever muscle it operates, even if that is the muscle controlling the big toe. Autonomic motor neurons are not as long, and usually two neurons are needed to stretch from the spinal cord to the muscle or gland being turned on or off.

Many of the connections among neurons in the peripheral nervous system are made in special structures called **ganglia** (singular, ganglion). Most ganglia are large collections of connecting neurons located in specific regions of the body, and are part of the autonomic nervous system. In some cases, the ganglia are located close to the spinal cord, and thus close to the target organ. SEE ALSO ADRENAL GLAND; CENTRAL NERVOUS SYSTEM; EYE; HEARING; MUSCLE; NERVOUS SYSTEMS; NEURON; PAIN; SPINAL CORD; TOUCH

Curt Walker

ganglia cluster of nerve cell bodies

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Peroxisomes

Peroxisomes (microbodies) are **cytoplasmic organelles** involved in **metabolism** of hydrogen peroxide, H_2O_2. The peroxisome is about 0.5 **microns** in diameter, and is surrounded by a membrane. They are widely distributed in most animal and plant cells. Although peroxisomes possess more than sixty **proteins**, their function requires at least one H_2O_2-generating **enzyme**, flavinoxidase, and an H_2O_2-degrading enzyme, catalase, a peroxisome. Peroxisomal proteins are synthesized on free polyribosomes and a peroxisomal targeting signal position enables them to be targeted to peroxisomes post-translationally.

Peroxisomes are major sites of oxygen consumption in the cell and participate in several metabolic functions that use oxygen. Oxygen consumption in the peroxisome leads to H_2O_2 production, which is then used to oxidize a variety of molecules. Important reactions in the peroxisome include **oxidation** of long-chain and very long-chain fatty acids, metabolism of glyoxalate, degradation of uric acid, and synthesis of ether **lipids** and cholesterol, among others. Alcohol is detoxified to acetaldehyde in part by action of peroxisomes. In plants, peroxisomes perform photorespiration.

cytoplasm material in a cell, excluding the nucleus

organelle membrane-bound cell compartment

metabolism chemical reactions within a cell

micron one-millionth of a meter; also called a micrometer

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

oxidation reaction characterized by loss of electrons, or reaction with oxygen

lipid fat or waxlike molecule, insoluble in water

In humans, defects in peroxisome biogenesis lead to at least twelve peroxisomal disorders, most of them lethal during childhood. In liver cells peroxisomes are few in number, but several drugs that lower serum lipids, and many other chemicals designated as peroxisome proliferators, induce a profound increase in peroxisome number by activating a nuclear receptor called peroxisome proliferator-activated receptor (PPAR). Sustained activation of PPAR and induction of peroxisome proliferation in liver leads to the development of liver cancer in rats and mice. SEE ALSO ALCOHOL AND HEALTH; C4 AND CAM PLANTS; LIPIDS; METABOLISM, CELLULAR; ORGANELLE

Janardan Reddy

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Pharmaceutical Sales Representative

The people who tell others about new medicinal preparations usually work for pharmaceutical manufacturing companies as pharmaceutical sales representatives. To keep informed about new products, pharmaceutical sales representatives are continuously learning as part of their jobs.

Pharmaceutical sales representatives talk to those who influence the prescription and sale of medicines. Such people include: those who write prescriptions (doctors, nurse practitioners, and dentists), the pharmacists who legally sell the preparations, and the policymakers who determine which drugs are covered by health management organizations and health insurance plans. Some are involved in advertisement of specific drug preparations directly to consumers.

A four-year bachelor's degree (B.S. or B.A.) with a major in chemistry, microbiology, animal biology, or pharmacology is the usual minimum preparation for this career. A better general understanding of the actions of drug preparations is obtained through an entry-level pharmacy degree (which is now in most states a Doctor of Pharmacy [Pharm.D.] degree), requiring six years after high school to complete. People with nonscience baccalaureate majors such as business or marketing will have the most "catching up" to do. In high school a person interested in a pharmaceutical sales career should take college preparatory courses with a science and mathematics emphasis. SEE ALSO CLINICAL TRIALS; PHARMACOLOGIST

Margaret A. Weck

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A scientist performing pharmacological research.

hormone molecule released by one cell to influence another

Pharmacologist

A pharmacologist practices the science of pharmacology, which is the study of drug, **hormone**, and chemical actions on biological systems. A pharmacologist must have knowledge in the sources, chemical properties, biologi-

cal effects, and therapeutic uses of drugs. The pharmacologist must be multidisciplinary with experience and/or knowledge in experimental techniques such as analytical chemistry, biochemistry, cellular and molecular biology, genetics, immunology, medicinal chemistry, microbiology, pathology, and physiology. Pharmacologists can be subcategorized as doing biologic, industrial, human, or regulatory research.

Pharmacologists perform studies to examine drug interactions and define the mechanism involved in producing these interactions. In order to determine the mechanism of action of a particular drug, the pharmacologist may perform experiments on cellular *in vitro* systems. However, in order to identify the physiological, biochemical, or immunological response, it is often necessary to perform the experiments in *in vivo* experimental animal systems such as rats and mice (preclinical). Many pharmacologists consider toxicology to be an important part of pharmacologic research. Pharmacologists may perform this type of research in an academic (university) or industrial (drug company) environment.

Pharmacology training usually requires graduate degrees (M.Sc. and Ph.D.). Pharmacologists who study the therapeutic and toxic actions of drugs in humans are referred to as clinical pharmacologists. The clinical pharmacologist often has medical training (M.D.) with specialized training in the use of drugs in the treatment of disease. Clinical pharmacologists determine the correct routes of drug administration (e.g., oral or intravenous), assess their adverse effects, monitor drug levels, and establish therapies which prevent or treat overdoses as well as the consequences of interactions with other drugs. Some pharmacologists are involved with the administration of the rules and regulations relating to the development of new drugs. The pharmacologist unlocks the mysteries of drug actions, discovers new therapies, and develops new medicinal products, which inevitably touch upon all human lives. SEE ALSO BIOCHEMIST; POISONS; PHARMACEUTICAL SALES REPRESENTATIVE

David S. Lester

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Pheromone

Pheremones are chemical signals released by an organism that influence the behavior of another. Communication between living cells is often ultimately chemical in nature. Chemical substances produced by one cell travel to another cell where they bind to **protein** receptors in the cell membrane or within the interior of the cell and initiate a series of signal **transduction** mechanisms that elicit a response. Chemicals that travel within an organism between cells of its own body are variously termed paracrines, **neurotransmitters**, neuromodulators, or **hormones**. Pheromones are chemicals that are carried between individual organisms of the same species.

ELION, GERTRUDE BELLE (1918–)

American pharmacologist who received, along with George Hitchings and James Black, the 1988 Nobel Prize in medicine for developing drugs to treat autoimmune disorders, leukemia, malaria, urinary tract infections, herpes, and gout. Elion's name appears on forty-five patents.

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

transduction conversion of a signal of one type into another type

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

hormone molecule released by one cell to influence another

Female *Cecropia* moths broadcast a pheromone that serves as an attractant for flying males.

The response of the receiving organism is usually a change in its physiology or behavior.

Pheromones are often involved in the mating behavior between males and females in which the chemical serves as an attractant for one of the sexes. Following emergence from the cocoon, female *Cecropia* moths crawl a short distance away and broadcast a pheromone early in the morning that serves as an attractant for flying males. Males have olfactory ("smell") receptors on their antennae and they fly upwind and orient themselves to equalize the signals received by the two antennae. In this way, they can locate a virgin female from several miles away. Females of closely related species may use the same or a similar chemical but broadcast it at different times of the day. Males are genetically programmed to respond only at the appropriate time.

The female nearly always produces pheromones that serve as sex attractants, but males may produce pheromones that serve as aphrodisiacs. Mantispids are small predaceous insects that resemble miniature praying mantids. Courtship behavior is elaborate because the male must convince the female that he is a potential mate rather than an easy meal. The male produces a sweet musklike substance from his abdomen that helps to appease the female and reduce her predatory instincts.

Pheromones may be involved in mating even when the organisms do not actually meet. Many marine creatures such as sea urchins and oysters release eggs and sperm in the water in a process called spawning. Pheromones in these **secretions** will induce other members of the same species to simultaneously release their eggs or sperm, thereby increasing the likelihood that external **fertilization** will occur.

The preceding examples have involved pheromones carried in the air or water, but direct contact between the receiving organism and the pheromone must sometimes occur. Ants finding a source of food will lay

secretion material released from the cell

fertilization union of sperm and egg

down a trail with a secretion from their Dufour's gland by touching their abdomen to the ground as they return to the colony. Foragers leaving the colony can follow the pheromone trail back to the food source.

Sometime a pheromone can be "decoded" by another species and used against the animal that normally responds to it. The bolas spider twirls a silken thread tipped with a glob of sticky silk that it throws at insect prey to entrap them. The strand is coated with the same pheromone produced by certain female moths to attract males of their own species. When the amorous moths fly to the spider expecting to mate, they are instead captured and eaten. SEE ALSO CHEMORECEPTION; HORMONES; INSECT; SEXUAL REPRODUCTION; SYNAPTIC TRANSMISSION

Kurt Redborg

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Photoperiodism

The term "photoperiodism" was coined to describe a plant's ability to flower in response to changes in the photoperiod: the relative lengths of day and night. Because flowers produce seeds, flowering is crucially important for the plant to complete its life cycle. Although people had long known that plants such as tulips flower in the spring and chrysanthemums flower in the fall, until the early 1900s little was known about what actually caused flowering.

Beginning in 1910, Wightman Garner and Henry Allard conducted experiments to test the effect of day length on flowering. They discovered that plants such as barley flowered when the day length was longer than a certain critical length. These plants, which they named long-day plants (LDPs), flower mainly in the summer as the days are getting longer. Others, such as soybeans, flower when the day length is shorter than a certain critical length. These short-day plants (SDPs) flower in the fall as the days are getting shorter. Still others are not sensitive to the photoperiod and are called day-neutral plants.

Photoperiodism is responsible for the distribution of many plants worldwide. For example, ragweed (a SDP) is not found in northern Maine because the plant flowers only when the day length is shorter than 14.5 hours. In northern Maine, days do not shorten to this length until August. This is so late in the growing season that the first frost arrives before the resulting seeds are mature enough to resist the low temperatures, and so the species cannot survive there. By contrast, spinach (a LDP) is not found in the tropics because there the days are never long enough to stimulate the flowering process.

To investigate photoperiodism, plants can be grown in growth chambers, in which timers are used to control the length of the light and dark
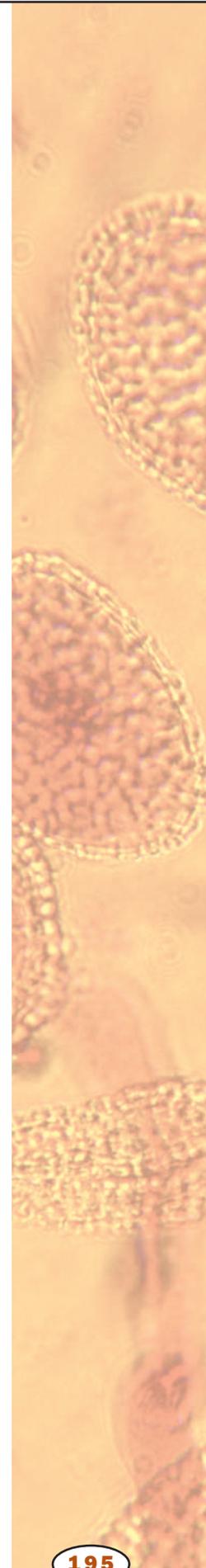
periods. Such research has shown that the dark period is more important than the light period. For example, if SDPs are grown under short-day conditions but the dark period is interrupted by a flash of light, the SDPs will not flower. The long night that normally accompanies a short day is interrupted by the flash. An interruption of the light period with dark has no effect. Thus, SDPs should more accurately be called long-night plants; and LDPs should be called short-night plants to emphasize the key role played by darkness in photoperiodism. Most plants require several weeks of the appropriate long-night or short-night cycle before they will flower.

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

Red light having a wavelength of 660 **nanometers** was found to be the most effective for interrupting the dark period, and this effect can be reversed by a subsequent exposure to far-red light (730 nanometers). These observations led to the discovery of phytochrome, the pigment responsible for absorbing those wavelengths and apparently the light sensor in photoperiodism. It has been suggested that photoperiodism results from an interaction between phytochrome and the plant's biological clock, which measures the time between successive dawns (rich in red light) and successive dusks (rich in far-red light). Under the appropriate conditions, these interactions are thought to activate the **genes** for flowering.

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

Many other processes in plants and animals are now known to be affected by the photoperiod. SEE ALSO FLOWERS; PLANT DEVELOPMENT

Robert C. Evans

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Photosynthesis

Photosynthesis is the process by which plants use the energy of light to produce **carbohydrates** and molecular oxygen (O_2) from carbon dioxide (CO_2) and water:

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

$$6CO_2 + 6H_2O \rightarrow \text{ sunlight} \rightarrow C_6H_{12}O_6 + 6O_2$$

Virtually all **ecosystems** on Earth depend on photosynthesis as their source of energy, and all free oxygen on the planet, including that in the atmosphere, originates from photosynthesis. The overall reaction is the reverse of respiration, which releases energy by oxidizing carbohydrates to produce CO_2 and water. Photosynthesis and respiration are linked ecologically, being the cellular metabolic processes that drive the carbon and oxygen cycles.

ecosystem an ecological community and its environment

Photosynthesis occurs in plants, photosynthetic protist (algae), and some bacteria. In plants and algae, it takes place within chloroplasts, whereas in

An overview of the photosynthetic process.

Energy-transduction reactions (thylakoid membrane)

Carbon-fixation reactions (stroma)
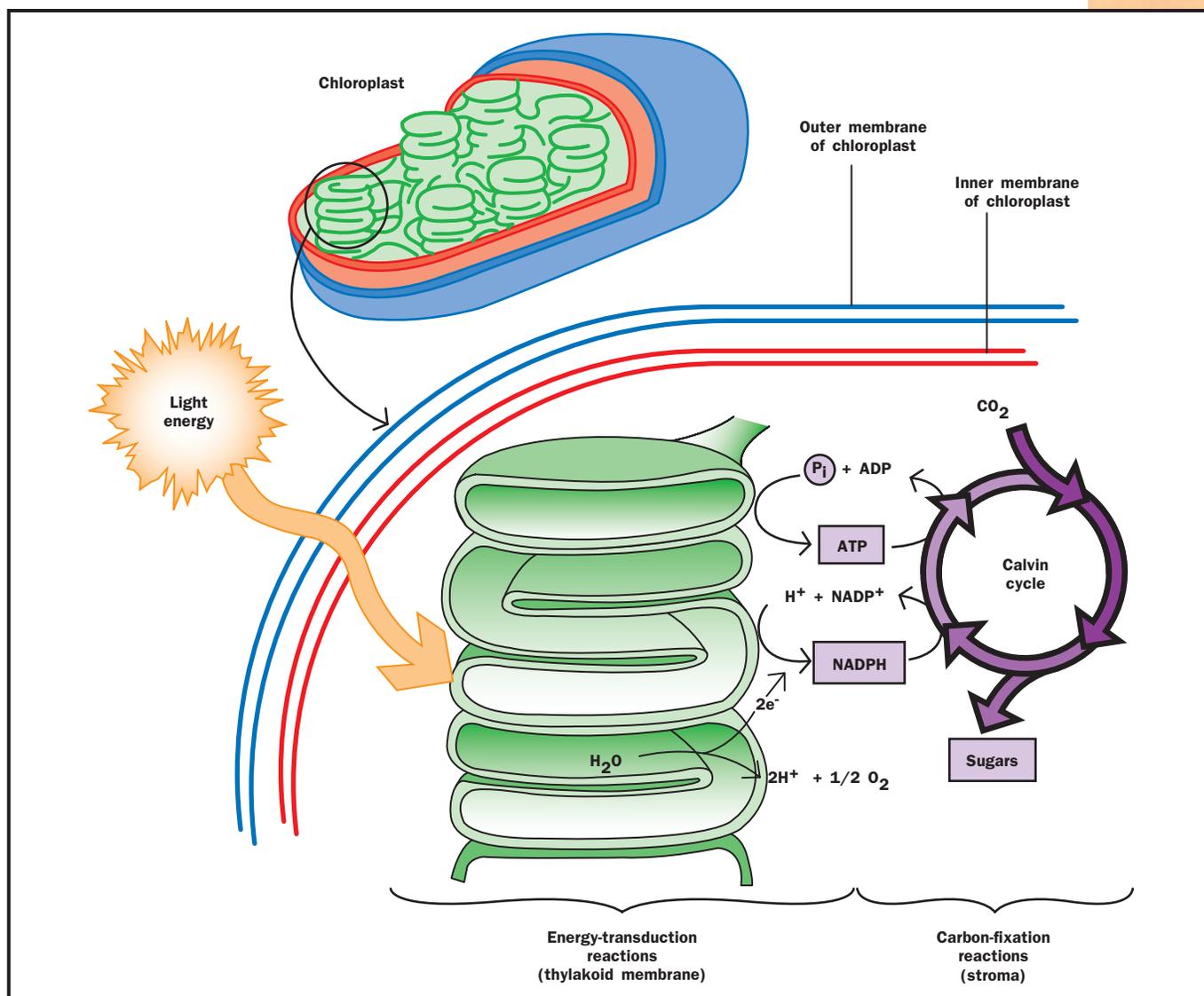
bacteria it occurs on the plasma membrane and in the **cytosol**. The remainder of this discussion will refer to photosynthesis in chloroplasts of plants.
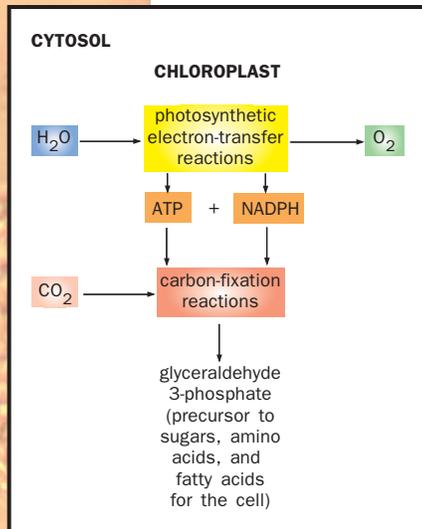
Overview

Photosynthesis is divided into two sets of reactions: the light-dependent (light) reactions and the light-independent (dark) reactions. As their names imply, the first set depends directly on light, whereas the second set does not. Nevertheless, even the dark reactions will cease if the plants are deprived of light for too long because they rely on the products of the light reactions.

The light reactions, which convert the energy in light into chemical energy, take place within the thylakoid membranes of the chloroplasts, whereas the dark reactions, which use that chemical energy to fix CO_2 into **organic** molecules, take place in the stroma of the chloroplast. In the light reactions, the energy of light is used to "split water," stripping a pair of electrons from it (and causing the two hydrogens to be lost), thus generating molecular

cytosol fluid portion of a cell, not including the organelles

organic composed of carbon, or derived from living organisms

CYTOSOL

CHLOROPLAST

H_2O → photosynthetic electron-transfer reactions → O_2

ATP + NADPH

CO_2 → carbon-fixation reactions

glyceraldehyde 3-phosphate (precursor to sugars, amino acids, and fatty acids for the cell)

Photosynthesis in a chloroplast.

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

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

ion an electrically charged particle

oxidative phosphorylation use of oxygen to make ATP

oxygen. The energy in light is transferred to these electrons, and is then used to generate adenosine triphosphate (**ATP**) and the electron carrier NADPH. These two products carry the energy and electrons generated in the light reactions to the stroma, where they are used by the dark reactions to synthesize sugars from CO_2.

The Light Reaction

The light reactions rely on colored molecules called pigments to capture the energy of light. The most important pigments are the green chlorophylls, but accessory pigments called carotenoids are also present, which are yellow or orange. The accessory pigments capture wavelengths of light that chlorophylls cannot, and then transfer the energy to chlorophyll, which uses this energy to carry out the light reactions. These pigments are arranged in the thylakoid membranes in clusters, along with **proteins** and electron carriers, to form light-harvesting complexes referred to as photosystems. Each photosystem has about two hundred chlorophyll molecules and a variable number of accessory pigments.

In most plants there are two photosystems, which differ slightly in how they absorb light. At the center of each photosystem is a special chlorophyll molecule called the reaction center, to which all the other pigments molecules pass the energy they harvest from sunlight. When the reaction-center chlorophyll absorbs light or receives energy from its accessory molecules, a pair of electrons on it becomes excited. These electrons now carry the energy from light, and are passed to an electron acceptor molecule.

The fate of these electrons depends on which photosystem they arose from. Electrons from photosystem I are passed down a short electron transport chain to reduce $NADP^+$ to NADPH (which also gains an H^+ **ion**). Electrons from photosystem II are passed down a longer electron transport chain, eventually arriving at photosystem I, where they replace the electrons given up by photosystem I's reaction center. Along the way, the energy released by the electrons is used to make ATP in a process called photophosphorylation. Many of the molecular details of this ATP-generating system are similar to those used by the mitochondrion in **oxidative phosphorylation**. (Phosphorylation refers to the addition of a phosphate group to adenosine diphosphate [ADP] to form ATP.) Like the mitochondrion, the chloroplast uses an electron transport chain, and ATP synthetase to create ATP.

The end result of excitation of both photosystems is that electrons have been transferred from chlorophyll to $NADP^+$, forming NADPH, and some of their energy has been used to generate ATP. While photosystem I gains electrons from photosystem II, the electrons lost by photosystem II have not been replaced yet. Its reaction center acquires these electrons by splitting water. During this process, the electrons in water are removed and passed to the reaction center chlorophyll. The associated hydrogen ions are released from the water molecule, and after two water molecules are thus split, the oxygen atoms join to form molecular oxygen (O_2), a waste product of photosynthesis. The reaction is:

$$2H_2O \rightarrow O_2 + 4H^+ + 4e^-$$

three molecules

| CO₂ | 1C |

three molecules

| ribulose 1, 5-bisphosphate | 5C |

six molecules

| 3-phosphoglycerate | 3C |

3 | ADP

3 | ATP

6 | ATP

6 | ADP

three molecules

| ribulose 5-phosphate | 5C |

six molecules

| 1,3-diphosphoglycerate | 3C |

6 | NADPH

6 | NADP⁺

2 | Pᵢ

6 | Pᵢ

five molecules

| glyceraldehyde 3-phosphate | 3C |

six molecules

| glyceraldehyde 3-phosphate | 3C |

three molecules of CO₂ fixed give a net yield of one molecule of glyceraldehyde 3-phosphate at a net cost of nine molecules of ATP and six molecules of NADPH

one molecule

| glyceraldehyde 3-phosphate | 3C |

$$H - C = O$$
$$H - C - OH$$
$$CH_2O \; (P)$$

SUGARS, FATTY ACIDS, AMINO ACIDS

The Dark Reactions

The NADPH and ATP generated in the light reactions enter the stroma, where they participate in the dark reactions. Energy and electrons provided by ATP and NADPH, respectively, are used to incorporate CO_2 into carbohydrate via a cyclic pathway called the Calvin-Benson cycle. In this complex pathway, the CO_2 is added to the five-carbon sugar ribulose bisphosphate to form a six-carbon unstable intermediate, which immediately breaks down to two three-carbon molecules. These then go through the rest

The carbon fixation cycle transforms simple, inorganic compounds of carbon into more complex forms of organic matter.

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

of the cycle, regenerating ribulose bisphosphate as well as the three-carbon sugar glyceraldehyde phosphate. It takes three turns of the cycle to produce one glyceraldehyde phosphate, which leaves the cycle to form **glucose** or other sugars.

Some plants bind CO_2 into a four-carbon compound before performing the Calvin-Benson cycle. Such plants are known as C4 plants or CAM plants, depending on the details of the CO_2 capture process. SEE ALSO BIOGEOCHEMICAL CYCLES; C4 AND CAM PLANTS; CHLOROPLAST; OXIDATIVE PHOSPHORYLATION

David W. Tapley

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Physical Therapist and Occupational Therapist

Physical therapists and occupational therapists are health care professionals who help people with a wide range of diseases, injuries, or disabilities maintain or improve their health and ability to carry out everyday tasks. They assess a patient's overall condition, develop a treatment plan, help the patient carry out the plan, and determine if the plan is working.

Physical and occupational therapists work in hospitals, clinics, schools, long-term care homes, research institutions, and in private practice. Both professions can be physically demanding and require strong interpersonal skills and a solid background in biology, chemistry, physics, psychology, and mathematics. Although some schools still offer four-year baccalaureate degrees, by 2002 (for new physical therapists) and 2007 (for new occupational therapists) all students will have to complete at least a master's degree in their field. After graduation, students must pass a licensing exam in order to treat patients. Students interested in these fields can do volunteer work to learn more about the work and gain experience before committing to a full training program.

Physical therapists work with patients to relieve pain and improve joint mobility, balance, coordination, movement, and overall health. For example, they may help a person recovering from shoulder surgery regain normal range of motion, a stroke patient learn to walk again, or a spinal cord injury patient to become as independent as possible.

Physical therapists use many techniques and tools to accomplish their goals, including exercises, massage, hot and cold packs, ultrasound, electrical stimulation, and assistive devices (crutches, prostheses, and wheelchairs).

Occupational therapists work with patients to improve their ability to carry out activities associated with daily living or employment. For ex-

ample, they may help a person who recently lost his vision learn to navigate his home, a developmentally disabled student participate in school, or a patient with head trauma learn to eat, dress, and bathe again. Occupational therapists use many tools to accomplish their goals, including assistive devices, computers, and a variety of everyday objects. SEE ALSO DOCTOR, FAMILY PRACTICE; MEDICAL ASSISTANT; NURSE; NURSE PRACTITIONER

John M. Ripper

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Physician Assistant

A physician assistant (PA) career has been rated by *U.S. News and World Report* as one of the fastest growing and most desirable careers for the future. Job opportunities include work in clinics, care for patients in hospitals, and care for patients in nursing homes. Many of the PA job duties are very much like the job of a doctor. Physician assistants see patients, take a history, do a physical exam, make a diagnosis, and decide on the treatment needed. The difference between a physician and a physician assistant is the amount of education required, the physician supervision, and the level of responsibility. Every PA needs to have a supervising physician, someone who oversees his or her work. The PA and physician work together as a team.

Most physician assistant programs require an undergraduate degree in one of sciences, such as biology or chemistry. Many PA programs require certain courses to get into a PA school, such as general biology, microbiology, general and organic chemistry, biochemistry, anatomy, physiology, psychology, and statistics. The PA education is anywhere from two to three years in length after a minimum of three years of college. All PA programs award a certificate of completion at the end of the program. Some programs also award a degree along with the certificate.

Getting into PA school is quite challenging. As of 2000, there were 125 programs in the United States. The class size for each PA program averages thirty-one. In order to be considered, one needs to get good grades in college, at least consistent Bs. Volunteering and working in the health care field, such as in a nursing home, increase one's chances of acceptance into a program. Many prospective students talk with PAs before starting a program so that they get a better idea of what PAs do on the job. SEE ALSO DOCTOR, FAMILY PRACTICE; NURSE; NURSE PRACTITIONER

Dawn B. Ludwig

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Physiological Ecology

The earth offers a huge variety of possible environments to inhabit: the hot arid environments of the desert, the salty environment of the oceans, the darkness of the deep sea, low oxygen environments of mountain peaks, and the frigid environments of the Arctic and Antarctic poles. This diversity of living conditions is reflected in the intriguing physiological adaptations developed by animals that live in these environments.

Adaptions to Cold

Temperature has a widespread impact on design. Two basic approaches to dealing with the challenge of temperature are to either maintain a constant and relatively high body temperature independent of ambient temperature (endothermy) or to let body temperature fluctuate with environmental temperature (ectothermy).

Endothermy.   Endotherms maintain a high internal temperature through metabolic heat generation. Most of this heat comes from **metabolism** in the gut and brain. In cold weather, increased muscular activity through shivering or simply exercising provides a mechanism to increase metabolic heat production.

metabolism chemical reactions within a cell

Some endotherms, like the arctic fox, are cold-weather specialists. Their most obvious strategy against the cold is insulation provided by a thick layer of fur. Aquatic animals rely predominantly on blubber for insulation as fur loses much of its insulation value upon immersion in water.

Another cold weather strategy is to temporarily decrease metabolic rate and body temperature. This regulated decrease in body temperature decreases the temperature difference between the animal and the air and therefore minimizes heat loss. Furthermore, having a lower metabolic rate is less energetically expensive. Many animals survive cold frosty nights through torpor, a short-term temporary drop in body temperature. Other animals such as marmots take a much more drastic approach: They hibernate through the cold months, letting their body temperature fall to a few degrees above ambient temperature. Contrary to popular belief, bears are not true hibernators as they undergo only a slight drop in body temperature and this activity can only be considered a deep sleep.

Ectothermy.   Ectotherms, which rely mostly on external sources of heat, adopt much different strategies to the cold. Ectotherms have little or no insulation. This is helpful to gain heat from the environment but ectotherms have difficulty coping with cold temperatures. Without the ability to prevent heat loss, cold-weather ectotherms either must be able to tolerate freezing or to be able to live in sub-freezing environments without ice formation in their bodies. Freeze-tolerant animals like the wood frog can survive the freezing (crystallization) of up to 65 percent of their body water. Freeze-intolerant animals, including many antarctic fish, avoid freezing by having antifreeze compounds in their plasma to lower the freezing and supercooling point of their tissues.

Adaptations to Heat and Dryness

A major challenge in hot and dry environments is the balance of water and temperature regulation. For endotherms, the main cooling mechanism is
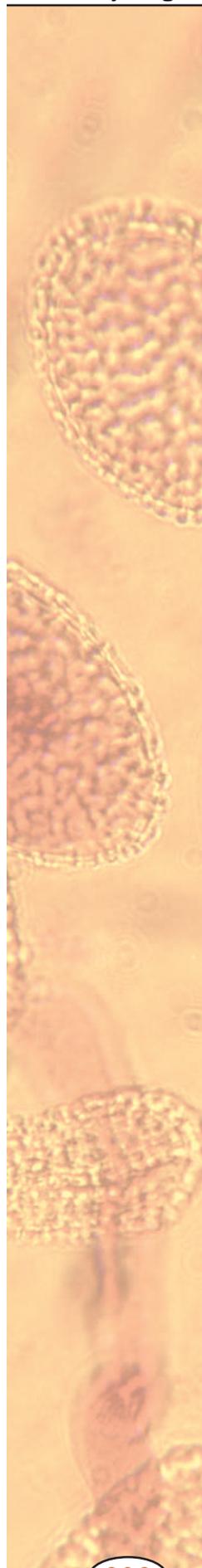
An African dromedary. Animals adapted to hot and dry environments have mechanisms for minimizing water loss while surviving the heat.

evaporation of water, either across respiratory surfaces or across the skin in those animals possessing sweat glands (mammals). Animals with a body covered by fur have limited ability to sweat, and rely heavily on panting to increase evaporation of water across the moist surface of the tongue and mouth. Birds have no sweat glands and therefore all birds pant. Animals adapted to hot and dry environments have mechanisms for minimizing water loss while surviving the heat. Interestingly, dense fur on desert inhabitants may also help to insulate the animal from heat gain.

Long loops of Henle of the kidney are another adaptation to arid environments. These long tubes are capable of super-concentrating urine, and enabling desert dwellers such as the kangaroo rat to conserve water. Big noses also help in the heat. A camel's elongated nose is an adaptation to minimize water loss across the respiratory surface of the nasal passages and even to keep the brain cool. Camels also are known to let their body temperature rise during the day and dissipate the extra heat load during the cool night through conduction (contact with a cool surface), which does not require water.

Small animals, with their high surface area-to-volume ratio, are in great danger of heat overload in hot environments. Most small animals therefore remain in burrows during the day and come out at night when the temperature is lower. (The **nocturnal** lifestyle of desert-adapted rodents explains why gerbils keep their owners up at night.)

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

Adaptations to Marine Environments

Marine environments pose a similar problem to an arid environment, the lack of fresh water. Bony fish osmoregulate (control salt regulations) in this high-salt environment by drinking seawater and eliminating salt through pumps in the gills. Similarly, marine birds drink seawater and eliminate salt

lipid fat or waxlike molecule, insoluble in water

enzyme protein that controls a reaction in a cell

hemoglobin oxygen-carrying protein complex in red blood cells

through glands located in their eye orbit. Sharks have the curious arrangement of salt glands in the rectum.

The ocean floor provides the strange environment of high ambient pressure and little or no light. One adaptation to lack of light has been the loss of eyes and pigmentation in some deep-sea fish. Other organisms have adapted to low light levels by possessing bioluminescent systems, either by having luminous organs or carrying bioluminescent bacteria. Such a system is useful for species recognition, luring prey, startling predators and mating. Deep-sea life also requires an adaptation to the extremely high pressure found at depths. Barophilic, or pressure-loving, organisms have adapted ways to avoid problems caused by high pressure. One adaptation is the modification of the set of **lipids** in cell membranes, designed to maintain fluidity despite the high pressure. Relatively pressure-insensitive **enzymes** are also found in organisms that live at great depths.

Adaptations to Low Oxygen Concentration

Just as high pressure influences organismal design, the low barometric pressure (and thus low oxygen availability) of the skies also presents an evolutionary force on physiology. A dramatic example of high altitude adaptation is seen in the bar-headed goose, a bird whose migration path between India and Tibet requires flight over Mount Everest. Research suggests that these birds maintain a phenomenal blood supply to flight muscles, and their blood has a unique **hemoglobin** structure, which optimizes oxygen transport in high-altitude conditions. Warm, stagnant bodies of water also present a low-oxygen environment and fish inhabiting these waters survive by managing to breathe both air and water. Lungfish, as the name suggests, possess both gills to breathe water and lungs to breathe air. It is likely that an organism similar to this air-breathing fish gave rise to terrestrial vertebrates millions of years ago.

Every organism on Earth represents a successful path to adapting to a specific environment, which helps to explain the impressive biodiversity of life present today. SEE ALSO ADAPTATION; BONY FISH; CARTILAGINOUS FISH; KIDNEY; OSMOREGULATION; TEMPERATURE REGULATION

Maureen E. Basha

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Pituitary Gland

The pituitary gland is one of the principal glands of the **endocrine** system. It releases at least nine **hormones** affecting a wide variety of body functions, including growth, reproduction, and levels of **electrolytes** and water in the body fluids. The pituitary sits near the center of the head, behind the nose and beneath the brain, just below the hypothalamus. The hypothalamus is a brain structure from which the pituitary receives chemical signals that control its action. Nerve endings from the hypothalamus stimulate the posterior portion of the pituitary to secrete oxytocin and antidiuretic hormone (ADH). Capillaries from the hypothalamus carry releasing factors and inhibiting factors to the **anterior** portion of the pituitary, stimulating or inhibiting release of eight other hormones (see Table 1). All the hormones of the pituitary gland are peptides, small chains of **amino acids**.

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

hormone molecule released by one cell to influence another

electrolytes ions in body fluids

anterior toward the front

amino acid a building block of protein

Hormones Released by the Pituitary Gland

Hormone	Site of Action	Effects
Posterior Pituitary		
Oxytocin	uterus	stimulates contraction during labor
	breast	stimulates contraction to express milk
Antidiuretic hormone (ADH)	kidney	stimulates retention of water
Anterior Pituitary		
Corticotrophin (adrenocorticotrophic hormone, ACTH)	adrenal cortex	stimulates release of cortisol
Thyroid-stimulating hormone (TSH)	thyroid	stimulates release of thyroxine
Growth hormone (GH)	bone	stimulates growth
Follicle-stimulating hormone (FSH)	female ovaries	stimulates follicle to mature an egg, estrogen production
	male testes	stimulates sperm production
Luteinizing hormone (LH)	female ovaries	stimulates ovulation, progesterone production
	male testes	stimulates testosterone production
beta-Endorphin	brain	reduces pain

Both the hypothalamus and the pituitary are involved in complex **feedback** loops with other glands in the body, sending and receiving hormonal signals to maintain homeostasis. Because of its central role in so many systems, pituitary abnormalities can lead to a variety of disorders. Disorders may lead to either **hyposecretion** or **hypersecretion**. Deficient growth hormone, for instance, leads to dwarfism, while excess causes gigantism. SEE ALSO ENDOCRINE SYSTEM; GROWTH; HOMEOSTASIS; HORMONES; HYPOTHALAMUS

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

hyposecretion lack of secretion

hypersecretion excess secretion

Richard Robinson

Plankton

Plankton are small aquatic organisms that live in both freshwater and marine environments. The word "plankton" is derived from the Greek word

Marine plankton. Plankton are a critical food resource for other aquatic organisms that live in freshwater and marine environments.
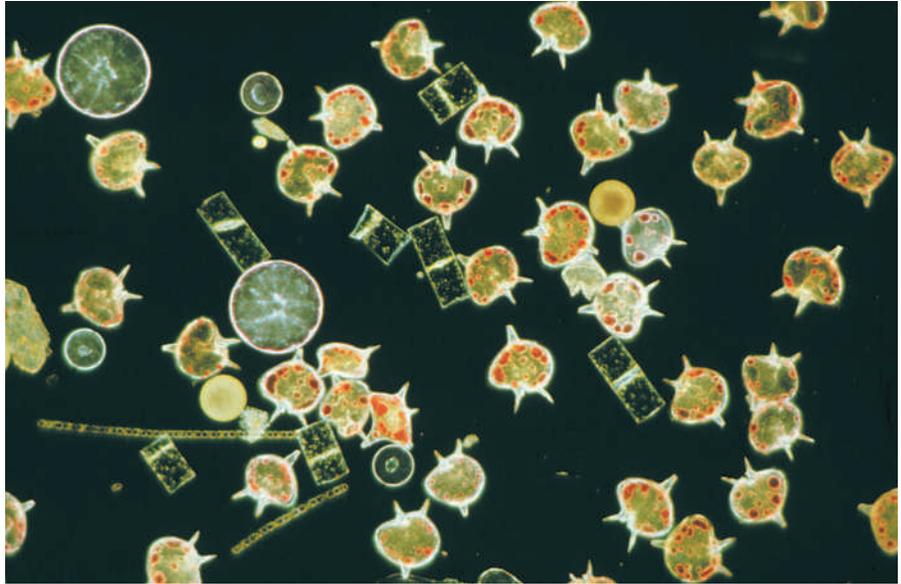
appendage attached organ or structure

phytoplankton microscopic floating creatures that photosynthesize

organic composed of carbon, or derived from living organisms

food web set of feeding relations in an ecosystem

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

fertilization union of sperm and egg

planktos, which means "drifting." In general, plankton have little or no means of locomotion and their distribution is determined largely by water currents and mixing. However, some plankton can swim through less turbulent waters using flagella and other **appendages**.

There are several broad categories of plankton. **Phytoplankton** are small plantlike plankton and are commonly referred to as algae. Phytoplankton are primary producers (they use energy from the sun to make **organic** food molecules). Bacterioplankton are very small (only seen through a microscope) and include bacteria, fungi, and viruses. Some bacterioplankton play important roles as primary producers and others as decomposers. Zooplankton are planktonic invertebrate animals (for example, the water-flea *Daphnia*). Some zooplankton consume phytoplankton, whereas others are predatory and consume smaller zooplankton. Ichthyoplankton are planktonic fish eggs and larvae. The ichthyoplankton are highly vulnerable to predation by invertebrate and vertebrate predators.

Plankton are important because they form the base of aquatic **food webs**. That is, plankton are a critical food resource for other aquatic organisms (such as fish) that live in freshwater and marine environments. Plankton are important to humans because they support recreational and commercial fisheries. Some humans consume plankton directly in the form of dietary supplements. For example, the phytoplankton species *Spirulina* has been marketed as a source of vitamins and **protein**.

Plankton are also important in processes that control the distribution and movement of energy and essential nutrients such as carbon, nitrogen, and phosphorus. A significant amount of the total global carbon is stored in the ocean. Some researchers have proposed that it is possible to increase the uptake of carbon dioxide generated by human combustion of fossil fuels by increasing production of ocean plankton through **fertilization**. Researchers debate whether this proposal is practical at a large scale. SEE ALSO ALGAE; BIOGEOCHEMICAL CYCLES; ECOSYSTEM; ESTUARIES; OCEAN ECOSYS-

Janet M. Fischer

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Plant

Plants (of the kingdom Plantae) are multicellular, eukaryotic organisms that develop from an embryo and that have cell walls and chloroplasts. Plants are distinguished from algae (from which they are descended) by a higher degree of multicellular complexity and from fungi by the ability to photosynthesize (those few plants that have lost this ability evolved from others that could).

Characteristics of Plants

Almost all plants live on land and have adapted to the conditions on land through the development of a waxy cuticle to prevent drying out, structures to absorb and transport water throughout their bodies (the bryophytes are an exception), and rigid internal support to remain erect without the buoyancy available in water. This rigidity is provided in large part by the cell wall, which is composed of **cellulose**, a **complex carbohydrate**, and **lignin**, a phenolic compound that stiffens the cellulose fibers.

The plant life cycle has two distinct multicellular phases: a **haploid** phase (in which **chromosomes** are present only as single copies) and a **diploid** phase (in which chromosomes are present in pairs). The haploid organism produces **gametes** that fuse to form an embryo, which develops into the diploid organism. The diploid organism produces haploid spores that germinate to form the haploid organism. This "alternation of generations" is found only in plants and some algae.

Almost all plants photosynthesize, using the sun's energy to power the production of sugar from carbon dioxide and water. Photosynthesis occurs in chloroplasts, membrane-bound **organelles** that contain the green pigment chlorophyll. Chloroplasts are descended from free-living photosynthetic bacteria that became symbiotic partners of ancient single-celled plant ancestors. Evidence of the chloroplast's bacterial origin is found in the presence of deoxyribonucleic acid (DNA) within it, as well as its size and structure.

The photosynthetic production of sugars by plants is the basis for all terrestrial food chains. Photosynthesis also produces oxygen, needed by animals, fungi, and other organisms (including plants themselves) to release the stored energy in those sugars.

Diversity

Plants are classified into twelve phyla (sometimes called divisions) in two major groups. The bryophytes are the most primitive group, lacking vascular

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

complex carbohydrate molecule formed by linking simpler carbohydrates such as sugars

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

haploid having single, nonpaired chromosomes in the nucleus

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

diploid having pairs of chromosomes in the nucleus

gamete reproductive cell, such as sperm or egg

organelle membrane-bound cell compartment

tissues for the transport of water. There are three phyla of bryophytes—the mosses, liverworts, and hornworts—that together comprise about 24,000 species. In contrast, plants in the second group, the tracheophytes, have well-developed vascular systems. The tracheophytes contain nine phyla and are divided into two groups: those without seeds and those with them. Ferns, which reproduce without seeds, contain approximately 13,000 species. Three other phyla of seedless vascular plants (Psilophyta, Lycopodophyta, and Equisetophyta) together include just over 1,000 species.

Seeds are structures that contain an embryo and food reserves wrapped in a protective seed coat. In the **gymnosperms**, the seed develops on structures exposed to the environment. Gymnosperms include Ginkophyta, which contains only one species, *Ginkgo biloba*; Cycadophyta (220 species); Gnetophyta (68 species); and Coniferophyta (588 species). Conifers bear seeds in cones and include many familiar needle-bearing evergreens, such as pine, spruce, and fir. Anthophyta, or angiosperms, enclose their seeds within ovaries. The angiosperms are the flowering plants and are the most diverse of all plant phyla, with about 235,000 species. SEE ALSO ALGAE; ALTERNATION OF GENERATIONS; ANGIOSPERMS; BIODIVERSITY; BRYOPHYTES; FUNGI; GYMNOSPERMS; PTERIDOPHYTES; SEEDLESS VASCULAR PLANTS

Richard Robinson

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Plant Development

Plant development is an umbrella term for a broad spectrum of processes that include: the formation of a complete embryo from a **zygote**; seed germination; the elaboration of a mature vegetative plant from the embryo; the formation of flowers, fruits, and seeds; and many of the plant's responses to its environment. Plant development encompasses the growth and differentiation of cells, tissues, organs, and organ systems. Plant development shares many similarities with developmental processes in animals, but the fact that plants are nonmotile, photosynthetic organisms requires certain novel developmental processes in addition to the common ones.

Embryo and Seed Development

Embryogenesis, the formation of a multicellular embryo from a single-celled zygote, is one of the most dramatic and best-characterized aspects of plant development. Four key developmental processes take place during embryogenesis. First, the zygote expresses **apical**-basal polarity, meaning that the apical and **basal** ends of the zygote cell differ structurally and biochemically. When the zygote divides, it typically divides asymmetrically, giving rise to a small apical cell with dense **cytoplasm** and a large basal cell with watery cytoplasm. Although these two cells have identical nuclei, their fates differ dramatically. The apical cell gives rise to the embryo itself, while the basal cell gives rise to a short-lived structure called a suspensor and the tip of the root system. The **progeny** of the apical cell grow and divide to form a

gymnosperms "naked seed" plants, including conifers

zygote fertilized egg

apical at the tip
basal lowest level

cytoplasm material in a cell, excluding the nucleus

progeny offspring

Embryogenesis

Zygote — Apical, Basal

Globular stage embryo — Embryo, Suspensor

Heart stage embryo — Cotyledon, Stem, Root

Mature embryo — Shoot apical meristem, Root apical meristem
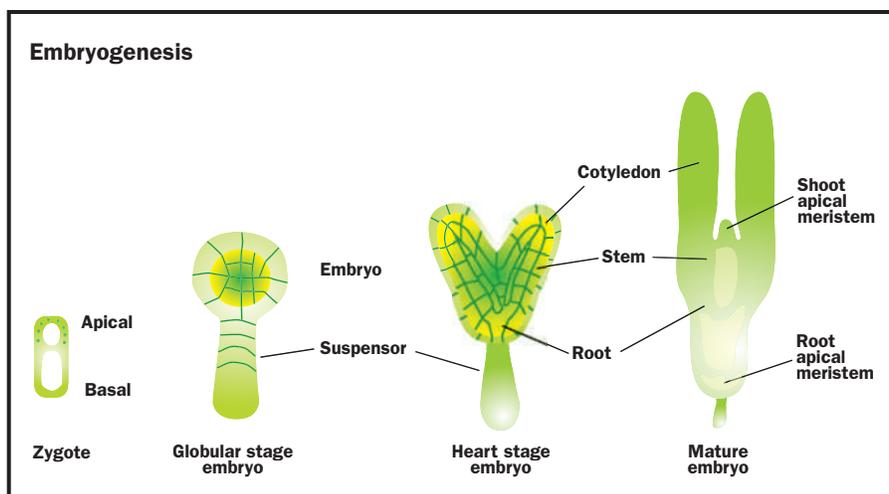
Embryo formation begins with cell division that establishes the apical-basal (top-bottom) axis. Further divisions elaborate on this basic plan, finally forming the cotyledons (seed leaves), as well as the apical meristems of root and shoot.

spherical mass of cells, the globular-stage embryo. Second, differential growth within the globular embryo gives rise to the "heart" stage embryo, the earliest stage when the precursors of **cotyledons**, root, and stem can be recognized. This key embryogenic process is called organogenesis. Third, distinctive planes of cell divisions bring about **histogenesis**, the process by which cells within embryonic cotyledons, root, and stem acquire different shapes, forming the precursors of the plant tissue systems. Last, the **apical meristems** of the shoot and root systems are formed at the apical and basal ends of the embryo.

After an embryo has reached full size, developmental changes continue to occur at the cellular level. Embryonic cells, particularly those of the cotyledons, begin to synthesize and store the **proteins**, **lipids**, and starch that will provide the energy and basic building blocks for germination and seedling growth. Next, the embryo begins to desiccate, sometimes losing up to 80 percent of its previous water content, and enters a phase of dormancy. Development and **metabolism** are arrested in dormant embryos, and seeds containing dormant embryos can survive for many years (sometimes centuries) and withstand extreme temperatures and drought.

Plant **hormones** are important regulators of embryogenesis and seed dormancy. The hormones auxin, gibberellic acid, and cytokinin all stimulate growth and are present in the embryo during the stages of embryogenesis. As the embryo matures, these hormones are degraded and abscisic acid is synthesized by the embryo. Abscisic acid provides a developmental signal for the embryo to initiate the synthesis of storage compounds and to undergo **desiccation**. Abscisic acid is present in dormant seeds and is thought to play an important role in maintaining seed dormancy.

Germination and Seedling Development

Embryo development and metabolism resume upon seed germination. Given the right combination of water availability, temperatures, and light, the desiccated seed begins to take up water and the embryo begins to grow and metabolize again. Some species have specific requirements for germination; for instance, many temperate zone tree species require several weeks of temperatures of 4 degrees Celsius (39.2 degrees Fahrenheit) or less in

cotyledon seed leaf, which stores food and performs photosynthesis after germination

histogenesis origin or production of tissues

apical meristem growing tip from which all plant tissues arise

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

lipid fat or waxlike molecule, insoluble in water

metabolism chemical reactions within a cell

hormone molecule released by one cell to influence another

desiccation drying out
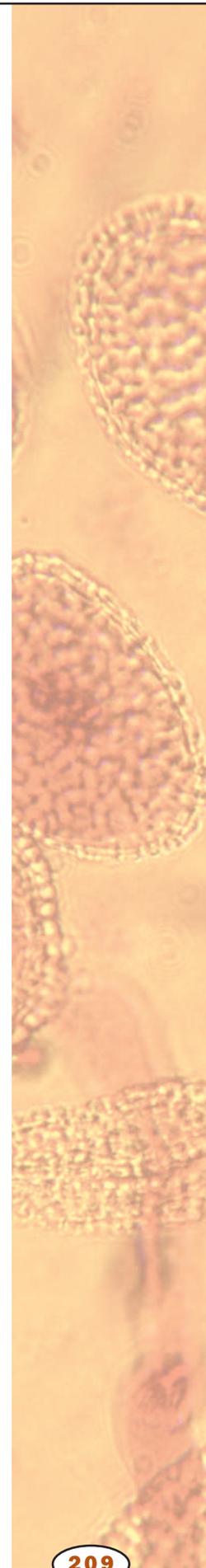
The root is the first portion of the plant to emerge during germination. Growth of the stem behind the cotyledons forms a "hook" that emerges from the soil, followed by emergence of the cotyledons, which begin to photosynthesize to feed further growth.

Germination

translation synthesis of protein using mRNA code

enzyme protein that controls a reaction in a cell
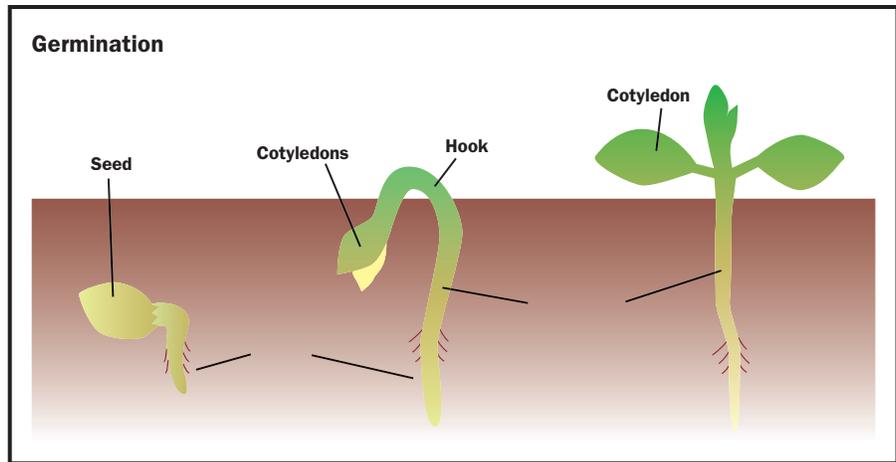
order to germinate. Other species require low levels of light in order to germinate. Once germination is initiated, the embryo follows a typical pattern of development. In many plants, the preformed embryonic root elongates first, forcing its way out of the seed coat and into the soil. Next, the embryonic stem, usually the part below the attachment of the cotyledons (the hypocotyl), elongates. Once the hypocotyl has carried the cotyledons into the light, they expand, providing a broad surface for photosynthesis.

Environmental factors and their **translation** into hormonal signals are important for seedling development. For instance, germination in the dark results in developmental events that help the seedling push its way through the soil into the light. The hypocotyl elongates quickly and maintains a "hook" near its tip that protects the cotyledons and shoot apical meristem region. Cotyledon expansion is suppressed so that they are not damaged as they are pulled through the soil. In contrast, if the same seeds germinate in the light, the hypocotyl hardly elongates at all and does not form a hook, while the cotyledons quickly expand. The hormone gibberellic acid plays an important role in seed germination and early seedling growth. Gibberellic acid induces the synthesis of **enzymes** required for the metabolism of stored foods, thus providing energy for seedling growth. Gibberellic acid also induces cell division and cell expansion in dark-grown hypocotyls, maintaining their rapid growth through the soil.

Apical Meristems and Development

The early stages of germination simply involve the enlargement of the root, hypocotyl, and cotyledons that were preformed in the embryo. Post-embryonic development, however, is focused on the apical meristems. The shoot apical meristem is the source of all the leaves, stems, and their component cells formed during the lifetime of the plant. The meristem itself is composed of a small population of perpetually embryonic (meristematic) cells. These cells grow and divide, giving rise to new cells, but never mature themselves. Thus there is always a source of new cells at the tip of the shoot. The root tip has a similar population of meristematic cells that gives rise to all root tissues. Both of these meristems are characterized by an indeterminate growth pattern: one that is not finite, but, in theory at least, could continue throughout the lifetime of the plant.

Apical meristems are involved in several distinct developmental processes. The meristems are the location of cell proliferation and thus the source of all new cells in the shoot and root systems. The regions below the meristems are the sites of active growth, as new shoot and root tissue rapidly expands. The shoot apical meristem plays a role in organogenesis, the formation of new leaves and axillary buds in a precise spatial pattern. In contrast, the root apical meristem is not involved in organogenesis; **lateral** roots are initiated by pericycle cells, which are themselves derived from the meristem, usually several centimeters away from the meristem. The apical meristems also play a role in histogenesis by giving rise to cells that undergo distinct patterns of differentiation to form the specialized tissue types of the shoot and root. While the embryo initially gives rise to the precursors of dermal, ground, and vascular tissues (protoderm, ground meristem, and procambium, respectively), these tissue precursors continue to be formed by the apical meristems and represent the first stages of cell and tissue differentiation.

Cell Growth and Cell Division

Growth is defined as an irreversible increase in mass that is typically associated with an increase in volume. Plant cell growth is associated with meristems and must be carefully regulated in order for organogensis and histogenesis to occur in the appropriate patterns. The plant regulates growth by regulating the **extensibility** of its cell walls. A cell that has nonextensible cells walls can take up some water, but eventually the physical pressure of the water inside the cell pressing out on the cell wall (the **turgor** pressure) prevents the entry of additional water and any further change in volume. In contrast, a cell that has extensible cell walls can take up a substantial volume of water and thus increase in size. Turgor pressure that would otherwise prevent water entry momentarily decreases because the walls keep stretching.

Typically cell growth occurs in small increments: (1) wall extensibility increases, reducing turgor pressure; (2) reduced turgor pressure allows water to enter the cell, increasing cell volume; (3) wall extensibility decreases, allowing the cell to build up turgor and preventing further water entry; and (4) the cell undergoes a cycle of synthesis of cytoplasmic and wall components, adding to the cell's mass. This cycle of incremental growth is repeated many times until the cell reaches its final size.

The plant hormones auxin and gibberellin are produced in the vicinity of the apical meristems and usually act in concert to induce cell growth. Both hormones regulate wall extensibility, but carry out this function in different ways. Auxin induces the activity of cell membrane H^+ adenosine triphosphatase (ATPase) molecules. Proton (H^+) extrusion lowers the pH of the cell wall, thus activating the cell wall enzyme expansin. Expansin cleaves the **hydrogen bonds** between two cell wall components: The **cellulose** microfibrils and the **hemicellulose** molecules that link adjacent cellulose microfibrils. Breakage of these bonds allows these structural wall components to reposition themselves farther apart, increasing wall extensibility. Gibberellic acid, on the other hand, stimulates the activity of another cell wall enzyme called xyloglucan endotransglycosylase (XET). Xyloglucans are a type of hemicellulose that is cleaved by the XET enzyme. Breakage of the

Apical Meristems

Apical meristem
Leaf primordium
Axillary bud
Protoderm
Ground meristem
Expansion zone
Procambium
Shoot apical meristem

Lateral root primordium
Protoderm
Ground meristem
Procambium
Apical meristem
Root cap
Root apical meristem
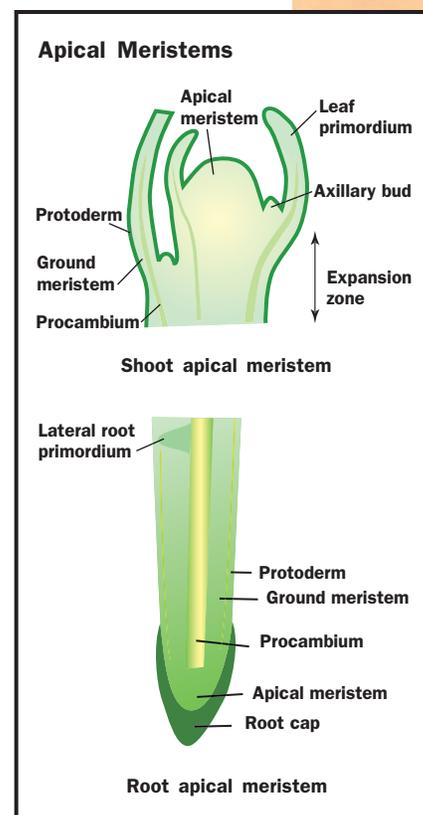
Structure of root and shoot apical meristems.

lateral side-to-side

extensibility ability to expand or grow larger

turgor internal pressure

hydrogen bond weak bond between the H of one molecule or group and a nitrogen or oxygen of another

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

hemicellulose complex carbohydrate related to cellulose and found in cell walls of plants and some other organisms

Cell Growth and Wall Extensibility

Cellulose microfibril

Hemicellulose

Hydrogen bonds

Auxin

Gibberellin

Expansin

XET
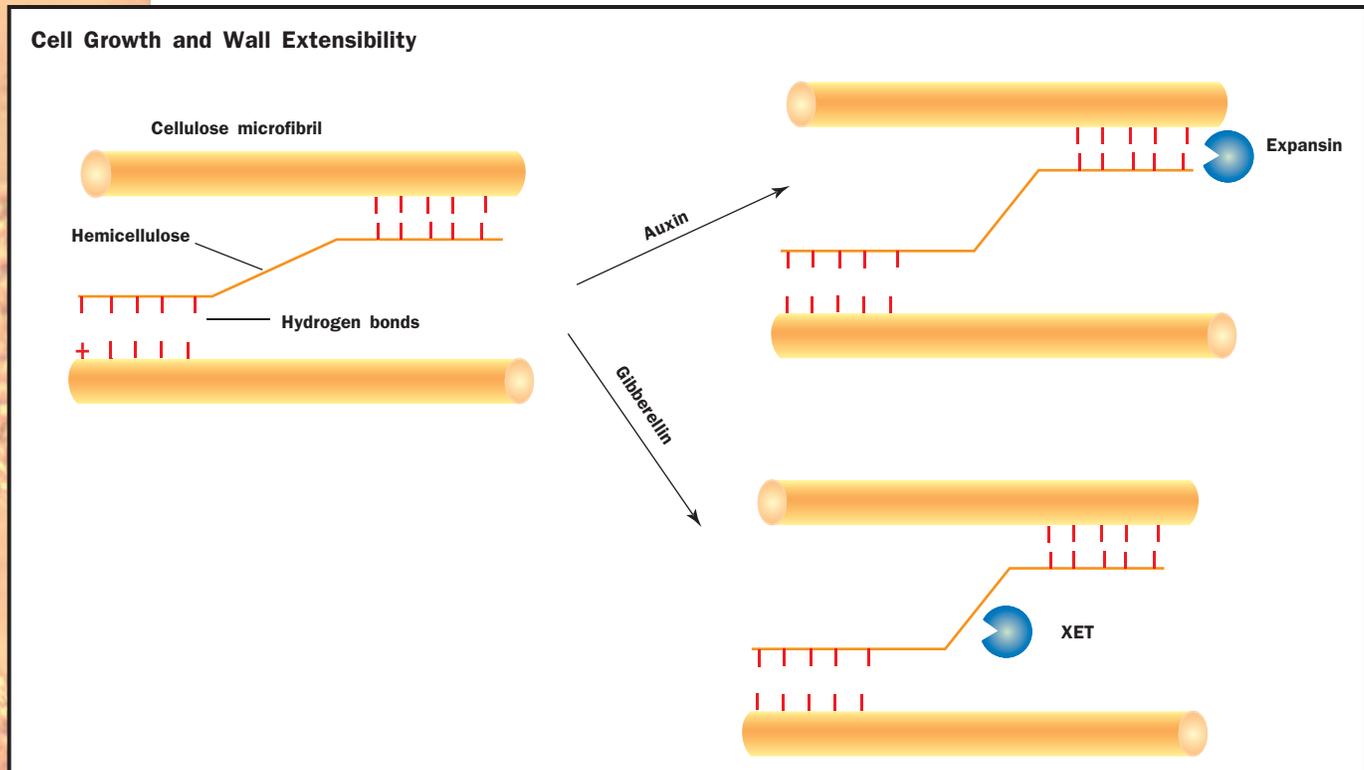
The hormones auxin and gibberellin each promote cell expansion by loosening the bonds between adjacent cell wall molecules. Each hormone acts on a different molecular target.

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

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

cell cycle sequence of growth, replication, and division that produces new cells

mitosis separation of replicated chromosomes

hemicellulose molecules also allows the cellulose microfibrils to move farther apart, increasing wall extensibility.

Cell division and cell growth are often tightly linked. When the rate of cell division is balanced by cell growth, as in the apical meristems, average cell size does not increase. As the meristem grows away from earlier formed cells, the ratio of growth to division increases, resulting in overall cell enlargement. As the tissues mature further, cell division ceases completely, giving rise to zones of pure cell enlargement where most of the visible growth of the plant occurs. This relationship between division and growth, coupled with observations of the predictable planes of cell division during histogenesis, indicates that cell division is carefully regulated during plant development.

Molecules called cyclin-dependent **kinases** (CDKs) are key regulators of cell cycling (including cell division) in plants. CDKs are activated by association with a regulatory subunit called a cyclin and by **phosphorylation** and dephosphorylation events. The plant hormone cytokinin appears to regulate the **cell cycle** by interacting with the CDKs. Cytokinins enhance the synthesis of the cyclin subunits that are required for the cell to enter the deoxyribonucleic acid (DNA) synthesis phase of the cell cycle. Cytokinins also enhance the CDK dephosphorylation step that is required for the cell to progress into **mitosis**. Both of these processes are inhibited by the hormone abscisic acid; thus a "developmental tug-of-war" occurs between a division-enhancing hormone and a division-suppressing hormone. The delicate balance between them determines the rate of cell division and this type of interaction is probably typical of the hormonal regulation of many aspects of plant development.

Differentiation

Differentiation is the process whereby cells, tissues, and organs become different from each other and from their precursors. The concept can be applied to organogenesis since cotyledons, foliage leaves, **sepals**, and petals may all develop from similar appearing precursors, the leaf primordia. As these organs mature, they become different from each other in size, shape, and the development of distinctive cell types. For instance, the epidermis tissue of petals is sharply differentiated from that of cotyledons, foliage leaves and sepals that are photosynthetic organs. Correlated with a photosynthetic function, the epidermis of these organs is made up of flat, transparent cells that allow the penetration of light into internal tissues. Specialized **guard cells** that allow CO_2 to enter the leaf are also present. In contrast, the epidermal cells of petals contain brightly colored carotenoid or anthocyanin pigments. These cells also have a **papillate** shape that imparts a velvetlike sheen to the petal surface. Since petals carry on minimal photosynthesis, they often lack guard cells.

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

The process of differentiation is best understood on a cellular level. For instance, guard cells are highly specialized epidermal cells. Early in the development of a leaf, protodermal precursor cells undergo a distinctive pattern of cell divisions. At first the cell divisions are asymmetric, producing one large and one small derivative. The large derivative stops dividing and differentiates as an unspecialized epidermal cell, while the small derivative undergoes another asymmetric division. At an unknown stop signal, the small derivative undergoes a symmetric division, giving rise to two equal sized cells that become the guard cells. Unlike their plain neighbors, these cells develop a distinctive kidney shape, unevenly thickened cell walls, large, conspicuous chloroplasts, and finally form a pore (the **stomatal** aperture) between them.

guard cells paired cells on leaves that control gas exchange and water loss

papillate small, nipple-like projection

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

Uniqueness of Plant Development

Although plants share many features of development with animals such as apical-basal polarity, regulation of the balance between cell growth and cell division, formation of distinctive patterns of organs, cells and tissues, and differentiation, some aspects of development are unique to plants. Among these are:

- The formation and maintenance of the perpetually embryonic regions, the apical meristems. The meristems have an indeterminate growth pattern that result in the occurrence of growth, organogenesis, and histogenesis throughout the life of the plant.

- Plant cells have rigid cell walls that prevent cell movement. Thus organogenesis and histogenesis must occur through differential growth and regulation of the planes of cell division. Cell-cell communication is important in plant development, but cell recognition is likely less important than it is in animals since plant cells keep the same neighbors throughout their life.

- Plant cells are totipotent; that is, able to differentiate as a different cell type if given the appropriate stimulus. Totipotency is likely a reflection of the plant's sedentary lifestyle. Plants can't escape predators and other kinds of damage, but they can readily repair wounds

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Differentiation of Guard Cells

Guard cells regulate passage of gasses into and out of the leaf through pores in the surface. Guard cells form by a series of cell divisions from undifferentiated protoderm, including a final symmetric division that forms the two identical cells.

and reconnect vascular strands by differentiating the appropriate cell types. SEE ALSO CELL CYCLE; CELL WALL; FLOWERS; HORMONES, PLANT; LEAVES; PHOTOPERIODISM; REPRODUCTION IN PLANTS; ROOTS; SEEDS; SHOOTS

Nancy G. Dengler

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Plant Nutrition

organic composed of carbon, or derived from living organisms

inorganic not bonded to carbon

C4 and CAM plants plants that employ accessory systems for trapping carbon for photosynthesis

Green plants, unlike animals, are able to manufacture their major **organic** constituents entirely from **inorganic** raw materials that are obtained from soil, water, or atmosphere using energy provided by photosynthesis. Of over fifty elements found in plant tissues, only sixteen are considered essential nutrients for all plants. Of these sixteen, nine are macronutrients, and seven are micronutrients. Macronutrients are required in high amounts and each is present at levels of greater than 0.2 percent of plant dry weight. Most macronutrients are important constituents of organic molecules, and most have more than one role. Micronutrients are required in small amounts often have special purposes. The seven known micronutrients each make up less than 0.1 percent of plant dry weight. A few other elements (nickel, silicon, and sodium) are considered essential only for some plants. Soybeans require nickel; horsetails require silicon; **C4 and CAM plants** require sodium.

Essential Elements for Proper Plant Nutrition: Roles, Available Forms, and Deficiency Symptoms

Essential Element*	Role	Symbol	Form absorbed	Deficiency symptoms	Leaves affected
Macronutrients					
Hydrogen	Component of organic compounds and water; chemiosmotic synthesis of ATP in mitochondria and chloroplasts	H	H_2O		
Carbon	Component of organic compounds	C	CO_2		
Oxygen	Component of organic compounds and water; electron acceptor in respiration	O	O_2, CO_2, H_2O		
Nitrogen	Component of proteins, phospholipids, nucleic acids, some hormones, and chlorophyll	N	NO_3^-, NH_4^+	Plants stunted; foliage light green, roots long and slender	Old
Potassium	Enzyme activator, involved in starch formation; regulates osmotic balance and movement of guard cells	K	K^+	Stems slender, numerous small necrotic spots form near the margins of leaves	Old
Calcium	Component of middle lamella (Capectate); controls activity of many enzymes; maintains membrane integrity; 2nd messenger	Ca	Ca^{2+}	Plants stunted; terminal bud dies; young leaves hooked; root tips die	Young
Magnesium	Component of chlorophyll; component of middle lamella (Mg-pectate); activates many enzymes	Mg	Mg^{2+}	Leaves with chlorotic spots; tips and margins of leaves turned upward	Old
Phosphorus	Component of nucleic acids, phospholipids, coenzymes; involved in sugar metabolism	P	$H_2PO_4^-$ HPO_4^{2-}	Plants stunted, foliage purple/dark green	Whole plant affected
Sulphur	Components of the amino acids cysteine and methionine; component of coenzyme A	S	SO_4^{2-}	Young leaves light green, no necrosis	Young
Micronutrients					
Chlorine	Involved in water balance; possibly involved in photosynthetic reactions in which O_2 is released	Cl	Cl^-	Leaves wilted, chlorotic, ultimately necrotic; roots thickened	Whole plant affected
Iron	Component of cytochromes ferredoxin and nitrogenase; cofactor of peroxidase; involved in chlorophyll synthesis	Fe	Fe^{2+}, Fe^{3+}	Stunted growth; interveinal chlorosis of young leaves	Young
Boron	May be involved in sugar transport; regulates enzyme function	B	H_2BO_4	Terminal bud dies; leaves may be twisted, base of young leaves chlorotic; root tips discolored	Young
Manganese	Activator of enzymes; involved in electron transfer, chlorophyll synthesis, and the photosynthetic evolution of O_2	Mn	Mn^{2+}	Interveinal necrosis of young leaves	Young
Zinc	Activates many enzymes; involved in the formation of pollen	Zn	Zn^{2+}	Stems with short internodes; leaves thick; leaf margins distorted	Old
Copper	Component of plastocyanin; present in lignin of xylem elements; activates enzymes	Cu	Cu^+, Cu^{2+}	Young leaves permanently wilted; foliage dark green; terminal branches unable to stand erect	Young
Molybdenum	Involved in nitrogen reduction	Mo	MoO_4^{2-}	Young leaves twisted, chlorotic	Young

Elements are listed in order of decreasing number of atoms relative to molybdenum.

For an element to be considered an essential nutrient, it must meet the following three criteria: (1) The element must be necessary for normal plant development through a complete life cycle; (2) no other element can substitute for that element; and (3) the element must play a role in **metabolism** within the plant. Studies to demonstrate whether an element is essential

metabolism chemical reactions within a cell

electron transport system membrane-bound system of proteins that extracts energy from high-energy electrons, found in mitochondria and chloroplasts

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

middle lamella layer of material between two plant cells that holds them together

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

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

guard cells paired cells on leaves that control gas exchange and water loss

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

ion an electrically charged particle

gradient difference in concentration between two places

anthocyanins colored compounds made by plants

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

are often very difficult to conduct. Special hydroponic culture in growth chambers that eliminate contamination from the air allows scientists to eliminate a particular element and determine plant response to the deficiency.

Roles of Nutrients

Structural and Metabolic Components. Carbon, hydrogen, and oxygen comprise a major portion of organic compounds that make up plant cells. Nitrogen and phosphorus are found in phospholipids and nucleic acids. Copper and iron are components of **electron transport systems** in **mitochondria** and chloroplasts. The **middle lamella** that cements adjacent plant cells together is rich in calcium and magnesium pectate. Magnesium is also a component of chlorophyll.

Enzymatic Role. Many **minerals** serve as **enzyme** activators. Potassium, for example, is involved in the activation of many enzymes. Calcium binding **protein** (calmodulin) regulates many cellular activities. Manganese is essential in the photosynthetic release of O_2 in photosystem II.

Osmotic Role. Potassium plays a major role in opening and closing movements of **guard cells** of the **stomatal** apparatus. Hydrogen **ion gradients** are important in the generation of adenosine triphosphate (ATP) in mitochondria and chloroplasts.

Deficiency Symptoms

Chlorosis, a yellowing of leaf and stem tissue, is a common symptom of mineral deficiencies. In nitrogen deficiency a general chlorosis is exhibited, but in iron-deficient plants, chlorosis is confined to areas between leaf veins. Occasionally, plants will develop a purple coloration due to the production of large amounts of **anthocyanins**, when certain elements, such as phosphorus, are deficient. Necrosis (death of tissue) may follow chlorosis as deficiencies become more acute. In potassium-deficient plants necrosis occurs along leaf margins, but in manganese-deficient plants necrosis occurs between veins.

For several essential nutrients, young leaves show symptoms first, which means that the element is not easily translocated from old to young leaves, as is the case with iron deficiency. Nitrogen, potassium, and magnesium are easily loaded into sieve tube members of the **phloem** and translocated from old leaves to younger developing leaves. In those cases the older leaves exhibit the symptoms. SEE ALSO C4 AND CAM PLANTS; CHLOROPLAST; PHOTOSYNTHESIS; TRANSLOCATION

George H. Wittler

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Plant Pathogens and Pests

Plants, being immobile, are unable to escape pests (herbivores) that eat them, or microorganisms (pathogens) that cause plant diseases. On a global basis, it is estimated that plant diseases annually cause an 11 to 16 percent reduc-

tion in the value of rice, wheat, corn, and potato harvests. Additional losses to these major food crops as a result of pests (primarily insects and mites) are estimated at 9 to 21 percent. The magnitude of these losses, despite people's best efforts at prevention, are of major concern.

Diseases

Diseases of plants are caused by fungi, bacteria, viruses, mollicutes, and **nematodes**. Fungi are eukaryotic, spore-bearing, heterotrophic organisms that produce extracellular **enzymes** to break down plant or animal products to small molecules (for example, sugars and **amino acids**), which they absorb as nutrients. Fungi may grow as unicellular yeasts, but more commonly they grow as multicellular chains of elongated cells that form threadlike structures collectively called mycelium. Important diseases caused by fungi include Dutch elm disease, apple scab, and wheat stem rust. Fungilike protists (primitive eukaryotic microorganisms) also cause many serious diseases, of which the best known is the late blight of potato, which caused the Irish potato famine in the 1840s. Since the 1980s, late blight (caused by *Phytophthora infestans*) has become the single most important biological constraint to global food production and the cause of one of the biggest uses of pesticides.

Bacteria, although differing from fungi in being unicellular **prokaryotic** organisms, also cause disease by extracellular digestion of plant tissues. These bacteria are highly infectious and are easily spread on seed and by wind-blown rain, irrigation water, and insects. Fire blight of apple and pear, caused by *Erwinia amylovora*, is a serious problem because the bacterium is so easily spread by rain and insects. Most bacterial plant pathogens survive as **saprophytes** living on crop debris and in soil. Mollicutes, which can be described as prokaryotes lacking cell walls, cause diseases of plants by living within the **phloem** cells from which they obtain their nutrients. Mollicutes are very effectively carried from plant to plant by insects in which they can also reproduce.

The viruses that cause plant diseases are also often carried by insects and other pests, as well as by **grafting** and on cutting tools, machinery, or in seed. Most such viruses consist of ribonucleic acid (RNA), surrounded by a **protein** coat (the capsid). A few plant pathogenic viruses contain deoxyribonucleic acid (DNA) rather than RNA. All viruses are **intracellular** and are **obligate parasites** as they are dependent on the plant cell for their reproduction.

Plant pathogenic nematodes are small (approximately 1-millimeter long) wormlike animals that live in soil and feed on plant roots by piercing the cells with a needlelike structure called a stylet through which they suck up the cell contents. Nematodes, which may feed from outside or inside the root, cause enormous damage to roots, thus reducing nutrient and water uptake. Root knot nematodes, one of the most damaging pathogens, stimulate division and expansion of root cells to create "galls" in which the female nematodes remain to feed and produce eggs.

nematode worm of the Nematoda phylum, many of which are parasitic

enzyme protein that controls a reaction in a cell

amino acid a building block of protein

prokaryotic without a nucleus

saprophyte plant that feeds on decaying parts of other plants

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

grafting attachment and fusing of parts from different plants

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

intracellular within a cell

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

parasite organism living in close association with another from which it derives most of its nutrition
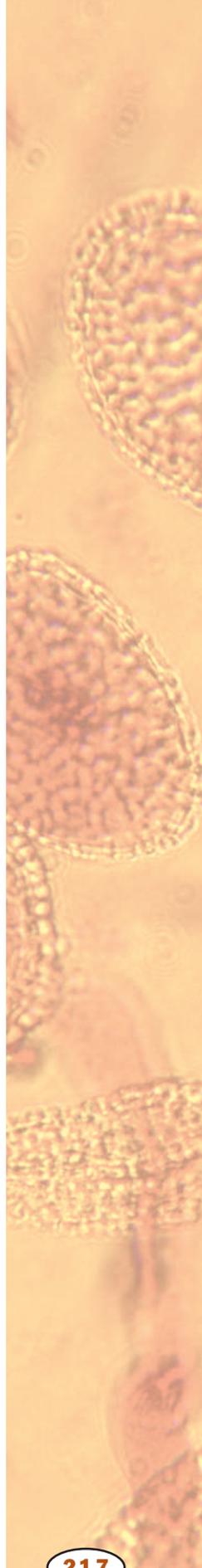
arthropods organisms with jointed appendages and exoskeletons, including insects, spiders, and crustaceans

Stink bugs have the ability to emit a foul-smelling substance from a pore on each side of their thorax. They often have symbiotic relationships with bacteria, which aids the insect in the production of nutrients.

Pests

Plant pests include the **arthropods** (such as insects and mites), slugs, snails, sowbugs, and pillbugs. Only a small proportion of insects are plant pests with the most conspicuous being the butterflies and moths. The larvae (caterpillars) of butterflies and moths cause severe damage by feeding on foliage until they pupate. The adults rarely feed on foliage. The most common butterfly pest in North America is the cabbage white, which is seen in great numbers in the summer. Beetles also damage plants as both larvae and adults chew on plant tissue. The Colorado potato beetle is the most notorious of these pests. Juvenile (nymphs) and adult grasshoppers are also foliage-eating insect pests. Larvae of flies feed and burrow into roots, bulbs, and stems of plants and thus cause considerable damage.

The least conspicuous insect pests are those that pierce the stem or leaf and suck nutrients from the plant. Nymphs and adults of aphids, leaf hoppers, stink bugs, and plant bugs cause extensive damage in this manner and, as well, they carry plant pathogens, especially viruses, from plant to plant. Insects called thrips also pierce plant parts and are important in transmitting viruses.

Mites differ from insects, as the adults have four pairs of legs (versus six for insects) and lack an antennae. Larvae of mites feed and molt to form six-legged nymphs before becoming adults. The mites that feed on plants have rasping and sucking mouth parts that damage plants and they also transmit plant pathogens as they feed. Both thrips and mites are very small and, as a result, often avoid detection until the plant growth is visibly affected.

Damage to plants caused by slugs and snails is very obvious, but is generally limited to crops growing in very damp situations and those, such as strawberries, in contact with the soil. Slugs and snails glide on an obvious slime trail of secreted mucus and feed at night, or on very cloudy days, to avoid drying out. Also at home in damp environments are the sowbugs and pillbugs. These oval (pill-sized) bugs have a small head, two pairs of antennae, and seven pairs of legs. These species are more important as decomposers of rotting vegetation than as plant pests.

Control

Crop management to reduce damage by diseases and pests is based on integrated control strategies involving exclusion, eradication, and protection. Whenever possible, growers attempt to exclude the pathogen or pests from their land by purchasing pathogen- and pest-free planting material (seeds, seedlings, grafting material, tubers, and bulbs). When a pathogen or pest is present in fields or orchards, every effort is made to eradicate it by cultivation practices designed to "starve" the organism, for example, by planting a crop on which it can not obtain nutrients. When such methods fail, pesticides may be required to reduce pathogen populations; for example, nematocides to kill root-knot nematodes. Many pests and pathogens (for example, apple scab and wheat stem rust fungi, fire blight bacterium) are, however, so widespread and so readily distributed from field to field that exclusion and eradication are impossible. Ideally, for these problems, plant varieties that are genetically resistant to the pathogen or pest are available.

Alternatively, growers may be able to reduce crop losses by cultural practices that make the environment unfavorable for the agent; for example, spacing plants to prevent the high humidity conducive to plant disease. If such methods are unsuccessful, the grower may be required to use biological control (for example, the bacterium *Bacillus thuringiensis* for moth and beetle control) or chemical pesticides (fungicides to control late blight of potato, or insecticides to control grasshoppers). Bioengineering techniques are enhancing researchers' ability to produce genetically resistant crop plants, and this technology will eventually decrease reliance on chemical pesticides. SEE ALSO DNA VIRUSES; EUBACTERIA; FUNGI; INSECT; NEMATODE; SECONDARY METABOLITES IN PLANTS; VIRUS

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Plant Pathologist

Plant pathologists specialize in the study of the nature, cause, and control of the diseases of plants. Plant pathologists are employed by colleges and universities, agricultural businesses, research organizations, government agencies, private enterprises, and as self–employed practitioners. They teach and conduct research; provide advice on the diagnosis and control of plant diseases; manage greenhouses, parks, golf courses, and farms; and serve as sales representatives and administrators.

A career as a plant pathologist typically begins with a Bachelor's degree in one of the chemical, biological, or physical sciences. Coursework or a major in plant pathology will result in greater employment opportunities. High school preparation should include four years of science and math. Preparation for most professional positions will include specialized graduate work leading to a master of science and/or doctor of philosophy degrees (Ph.D.). Graduate plant pathology specialities include virology, bacteriology, mycology, molecular plant pathology, epidemiology, biological control, and diagnosis. Individuals interested in a career in plant pathology should contact the plant pathology department at a university. SEE ALSO BOTANIST; MICROBIOLOGIST; PLANT PATHOGENS AND PESTS

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prokaryote single-celled organism without a nucleus

lipid fat or waxlike molecule, insoluble in water

intracellular within a cell

solute dissolved substance

bilayer composed of two layers
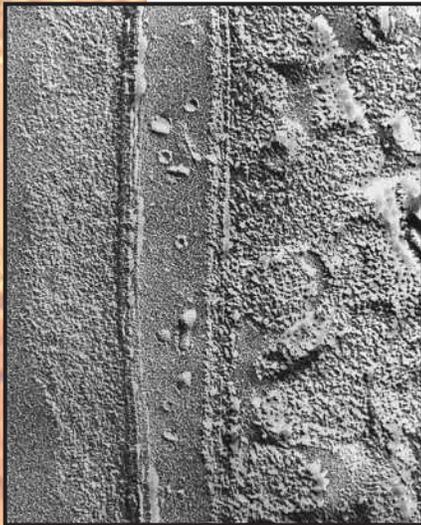
Freeze fracture image across the cell wall and membrane of a blue-green algae.

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

amino acid a building block of protein

ion an electrically charged particle

gradient difference in concentration between two places

metabolism chemical reactions within a cell

neuron nerve cell

action potential wave of ionic movement down the length of a nerve cell

Plasma Membrane

Plasma membranes envelop all plant and animal cells and all single-celled eukaryotes and **prokaryotes**, separating them from their environments. Structurally, they resemble other cellular membranes, but differ slightly in their **lipid** composition and more drastically in their protein content from one cell to another and from **intracellular** membranes. These compositional similarities and differences, in turn, are reflected in the ways in which plasma membranes carry out their functions, facilitating **solute** transport, conducting signals, and anchoring cells to their environments.

The Roles of Membrane Proteins

Like other membranes, plasma membranes are essentially lipid **bilayers** and exhibit a dynamic organization and fluidity characteristic of such "liquid crystalline" structures. The predominant lipids found in most plasma membranes include phospholipid and glycolipid; those in animal cells also contain significant amounts of cholesterol. Since cholesterol is a stiff, planar molecule and is thought to have a stabilizing influence on plasma membranes, scientists speculate its presence represents an adaptation by animal cells to the absence of the external cell wall that surrounds bacterial and plant cells. Plasma membranes also contain protein and glycoprotein in addition to lipid, of both the integral and peripheral varieties. These proteins perform the major functions associated with plasma membrane and they account for the major differences in plasma membranes among different cells of an organism.

Plasma membranes transport nutrients into (and out of) cells and are responsible for facilitating the removal of carbon dioxide, the waste product of respiration. To perform these functions, they contain integral membrane proteins (IMP) that serve as carriers for **glucose** and a variety of **amino acids** and for HCO_3- (bicarbonate, the soluble form of carbon dioxide). All cells typically maintain cytoplasmic concentrations of Na^+ (sodium) and K^+ (potassium) at very different levels than found in their immediate environment: higher in the case of K^+ and lower in the case of Na^+ These **ion gradients** are maintained by another group of IMP called pumps, which actively transport these ions up their gradients, using energy supplied by **metabolism**.

Membranes are also leaky to these ions, which diffuse across the plasma membrane and down their respective gradients through another class of IMPs called channels. Differences in the rates of ion diffusion produce differences in electrical charge across most membranes; these are measured as small differences in voltage and are called resting potentials. In so-called excitable cells, such as muscle fibers and **neurons**, channels may be opened by changes in resting potentials (or by signaling molecules binding to them). When this happens a wave of change in electrical potential may pass along the plasma membrane over the entire surface of the cell; these are called **action potentials** and represent the major way our nerves and sense organs communicate.

Proteins integral to plasma membranes are involved in other forms of signaling as well. In these instances, an external signaling molecule, such as a hormone, binds very selectively to that portion of the IMP extending into

the external environment (often involving the **carbohydrates** attached to the IMP). Such IMPs are more commonly called receptors, which differ in their binding specificity for various signaling molecules. When binding occurs, the receptor changes its overall structure (its **conformation**) and that portion projecting into the cytoplasm becomes reactive in some manner. The cytoplasmic region might become an activated **enzyme** or it might, in turn, become "sticky" for a soluble cytoplasmic enzyme. In any event, the presence of an external signal is conveyed across the plasma membrane and is amplified by the activation of cytoplasmic enzymes, which continue the signaling process by producing second messengers.

Under certain circumstances, the cytoplasmic "tails" of receptors are anchored to peripheral membrane protein components of the **cytoskeleton**, and the binding of a molecule to the extracellular surface releases the receptor from its anchorage. The IMP is then free to diffuse in the plane of the membrane and may become associated with other peripheral membrane proteins in the cytoplasm and **aggregated** into a specialized region of the plasma membrane called a coated pit. The coated pit then invaginates and forms a **vesicle**, by a process called endocytosis that removes the receptor (and its attached signal) from the cell surface.

Cell Junctions

Integral membrane proteins of the plasma membranes also anchor cells to their environment: that is, to neighboring cells and to the proteins and glycoproteins of the extracellular environment (the extracellular **matrix** or ECM). The cytoplasmic portions of these IMP in turn are usually attached to peripheral membrane components of the cytoskeleton (such as microfilaments and intermediate filaments). Although these IMPs are not usually called receptors, their binding with the IMP of an adjacent cell or with the peripheral membrane proteins of the ECM is very selective, and a complex terminology has developed to characterize the very specific nature of these cell-cell and cell-matrix interactions and the IMP involved.

Anchoring IMPs also resemble receptors insofar as changes in cell-cell and cell-ECM interactions mediated by these IMPs are often associated with changes in the cytoplasmic regions of the IMP, in this case to their attachments with the cytoskeleton. In this manner, some cells move from place to place (by changing their anchorage points), either normally in the case of circulating leukocytes and abnormally in the case of metastasizing cancer cells.

Clusters of anchoring IMPs and their cytoskeletal elements are often referred to as desmosomes when the associations involve other cells and hemidesmosomes when the clusters attach to the ECM. Certain intercellular IMP associations are so tight they effectively seal adjacent cells to each other (without causing fusion of their membranes), forming so-called tight junctions. Tight junctions are especially common in epithelial tissue where their presence in bands around all the epithelia cells produces a very effective barrier against leakage of materials across the tissue through the extracellular space.

Finally, certain IMPs may self-associate to form large, nonselective channels in the plasma membrane; such channels arise in close association with identical channels in neighboring cells, establishing cytoplasmic continuity among the cells so connected. These junctions are called gap junctions and

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

conformation three-dimensional shape

enzyme protein that controls a reaction in a cell

cytoskeleton internal scaffolding in a cell, composed of protein

aggregate clump together

vesicle membrane-bound sac

matrix a network, usually of threadlike fibers
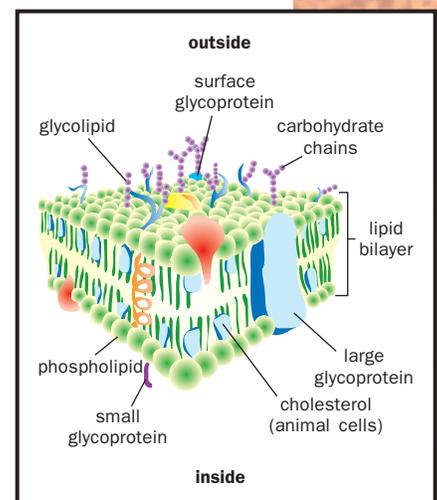
The plasma membrane is composed of a bilayer of phospholipid molecules, plus large numbers of embedded proteins, many of which have attached sugar molecules (glycoproteins). Animal cells also contain cholesterol, which increases rigidity.

they are thought to represent a major means of communications among neighboring cells making up a specialized tissue.

Receptors and anchoring IMPs, and the plasma membranes containing them, differ respectively in the signals they can receive, in the second messengers they produce and in the selective nature of their anchorages. To a lesser extent, this is true of transport IMPs as well. These IMPs are the products of differential gene activation and they thus represent a major way in which specialized cells differ from each other. SEE ALSO CELL JUNCTIONS; MEMBRANE STRUCTURE; MEMBRANE TRANSPORT

Chris Watters

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Platyhelminthes

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

bilaterally symmetric symmetric, or similar, across a central line

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

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

The **phylum** name Platyhelminthes literally means "flatworms." Members of this phylum are soft, thin-bodied, leaf or ribbonlike worms, including the familiar planaria of ponds and streams, as well as the flukes and tapeworms parasitic in human and other animal bodies. Some defining characteristics of the phylum are that flatworms are acoelomate (they have no body cavity), triploblastic (the body has three tissue layers), and **bilaterally symmetric** (they have symmetric right and left sides and usually a definite head), and they have organ systems, including an excretory, digestive, reproductive, and nervous system, but no respiratory system.

The class Turbellaria includes all free-living members of the phylum, as well as a few **parasites**. It includes many marine forms, whose beautiful colors serve as a warning of their toxicity to would-be predators, as well as the more drab freshwater planarians (*Dugesia*). Some Turbellaria can swim by undulations of the body margins, but most of them glide gracefully over surfaces along a trail of mucus, pushed by **cilia** on their ventral surface.

The class Trematoda, commonly called flukes, are unsegmented parasitic flatworms that usually parasitize a snail as an intermediate host (in which they reproduce asexually) and a human or other vertebrate as a definitive host (in which the worms mate and lay eggs). Many species have other hosts between these two, such as fish or frogs. Trematodes usually have a pair of suckers for crawling and clinging to the host's tissues. Many humans are infected with blood flukes, liver flukes, lung flukes, and other trematode parasites of great medical importance.

The Cestoda, commonly called tapeworms, are segmented, ribbonlike parasites usually found as adults in the small intestines of vertebrate animals. Unlike the other classes, they have no digestive tract, for they can absorb predigested nutrients from the host's intestine. The body consists of a long chain of segments, each with its own reproductive system. The anterior end is a knoblike holdfast called a scolex, equipped with suckers and often hooks for attachment to the host's intestine. In general, tapeworm infections are not as medically serious as trematode infections, but some tapeworms can be lethal. SEE ALSO ANIMALIA; BODY CAVITIES; NEMATODE; PARASITIC DISEASES; SYMBIOSIS

Kenneth S. Saladin

HYMAN, LIBBIE HENRIETTA (1888–1969)

U.S. zoologist famous for her authoritative six-volume treatise on invertebrates, whose own specialty was hydras and flatworms. Hyman went to college despite her family's objections. In her last years, she lived off the royalties from her textbooks and worked at the American Museum of Natural History.

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Poisonous Plants

Poisonous plants contain substances that can cause sickness or death if those substances are ingested or come into contact with the body of an animal. These substances are often referred to as "secondary compounds." Primary

Some Plants Poisonous to Humans and Animals

Plant name and occurrence	Poisonous plant parts and toxins	Comments
Alfalfa (*Medicago sativa*) - forage and silage	leaves and stems - phytoestrogenic compounds, saponins, bloat-causing proteins	livestock, poultry: bloat, photosensitization (sickness after ingesting plant and subsequent exposure to sunlight), phytoestrogens cause infertility, reduced egg-laying in poultry
Astragalus (*Astragalus lentigenosus*) - rangeland plant	above-ground plant parts - alkaloid: swainsonine	livestock: locoism (erratic behavior), birth deformities, abortion, and (above 2120 m) contributes to congestive heart failure in cattle
Castor bean (*Ricinius communis*) - garden plant	seeds and to a lesser extent the leaves - toxalbumin: ricin	humans, livestock, pets: illness and death; chewing a single seed may sicken a child
Crown-of-thorns (*Euphorbia milii*) - house plant	plant juices or sap - toxic diterpenes including 5-deoxyingenol	humans and pets: irritant in the sap causes irritation of the skin, eyes, mouth
Johnson grass (*Sorghum halepense*) - outdoor weedy grass	leaves and stems - cyanogenic glycoside: dhurrin; nitrate accumulation	livestock: in the animal body dhurrin is converted to cyanide (which may be lethal); can accumulate excessive amounts of nitrates causing death, abortion
Kochia (*Kochia scoparia*) - outdoor and garden plant	leaves, flowers, and seeds - alkaloids, oxalates, and saponins	livestock: photosensitization
Oleander (*Nerium oleander*) - house and garden plant	leaves and stems - glycosides: oleandrin, nerioside	livestock and humans: nausea, vomiting, dizziness, death (e.g. poisoning of humans after eating hot dogs roasted on oleander sticks)
Poison ivy (*Rhus radicans*), Poison sumac (*Rhus vernix*), Western poison oak (*Rhus diversiloba*), - outdoor plants	plant sap - allergin: urushiol containing catechols	humans: allergic reaction causing dermatitis, blisters (many humans develop symptoms after only one exposure); sap contaminates clothing, tools, etc.
Rhubarb (*Rheum raponticum*): - food plant	leaf blade, not the leaf stems - oxalic acid	livestock and humans: leaf stems (petioles) are edible; leaf blades contain oxalic acid crystals causing nausea, vomiting, abdominal pain
Spotted water-hemlock (*Cicuta maculata*) - outdoor plant	all parts, especially roots - alkaloids: cicutoxin, cicutol	animals and humans: most violently toxic plant in North America; symptoms can appear suddenly causing spasms, coma, and death

metabolism chemical reactions within a cell

compounds are chemicals involved in basic **metabolism**, whereas secondary compounds are chemicals that are generally waste products of metabolism. Secondary plant compounds, the toxic substances, have coevolved in higher plants in response to attack by herbivorous insects for over one hundred million years. Animals are poisoned when the animals' protection mechanisms (detoxification) are inadequate.

Secondary compounds include chemicals such as alkaloids, glycosides, oxalates, saponins, tannins, and toxalbumins. These chemicals are toxic in various ways to vertebrates. Some responses are dramatic (violent spasms, death) or subtle (reduced weight gain, birth defects). Other chemicals are only toxic after being altered inside the animal body (for example, cyanogenic glycosides, which produce cyanide) or if the animal is exposed to the sun (photosensitization). Researchers continue to discover new toxins from plants.

In 1986 it was estimated that poisoning of cattle, sheep, and horses grazing western U.S. rangelands cost ranchers $190 million per year. Most cases of human poisoning involve house and garden plants. In 1998 there were 122,578 plant-related calls to poison control centers in the United States, according to information from the American Association of Poison Control Centers. Only 109 of those cases were serious (but included four fatalities).

Some cases of plant poisoning are remarkable. During the nineteenth century tragic loss of human life occurred from a mysterious milk sickness in which cattle ingested white snakeroot and a toxin was passed on to humans through the milk. In 1971 near Garrison, Utah, more than twelve hundred sheep died after ingesting the rangeland plant halogeton. Although these toxic compounds are harmful to most species that ingest them, some insects are not harmed by some of the toxins and actually sequester the poison in their own body as a defense against their own predators.

Derek Bishop Munro

When white snakeroot is eaten by livestock, it can cause a sickness known as trembles. Symptoms in animals include depression, inactivity, labored breathing, loss of weight, and trembling.

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Poisons

Poisons are substances that are harmful to living organisms. It is said that "the dose makes the poison" because almost any substance can be poisonous at high enough concentrations, especially many substances used as medicines.

Poisons include compounds of biological origin and chemicals manufactured by humans. Biological poisons, also known as toxins, are produced by some members of every living kingdom, including bacteria, fungi, protists, plants, and animals. The chemical industries produce thousands of chemicals, many of which are poisonous. Regulation of workplace exposure to these is the responsibility of the Occupational Safety and Health Agency,

or OSHA. The Environmental Protection Agency (EPA) oversees cleanup of toxic wastes and spills.

Exposure

There are three major routes of exposure for poisons: absorption through the skin, inhalation into the lungs, and ingestion in the gut. Skin forms a barrier against many poisons, but its large surface area provides a route of entry for liquids especially. Inhalation provides a rapid route of entry directly into the bloodstream for small, **volatile** molecules. The **enzymes** and acids of the gastrointestinal tract inactivate some ingested poisons, but the long transit time and high surface area of the gut mean that an ingested poison is likely to enter the bloodstream if not inactivated.

volatile easily vaporized

enzyme protein that controls a reaction in a cell

Most poisons act acutely, meaning their toxic effects come on very quickly after exposure. In contrast, heavy metals such as lead and mercury accumulate slowly in the fatty tissue of the body, and chronic exposure to low doses can cause poisoning.

Mechanisms

Poisons disrupt metabolic processes or destroy tissue through chemical reactions with cells. While the number of specific mechanisms of action is large, there are several broad means by which many poisons exert their effects. The list below is not comprehensive.

Oxygen Deprivation.   The brain consumes large amounts of oxygen and cannot survive if deprived of it for more than ten minutes. Oxygen deprivation may occur if the respiratory muscles cannot deliver adequate air to the lungs, if the lungs cannot absorb adequate oxygen from the air, or if the blood cannot carry the oxygen to the brain.

Barbiturates and benzodiazepines, drugs prescribed as sedatives, depress activity in the brain center that controls the respiratory muscles, thus preventing those muscles from working sufficiently. Respiratory muscle paralysis may be caused by ingestion of botulinum toxin, one of the most poisonous substances known. It is formed by the bacterium *Clostridium botulinum*, a contaminant of improperly canned food. Botulinum toxin prevents release of acetylcholine by **neurons** at the neuromuscular junction. Without this neurotransmitter, the respiratory muscles cannot contract.

neuron nerve cell

Absorption of adequate oxygen can be interrupted when otherwise harmless gases, such as nitrogen or carbon dioxide, are present in high concentration. In 1986, a massive release of dissolved carbon dioxide from Lake Nyos in Cameroon, Africa, asphyxiated eighteen hundred people in the surrounding villages. **Hemoglobin** carries oxygen in the bloodstream. Carbon monoxide binds to hemoglobin, displacing oxygen and preventing its transport. Carbon monoxide is produced by combustion and is found in car exhaust and furnace smoke.

hemoglobin oxygen-carrying protein complex in red blood cells

Cardiac Toxicity.   The heart muscle relies on chemical signals to control the rate and force of its contractions. Digitalis, derived from the foxglove plant, is prescribed for congestive heart failure to increase heart output. In slightly larger doses, it is deadly. Related compounds are produced by
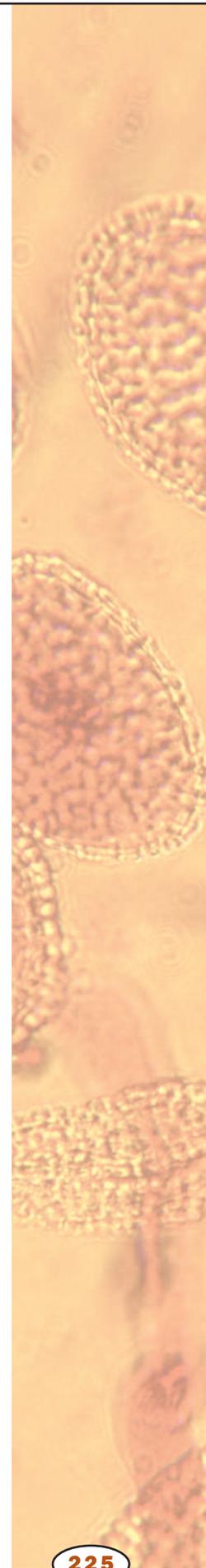
Digitalis, derived from the foxglove plant, is prescribed for congestive heart failure to increase heart output. In slightly larger doses, it is deadly.

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

oxidative phosphorylation use of oxygen to make ATP

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

ion an electrically charged particle

various South American frogs of the genus *Dendrobates*, and are used on arrow tips for hunting.

Mitochondrial Poisons. Most cells in the body are supplied with fuel by subcellular structures called **mitochondria**. One step of the energy-producing reactions, **oxidative phosphorylation**, relies on electron-carrying **proteins** called cytochromes. Cyanide binds permanently to these cytochromes, preventing them from carrying electrons and thus inactivating them. Another step in these reactions requires a buildup of H$^+$ **ions** across the mitochondrial membrane. Dinitrophenol, a chemical used in dye manufacture, is a membrane-soluble H$^+$ carrier. By carrying H$^+$ ions across the mitochondrial membrane, dinitrophenol interrupts this step. Impaired energy production affects all cells, especially brain and heart cells.

Liver and Kidney Poisons. The liver is the principal site of poison detoxification. It has many different types of enzymes that attack and degrade the wide variety of molecules to which the body may be exposed. Inhalants such as glues, gasoline, or other solvents cause direct tissue damage to the liver, leading to liver failure. The kidneys excrete most poisons or their breakdown products. Kidneys may be damaged from exposure to poisons, or by accumulation of compounds that cannot be excreted.

Mutagens and Carcinogens. Chemicals that cause changes in deoxyribonucleic acid (DNA) sequence, or mutations, are called mutagens. If these changes prompt the cell to begin dividing, the cell may become cancerous. Substances that cause cancer are called carcinogens. Inhaled asbestos fibers can cause lung cancer, as can chemicals in cigarette smoke.

Treatment

Antidotes are available for very few poisons. Snakebite, for instance, may be treated with antivenin, which provides antibodies that inactivate the poisonous venom. However, in most cases of poisoning, medical treatment focuses

on removing the poison from the body when possible, and maintaining respiration and circulation until the toxic effects are reduced as the compound is metabolized and **excreted** over time. Poison control centers in every state maintain telephone hotlines to deal with poisoning emergencies. If a victim is in medical distress, 911 should be called immediately. SEE ALSO ALCOHOL AND HEALTH; ANTIBODY; CANCER; HEALTH AND SAFETY OFFICER; LIVER; MUTATION; MITOCHONDRION; NEURON; OXIDATIVE PHOSPHORYLATION; PEROXISOMES; SYNAPTIC TRANSMISSION

Richard Robinson

excrete deposit outside of

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Pollination and Fertilization

Pollination is the transfer of pollen to the female organs of seed plants. In flowering plants (angiosperms, or "covered seeds"), immature seeds (ovules) are located within carpels. In contrast, nonflowering seed plants have uncovered **ovules** to which the pollen is transferred, making these "naked seeds" (gymnosperms).

Gymnosperms have simpler pollination as all transmit their pollen by wind. In contrast, angiosperm have a wealth of pollination methods involving many different agents to transfer pollen, including insects (entomophily), birds (ornithophily), bats (chirophily), wind (anemophily), and water (hydrophily). Attraction of animals usually occurs through a conspicuous floral display, with color and scent playing important roles. Yellow and blue flowers tend to attract bees, red flowers attract hummingbirds, pink flowers attract butterflies, and white flowers that stand out at night often attract moths and bats. Animal-based pollination is efficient and usually associated with a food reward to assure a continuing relationship. Frequently, this is a simple symbiotic relationship; however, other plants seem to practice deceit. For example, trap pollinators may hold insects hostage until a flower is pollinated successfully, when they are released. A most unusual mechanism are orchids that seemingly imitate the form and scent of female wasps, attracting amorous male wasps to mount the flower, inadvertently pollinating it. Aquatic plants frequently have filamentous pollen, which is more easily captured in water, and may release male flowers that float freely to their attached female counterparts.

When pollen is deposited on the stigma (in angiosperms) or the ovule (in **gymnosperms**), it germinates, forming a slender pollen tube through a weakened area of the pollen wall. The pollen tube elongates through "tip extension," penetrating between cells of the host parent. Within the pollen tube, two nonmotile sperm cells are ultimately formed and are conveyed through the tube, keeping pace with tip growth. The pollen tube uses chemotropic signals to determine the final pathway to the egg cell, deep within the ovule. In angiosperms, pollen tubes penetrate the stigma, style, and ovary until they are amid the ovules. In gymnosperms, pollen germinates
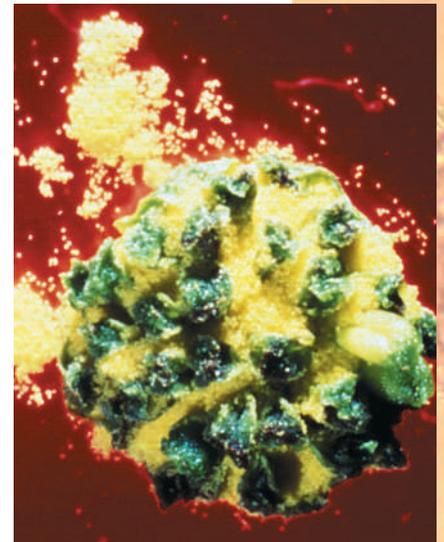
Pollen being released from the anther of a black walnut.

ovule multicellular structure that develops into a seed after fertilization

gymnosperms "naked seed" plants, including conifers

gametophyte a haploid plant that makes gametes by mitosis

zygote fertilized egg

endosperm nutritive tissue within a seed

fertilization union of sperm and egg

gamete reproductive cell, such as sperm or egg

directly on the ovule. Pollen tubes enter ovules through a tiny pore called the micropyle and then elongate into the female **gametophyte** (called the embryo sac in angiosperms). In gymnosperms, the pollen tube directly penetrates the egg cell, but in angiosperms, there are sterile cells in the embryo sac, called synergids, that initially receive the sperm.

At this point, one sperm cell is discharged from the pollen tube and fuses, with the egg cell to form the **zygote** (the immediate fusion product) and subsequent embryo, which will become the offspring plant. In angiosperms, the second sperm fuses with the central cell to form a nutritive **endosperm** during double **fertilization**. The endosperm is needed for successful embryo development.

During fertilization the male and female **gametes**: (1) contact one another, (2) adhere, (3) cells fuse, and finally (4) nuclei fuse. The act of fertilization triggers embryo development in all plants and endosperm development in angiosperms. SEE ALSO FLOWERS; PLANT DEVELOPMENT; REPRODUCTION IN PLANTS; SEEDS

Scott D. Russell

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Pollution and Bioremediation

When a substance is released to the environment at a rate in excess of what can be safely assimilated, that substance becomes an environmental pollutant.

Properties of Pollutants

bioaccumulate buildup within organisms

inorganic not bonded to carbon

organic composed of carbon, or derived from living organisms

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

hydrolysis splitting with water

enzyme protein that controls a reaction in a cell

Three properties make environmental pollutants especially hazardous: resistance to decomposition (persistence); ability to **bioaccumulate**, which is related to insolubility in water (hydrophobicity) and solubility in oil (lipophilicity); and the concentration or quantity at which toxic effects occur (potency). Elements like **inorganic** mercury cannot be further broken down but can only be changed in form, so once a source is reduced or eliminated pollutants' concentrations decrease over time only as a result of dilution or burial in accumulating soil or sediments.

Synthetic **organic** substances (SOCs), like the pesticide DDT, can persist in the environment because they are only very slowly decomposed by natural physical, chemical, and microbiological processes. Sunlight can break down some SOCs, while others react with water molecules under **acidic** or basic conditions in a process called **hydrolysis**. The **enzymes** of some microbes that decompose wood can also decompose SOCs. The products of these reactions tend to be more water-soluble and less fat-soluble than the parent compounds, reducing their tendencies to bioaccumulate. In general, the breakdown products are also less toxic, although there are exceptions to this rule.

Some air pollutants, like sulfur trioxide and nitrogen dioxide, react with the water vapor in the air to produce acid rain. The high acidity (low pH)

caused by acid rain in poorly buffered lakes has decimated fish populations. Acid rain also leaches metals from the soils in the watershed more efficiently than does normal rain, and some of these metals like copper are especially toxic to aquatic organisms.

The metal mercury presents an example of a pollutant that is persistent, bioaccumulates, *and* is extremely toxic. Mercury is released into the air in small quantities from burning coal and municipal, medical, and industrial waste, and into water as pollution from a variety of industrial chemical processes. Like other air pollutants, mercury can eventually deposit on watershed surfaces and be carried by storm runoff into the stream, wetland, or lake, or deposit on them directly. Once present in the lake, the inorganic mercury attaches to living (biotic) or nonliving (abiotic) particles and eventually settles into the sediments. There, oxygen-avoiding (anaerobic) bacteria synthesize methylmercury from inorganic mercury as a byproduct of their life processes. The methylmercury then moves out of the sediment and into the overlying water and is absorbed by microscopic plants and animals.

Methylmercury is rapidly taken up but only slowly eliminated from the bodies of aquatic animals, and elimination efficiency decreases with increasing size. Thus, at the top of the aquatic food chain, prized sport fish like the largemouth bass can bioaccumulate as much as ten million times the concentration of methylmercury in the water in which it lives. The birds that feed on top-predator fish, like the eagle and the osprey, can further biomagnify the methylmercury in their bodies. When eggs are laid, the methylmercury is deposited in the egg's albumin, or white.

Mercury is not only a threat to birds, but to all animals, including humans. Methylmercury crosses into the developing brain, disrupting brain (neural) development and thought processing. At low doses, methylmercury can slow the development of movement (motor) and learning (cognitive) skills. At high doses in humans, it can cause the severe retardation and twisted limbs now referred to as Minamata disease, after the small city (Minamata Bay) in Japan where the severest toxic effects of methylmercury poisoning were first observed.

Synthetic Organic Substances: Targets for Bioremediation

Typically, decomposition of SOCs occurs more rapidly by oxygen-loving (aerobic) bacteria and fungi than by the more primitive, oxygen-avoiding (anaerobic) bacteria. Unfortunately, many SOCs like the benzene in gasoline leach into the aquifers underlying leaking storage tanks or spills where there is little oxygen. This means that decomposition occurs only slowly, if at all. To speed up this process, engineers have developed ingenious systems to pump water supersaturated with oxygen (and sometimes with added bacteria) into the groundwater. Other systems rely on pumping the groundwater with substitute hydrogen peroxide for oxygen, which releases oxygen as it breaks down. Scientists are also working with the bacteria and fungi that decompose wood to develop a taste for SOCs. While weaning the organisms onto SOCs used to be a time-consuming process in the past, a new generation of genetically engineered organisms are being tested for their efficiency and safety.
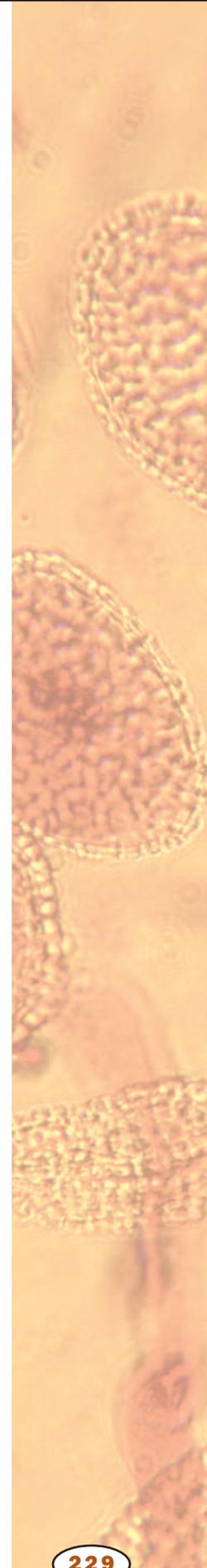
This General Electric plant in Pittsfield, Massachusetts, lay dormant from the 1970s, when the use of PCBs was banned, until the mid-1990s, when GE and civic leaders agreed to clean the site on the Housatonic River on which it sits.

volatile easily vaporized

Finally, some plants are capable of transporting **volatile** organic compounds (VOCs) like benzene through their roots and out their leaves, while others take up toxic metals through their roots and store them in their stems and leaves. The process of using plants to clean up (remediate) a contaminated site is called phytoremediation. These bioremediation alternatives are often preferable to such techniques as burying hazardous waste in clay-lined pits, stabilizing the contaminant in place using soil-cement mixtures, or turning the soil into glass one section at a time using a powerful electric current.

DDT: An Environmental Success Story

By the late 1930s the pesticide SOC named dichlorodiphenyltricholroethane (DDT) had been shown to be an effective pesticide against a wide variety of insects, including the mosquitoes, lice, and fleas that carried human diseases, and a wide variety of agricultural insect pests. By the mid-1950s, it was readily available to farmers, who hailed DDT as the beginning of a new era in agriculture, allowing them to plant more crops in greater densities with less pest damage, and the use of DDT expanded dramatically. It was also broadcast on lakes, ponds, and swamps for mosquito control. Soon thereafter, when environmental samples were analyzed from across the United States and then the world, scientists were shocked to learn that DDT was not only building up in the soils and soil organisms where it was being applied, but in the birds feeding on those soil organisms in the sediment and water in nearby lakes, in the fish in those lakes, and in the birds eating those fish.

This intrigued an unknown biologist named Rachel Carson, who in the late 1950s began to review the scientific literature and compile lay unpublished reports and anecdotal information on the toxic effects of DDT, ultimately resulting in her book *Silent Spring* (1962). In it she predicted that

the indiscriminate use of DDT and related pesticides threatened nontarget species like worm- and fish-eating birds with local extinction.

Studies showed that DDT mimicked the **hormone** that controlled calcium deposition in egg shell formation. DDT was not directly toxic to adult birds or their offspring, but it caused eggshell thinning, so that the shells broke under the weight of the nesting mother. At the same time, field scientists were able to document the serious declines in populations of fish-eating birds, even along the shores of the seemingly pristine Great Lakes.

hormone molecule released by one cell to influence another

Goaded by these revelations, within five years of the publication of *Silent Spring*, the state of Wisconsin was the first to ban all uses of DDT. By 1972, the then two-year-old U.S. Environmental Protection Agency (EPA) banned DDT across the United States, although manufacture and export are still lawful. One by one, DDT's chemical cousins—aldrin, endrin, heptachlor, chlordane, lindane, and toxaphene—were also banned. Clearly, *Silent Spring* was one of the most influential books of the twentieth century, giving birth to both the environmental movement and the environmental science that would guide the implementation of laws to restore and protect clean air, water, and soil and the proper disposal of hazardous waste.

Endocrine Disrupters: A New Challenge

In the 1990s Theo Colborn has refocused attention on chemicals that mimic, suppress, or amplify the action of animal hormones, so-called **endocrine** disrupters. When an organism is exposed to these endocrine signal scramblers in the egg or uterus, normal sexual development can be disrupted, resulting in increased incidences of infertility, underdeveloped sex organs, possession of both sets of sex organs (hermaphrodism), masculinization of females, and feminization of males.

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

In 1996, Colborn and her co-authors released *Our Stolen Future*, which summarized the scientific literature on the effects of endocrine disrupters to animals in the laboratory and in the wild and linked the occurrence of similar effects in humans to exposure to endocrine disrupters. While the controversy surrounding *Our Stolen Future* can only be compared to that of *Silent Spring*, so too its almost immediate impact on national policy. Because of the potentially serious consequences of human exposure to endocrine disrupting chemicals, Congress included specific language on endocrine disruption in the Food Quality Protection Act and amended Safe Drinking Water Act in 1996. The former mandated that EPA develop an endocrine disrupter screening program, whereas the latter authorizes EPA to screen endocrine disrupters found in drinking water sources. As of 2000, scientists are still in the process of developing the standardized tests required to screen for endocrine disrupter effects in the more than seventy thousand chemicals produced commercially each year. SEE ALSO CARSON, RACHEL; ENDANGERED SPECIES; ENDOCRINE SYSTEM; HORMONES; LIMNOLOGIST

Larry Fink

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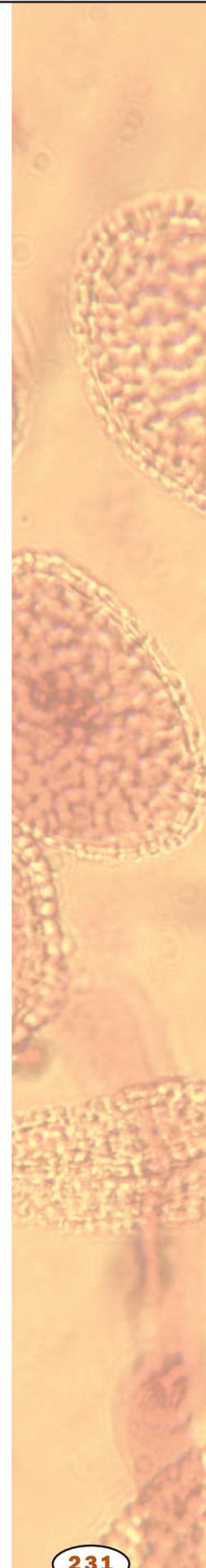
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Polymerase Chain Reaction

The polymerase chain reaction (PCR) is a process that allows one to make in a short amount of time many copies of a particular deoxyribonucleic acid (DNA) sequence. It was developed in 1985 by Kary Mullis and has provided scientists in diverse fields with a powerful tool for DNA amplification, analysis, and manipulation.

The technique involves repeated heating and cooling cycles and requires the DNA polymerase (known as *Taq*) from the organism *Thermus aquaticus*; these cycles are usually controlled by a machine known as a thermal cycler. Since high temperatures usually inactivate most **enzymes**, the DNA polymerase used in this procedure is isolated from a heat-tolerant bacterium.

The high temperature (90 to 92 degrees Celsius [194 to 197 degrees Fahrenheit]) disrupts the **hydrogen bonds** between the bases of DNA and results in the separation of the two DNA strands. Since all enzymes that duplicate DNA require short sequences known as **primers**, the priming sequences for the desired region are added and the temperature is then lowered. The primers anneal with sequences on each strand of the DNA, and *Taq* then uses added **nucleotides** to synthesize a new strand of DNA that is attached to the primers and **complementary** to each of the original strands.

The sample is then heated again to separate the strands and liberate the primer, and the sample is again cooled to allow another round of DNA duplication. Each round takes only a few minutes, and double the number of DNA strands each time. The process is repeated many more times with the

enzyme protein that controls a reaction in a cell

hydrogen bond weak bond between the H of one molecule or group and a nitrogen or oxygen of another

primer short nucleotide sequence that helps begin DNA replication

nucleotide the building block of RNA or DNA

complementary matching opposite

The polymerase chain reaction is a process that allows one to make many copies of a DNA sequence in a short amount of time.
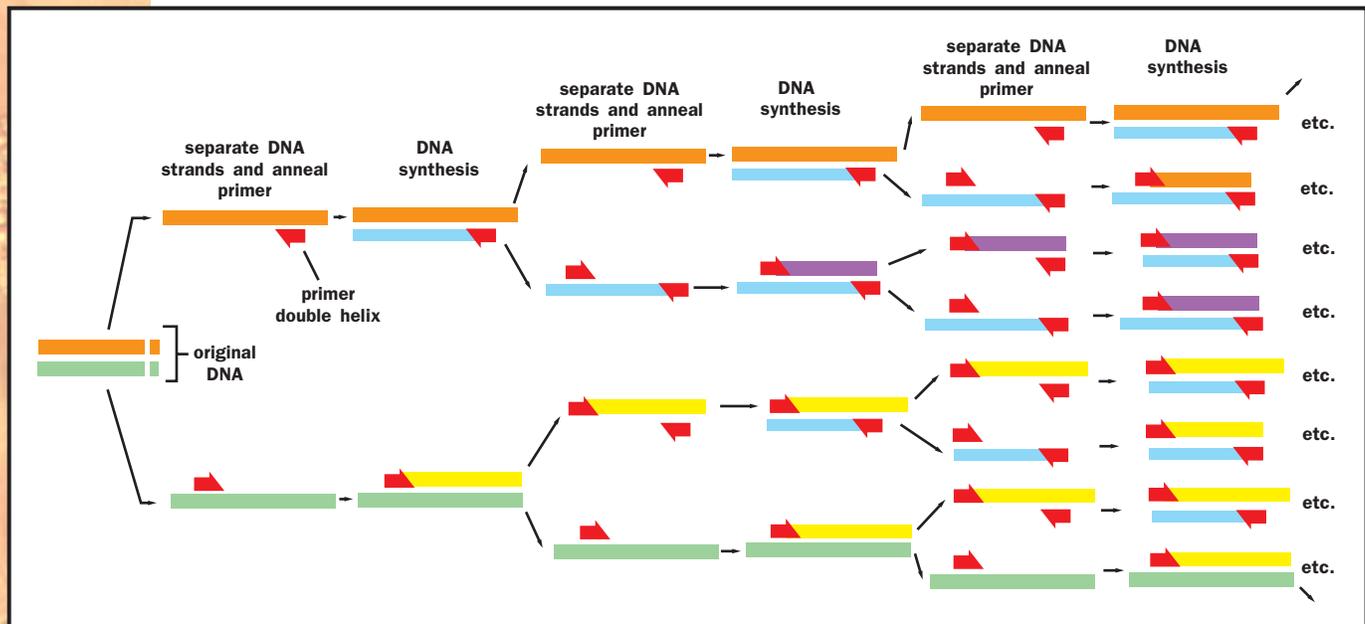
result that thousands, and even millions, of copies of a particular DNA sequence are produced within a few hours. The first two or three rounds of duplication produce DNA molecules of various lengths, but the final rounds produce identically sized molecules.

While early PCR techniques were limited to copying up to 1,000 **base pairs**, methods developed in the late 1990s have extended the limit up to 10,000 base pairs or more. The procedure will copy any DNA molecule and, consequently, the scientist must make certain that no extraneous DNA is present in the reaction tube.

PCR has allowed people to produce large amounts of DNA from a variety of sources: blood or semen from a crime scene; single embryonic cells for prenatal diagnosis; frozen ancient mammals; cells infected with viruses such as HIV (human immunodeficiency virus). SEE ALSO ARCHAEA; CLONE; DNA SEQUENCING; FORENSIC DNA ANALYSIS; REPLICATION

William R. Wellnitz

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

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Population Dynamics

A population is a collection of individual organisms of the same species that occupy some specific area. The term "population dynamics" refers to how the number of individuals in a population changes over time. Biologists study the factors that affect population dynamics because they are interested in topics such as conservation of endangered species (for example, the Florida panther) and management of fish and wildlife. In addition, basic knowledge about the processes that affect population dynamics can be used to predict future patterns of human population growth.

How Do Biologists Characterize Populations?

Biologists distinguish between two main types of populations: unstructured and structured. In an unstructured population, all individuals are subject to the same general ecological pressures. That is, the rates of growth, reproduction, and mortality are roughly the same for all individuals in the population. A bacterial colony is a good example of an unstructured population. Conversely, in structured populations, individuals can differ from one another in ways that make some individuals more susceptible to mortality or more likely to reproduce than others. Examples of structured populations include many insects, sea turtles, trees, and fish. In these cases, mortality is often much higher for younger (and/or smaller) individuals. In addition, reproduction is often delayed until individuals are older (and/or larger).

How Does Resource Abundance Affect Population Dynamics?

The abundance of environmental resources such as food, water, and space determines how population abundance changes over time. In the presence of unlimited resources, populations grow exponentially. If one plots the number of individuals in an exponentially growing population over time,

A. Exponential Growth

Number of individuals

Time

B. Logistic Growth

Number of individuals
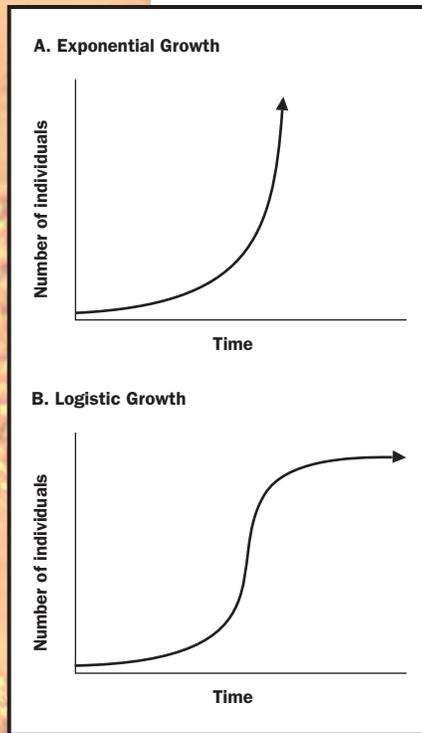
Time

The abundance of environmental resources determines the rate of population growth over time.

one finds a J-shaped curve where the slope gets ever steeper. This curve is described by the following equation:

$$N_t = N_0 e^{rt}$$

Where N_0 is the initial number of individuals, N_t is the number of individuals at a future time, r is the rate of increase, t is time, and e is the base of the natural logarithm (roughly 2.718). The rate of increase (r) is determined by the difference between birth and death rates of the population. In 1999 the U.S. Bureau of the Census estimated the rate of population increase (r) for the world human population to be 0.0129 (or 1.29 percent) per year. Few natural populations grow at exponential rates for extended periods of time because resources typically become limiting when population abundance is very high.

In an environment where resources become limited, populations exhibit a pattern of growth called logistic growth. In this case, if one plots the number of individuals in the population over time, one finds a sigmoidal, or S-shaped curve. When population abundance is low, the population grows exponentially. However, as population size increases, resources become limited, the population growth rate slows, and the population abundance curve flattens. The number of individuals present in the population when the growth rate slows to zero is referred to as K, the carrying capacity. The carrying capacity is the theoretical maximum number of individuals that the environment can support. Although estimates of K for humans are controversial, most are around 12 billion.

Using concepts from basic population biology, biologists have distinguished two strategies for population growth. Some species have characteristics that allow them to grow rapidly when an environment with abundant resources is newly created (for example, a new clearing in a forest). These species are referred to as r-selected species and typically reproduce at a young age and produce many offspring. Other species, called K-selected species, have characteristics that make them well suited for life in environments where there is intense competition for limited resources. These species are often strong competitors, reproduce later in life, and produce fewer offspring than r-selected species.

How Does Variability in Environmental Conditions Affect Population Dynamics?

A key assumption of the logistic population growth model for environments where resources are limiting is that environmental conditions are constant. In nature, environmental conditions may vary substantially over time. In such variable environments, the abundance of individuals in a population may also fluctuate over time. Some populations cycle in a predictable manner. Populations that fluctuate widely or have low abundance are especially vulnerable to extinction, an event in which population abundance declines to zero. Extinctions may be local (a population in a particular area is lost) or global (all populations of a species decline to zero and there are no living individuals of the species left on the planet). For example, the passenger pigeon, which was once one of the most numerous birds on Earth, went globally extinct in 1914 due to overhunting and habitat loss.

How Do Physical and Biological Factors Regulate Population Dynamics?

Patterns of population abundance are affected by a variety of biological and physical factors. For example, the abundance of a given species (for example, snails) might be controlled by the abundance of organisms that have a negative effect on the species of interest, such as competitors, predators, and diseases. Similarly, population abundance could be limited by the abundance of organisms that benefit the species of interest (for example, algae consumed by the snails).

In fact, some organisms require the presence of other species called **symbionts** with whom they live in direct contact. For example, corals use food molecules synthesized by symbiotic zooxanthellae (a type of algae), and zooxanthellae receive nutrients and protection from corals. However, not all populations are regulated by biological factors involving interactions with other species. Physical factors like water availability and temperature can control population abundance of some species.

Which type of factor (biological or physical) has a stronger effect on population dynamics? As one might suspect, the answer depends largely on the population that is studied. Some populations are regulated mostly by biological factors, others are controlled by physical factors, and most populations are affected by both biological and physical factors. SEE ALSO ALGAE; CORAL REEF; EXTINCTION; HUMAN POPULATION; THEORETICAL ECOLOGY

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symbionts organisms living in close association with another organism

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Population Genetics

The field of population genetics examines the amount of genetic variation within populations and the processes that influence this variation. A population is defined as a group of interbreeding individuals that exist together at the same time. Genetic variation refers to the degree of difference found among individuals, for instance in height, coat color, or other less observable traits. The particular set of genes carried by an individual is known as his or her genotype, while all the genes in a population together comprise the "gene pool."

Foundations

The foundation for population genetics was laid in 1908, when Godfrey Hardy and Wilhelm Weinberg independently published what is now known as the Hardy-Weinberg equilibrium. The "equilibrium" is a simple prediction of genotype frequencies in any given generation, and the observation that the genotype frequencies are expected to remain constant from

generation to generation as long as several simple assumptions are met. This description of stasis provides a counterpoint to studies of how populations change over time.

The 1920s and 1930s witnessed the real development of population genetics, with important contributions by Ronald Fisher, Sewall Wright, and John B. S. Haldane. They, with many others, clearly established the basic processes which caused populations to change over time: selection, genetic drift, migration, and mutation. The change in the genetic makeup of a population over time, usually measured in terms of **allele** frequencies, is equivalent to evolutionary change. For this reason, population genetics provides the groundwork for scientists' understanding of evolution, in particular microevolution, or changes within one or several populations over a limited time span.

The questions addressed by population genetics are quite varied, but many fall within several broad categories. How much genetic variation is found in populations, and what processes govern this? How will a population change over time, and can a stable endpoint be determined? How much and why do populations of the same species differ? The answer is always cast in terms of selection, drift, mutation, migration, and the complex interplay among them. Of the four, selection and genetic drift are usually given credit as the major forces.

allele a particular form of a gene

Selection

Simply put, selection occurs when some genotypes in the population are on average more successful in reproduction. These genotypes may survive better, produce more offspring, or be more successful in attracting mates; the alleles responsible for these traits are then passed on to offspring. There is broad theoretical consensus and abundant empirical data to suggest that selection can change populations radically and quickly. If one genetic variant, or allele, increases survivorship or fertility, selection will increase the frequency of the favored allele, and concurrently eliminate other alleles. This type of selection, called directional selection, decreases the amount of genetic variation in populations.

Alternatively, an individual carrying two different alleles for the same gene (a heterozygote) may have advantages, as exemplified by the well-known example of the sickle-cell allele in Africa, in which heterozygotes are more resistant to malaria. In this case, called overdominant selection, genetic variation is preserved in the population. Although a number of similar examples are known, directional selection is much more common than overdominant selection; this implies that the common action of selection is to decrease genetic variation within populations. It is equally clear that if different (initally similar) populations occupy different habitats, selection can create differences among populations by favoring different alleles in different areas.

Genetic Drift

Often overlooked by the layperson, genetic drift is given a place of importance in population genetics. While some analyses of genetic drift quickly become complicated, the basic process of drift is simple and involves random

Cheetahs, which have very little genetic variation, are presumed to have gone through several genetic bottlenecks.
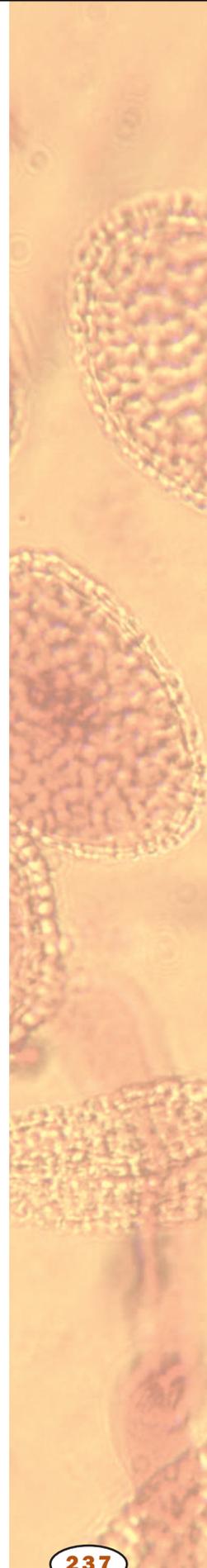
changes in allele frequency. In sexual species, the frequency of alleles contained in the **progeny** may not perfectly match the frequency of the alleles contained in the parents. As an analogy, consider flipping a coin twenty times. Although one might expect ten heads and ten tails, the actual outcome may be slightly different; in this example, the outcome (progeny) does not perfectly represent the relative frequency of heads and tails (the parents).

progeny offspring

What does this mean for populations? Start by considering neutral alleles, which have no impact on survival or reproduction. (An example is the presence or absence of a widow's peak hairline.) The frequency of a neutral allele may shift slightly between generations, sometimes increasing and sometimes decreasing. What outcomes are expected from this process? Suppose that a particular allele shifts frequency at random for a number of generations, eventually becoming very rare, with perhaps only one copy in the population. If the individual carrying this allele does not pass it on to any offspring or fails to have any offspring, the allele will be lost to the population. Once lost, the allele is gone from the population forever. In this light, drift causes the loss of genetic variation over time. All populations are subject to this process, with smaller populations more strongly affected than larger ones.

Perhaps better known than the pervasive, general effects of genetic drift are special examples of drift associated with unusually small populations. Genetic bottlenecks occur when a small number of individuals from a much larger population are the sole contributors to future generations; this

HALDANE, J. B. S. (1862–1964)

British biologist and author who immigrated to India. Haldane was famous for both his flamboyant personality and his influence on genetics and evolutionary biology. Haldane, along with Ronald Fisher, showed that evolution is the change in frequency of individual genes over time.

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

occurs when a catastrophe kills most of the population, or when a few individuals start a new population in different area. Genetic bottlenecks reduce the genetic variation in the new or subsequent population relative to the old. Cheetahs, which have very little genetic variation, are presumed to have gone through several genetic bottlenecks. Occasionally, these new populations may have particular alleles that are much more common than in the original population, by chance alone. This is usually called the founder effect.

Migration and Mutation

Migration may also be important in shaping the genetic variation within populations and the differences among them. To geneticists, the word "migration" is synonymous with the term "gene flow." Immigration may change allele frequencies within a population if the immigrants differ genetically. The general effect of gene flow among populations is to make all of the populations of a species more similar. It can also restore alleles lost through genetic drift, or introduce new alleles formed by mutation in another population. Migration is often seen as the "glue" that binds the subpopulation of a species together. Emigration is not expected to change populations unless the migrants are genetically different from those that remain; this is rarely observed, so emigration is often ignored.

The last important process is mutation. Mutation is now understood in great detail at the molecular level, and consists of any change in the deoxyribonucleic acid (DNA) sequence of an organism. These mutations range from single base substitutions to the deletion or addition of tens or hundreds of bases to the duplication or reorganization of entire **chromosomes**. Mutation is most important as the sole source of all new genetic variation, which can then be spread from the population of origin by migration. This importance should not be undervalued, although the impact of mutation on most populations is negligible at any given time. This is because mutation rates are typically very low.

Questions and Contributions

The real challenge of population genetics has been in understanding how the four processes work together to produce the observable patterns. For instance, genetic drift eliminates variation from populations, as do the most common modes of natural selection. How then can the abundance of genetic variation in the world be explained?

This question has many complicated answers, but some cases, such as the observation of deleterious alleles in humans (for example, alleles for phenylketonuria, a genetic disease), might be explained in terms of mutation and selection. Mutation adds these alleles to a population, and selection removes them; although the rate of mutation is likely to be nearly constant, the rate at which selection removes them increases as the abundance of the allele increases. This is certainly true for recessive alleles, which are only expressed when an individual has two copies. With only one, the allele remains unexpressed and therefore not selected. At some point, predictable from the mutation rate and physical consequences of the disease, the two opposing forces balance, producing the stable persistence of the disease allele at low frequency.

As a discipline, population genetics has contributed greatly to scientists' understanding of many disparate topics, including the development of resistance of insects to insecticides and of **pathogenic** bacteria to antibiotics, an explanation of human genetic variation like the alleles for sickle-cell **anemia** and blood groups, the evolutionary relationships among species, and many others. Of particular interest is the use of genetic data in conservation biology.

By definition, endangered and threatened species have reduced population sizes, making them subject to the vagaries of genetic drift and also to inbreeding. Inbreeding is mating between genetically related individuals, and often leads to inbreeding depression, a reduction of health, vigor, and fertility. Genetic drift leads to a loss of genetic variation, which limits what selection can do to produce adaptations if the environment changes. Keeping these two issues in mind, greatly reduced populations may be at increasingly greater risk for genetic reasons, leading to further declines. SEE ALSO CONSERVATION; ENDANGERED SPECIES; EVOLUTION; EXTINCTION; HARDY-WEINBERG EQUILIBRIUM; NATURAL SELECTION; SEXUAL REPRODUCTION

Paul R. Cabe

pathogen disease-causing organism

anemia lack of oxygen-carrying capacity in the blood

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Porifera

Porifera, or sponges, are the simplest and oldest of the multicelled animals, with fossils dating back to **Precambrian** times. They are aquatic and **sessile**, living permanently attached to submerged objects. More than 5,000 species are known, most of which occur in shallow coastal waters and in the deep sea. About 150 species live in fresh water. Sponges are found at all latitudes, even in polar regions.

Sponges are unique among animals because they lack a brain, nerves, muscles, organs, and specialized tissues. They rely upon highly specialized, but poorly coordinated cells. As the name Porifera ("pore bearers") suggests, the body is perforated. Numerous small pores (ostia) convey water into an internal canal system lined with flagellated collar cells (choanocytes). The flagella of these cells beat **synchronously** to produce currents that pump water through the sponge. Choanocytes filter water through their sievelike collars to remove suspended food particles (bacteria, protozoans, microscopic algae, **organic** particles). The particles are digested by wandering **amoeboid** cells (amoebocytes), which carry nutrients to various parts of the sponge. Filtered water and waste products are expelled through large vents (oscula).

Precambrian before the Cambrian era; before 600 million years ago

sessile attached and remaining in one place

synchronously at the same time

organic composed of carbon, or derived from living organisms

amoeboid like an amoeba, especially in movement via extension of portions of the membrane
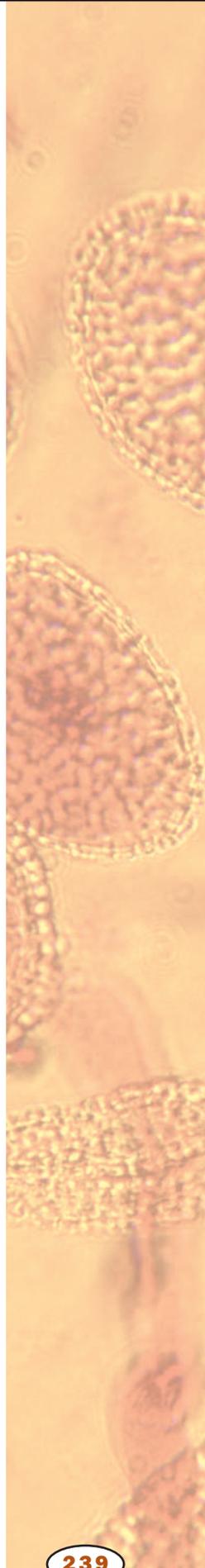
protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

zygote fertilized egg

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

substrate the molecule acted on by an enzyme

The skeleton supporting these canals and chambers is composed of needlelike spicules and/or elastic **protein** fibers (spongin). The spicules are made of silica or calcium carbonate and occur in various shapes and sizes characteristic of each species.

Sponges can reproduce both sexually and asexually. Clouds of sperm expelled into the water by one sponge are drawn into other sponges with water currents. Specialized cells (modified choanocytes) carry sperm to the eggs. **Zygotes** develop into **ciliated** larvae that are released into the water, where they are planktonic for a short period before settling onto a suitable **substrate** to become adult sponges. Asexual reproduction occurs by fragmentation and/or budding; for example, freshwater sponges use resistant buds (gemmules) for surviving winter or periods of drought. SEE ALSO ANIMALIA; CORAL REEF

Anthony Ricciardi

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Porter, Keith

Canadian cytologist
1912–1997

In 1945 Keith Porter, with Albert Claude and Ernest F. Fullam, published the first electron micrograph of a complete cell in the *Journal of Experimental Medicine*. The photograph gave a new vigor to the study of cells that had been "becalmed in the doldrums" (Willmer 1965, p. 8). Biologists began to study subcellular components using centrifugation, tissue culture, and electron microscopy techniques devised by Porter, Claude, and George Palade. These techniques led to the integration of cell structure and function and the modern science of cell biology.

Porter was born in Yarmouth, Nova Scotia, in 1912. In 1939 he joined the laboratory of cancer researcher James B. Murphy at The Rockefeller Institute (now University) to study cultured cells. However, conventional light microscopy was inadequate, and he began his mastery of the newly available electron microscope to examine fine cell structure. This demanded radical changes in specimen preparation. The cells had to be ultra thin and dry.

endoplasmic reticulum network of membranes within the cell

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

Porter was the first to identify the cell's **endoplasmic reticulum**, **cilia**, microtubules, and the microtrabecular lattice. To produce superior electron micrographs he devised methods of tissue culture and standards for cell preparation, founded the Tissue Culture Association, and designed the Porter-Blum microtome. He died in 1997. SEE ALSO CELL; ELECTRON MICROSCOPY

Carol L. Moberg

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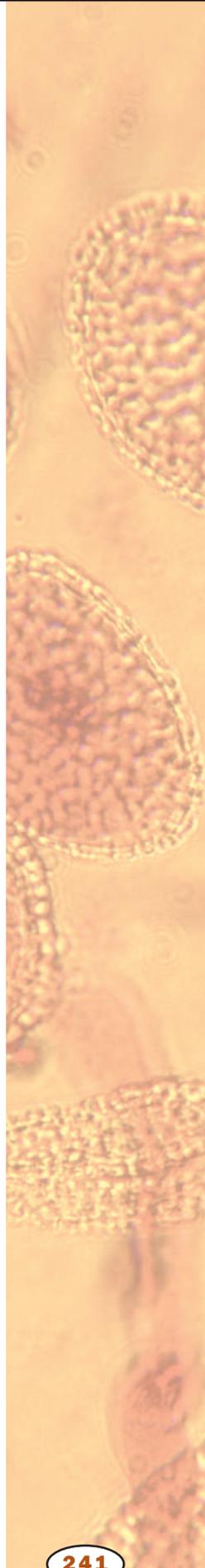
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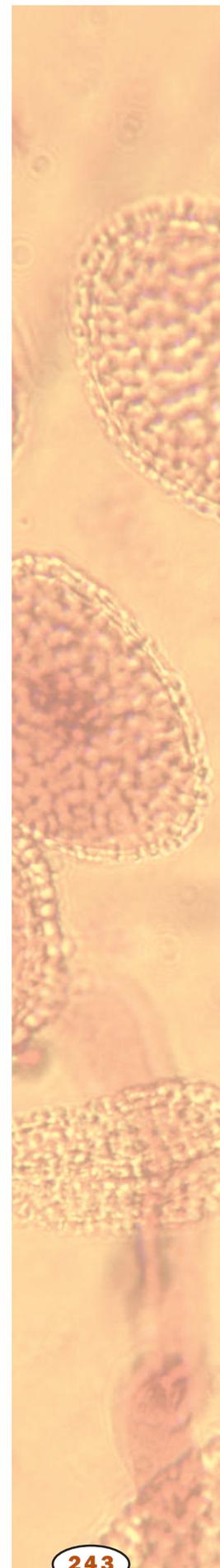
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AP/Wide World Photos; **p. 188** T4 bacteriophage virus, colored transmission electron micrograph. © Department of Microbiology, Biozentrum/Science Photo Library/Photo Researchers, Inc.; **p. 189** Compound eye of a fruit fly, scanning electron micrograph, SEM. © Dr. Dennis Kunkel; **p. 194** Drop of guttation, water extruded by a plant's root pressure, on a blade of grass. Alpine Lakes Wilderness Area, Washington, photograph. © Pat O'Hara/Corbis; **p. 196** Watson, Dr. James Dewey, with DNA model, 1962, photograph. UPI/Corbis-Bettmann; **p. 198** Dead tree trunks, stumps in deep blue water, golden leaves, photograph by Robert J. Huffman/Field Mark Publications; **p. 199** Biologists take samples from drugged polar bears for data about pesticides, photograph. © Galen Rowell/Corbis; **p. 201** Man walks across giant rollers used to crush wood pulp at the Ketchikan Pulp Company, photograph. © Kevin Fleming/Corbis; **p. 205** Zoo veterinarian Don Janssen examining the San Diego Zoo's 2-week old giant panda cub, photograph. AP/Wide World Photos.

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
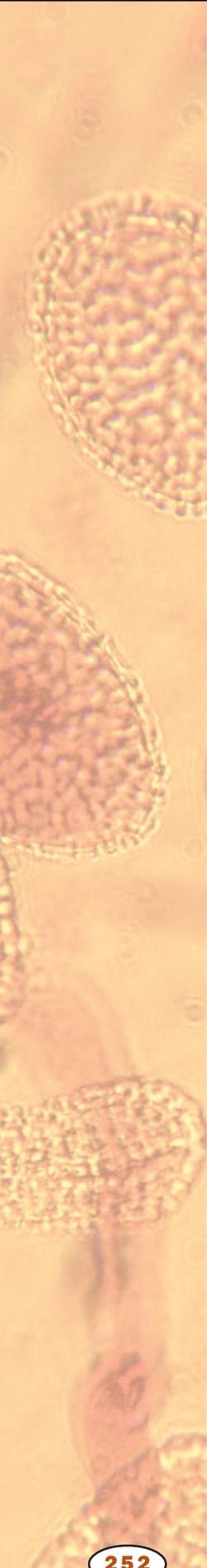
amoeboid like an amoeba, especially in movement via extension of portions of the membrane

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
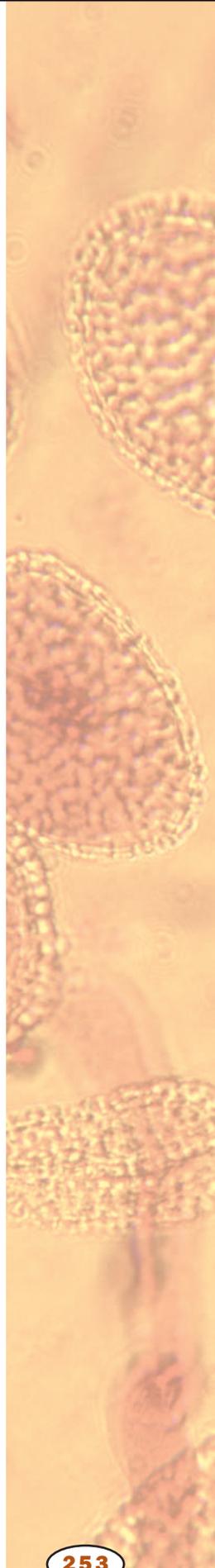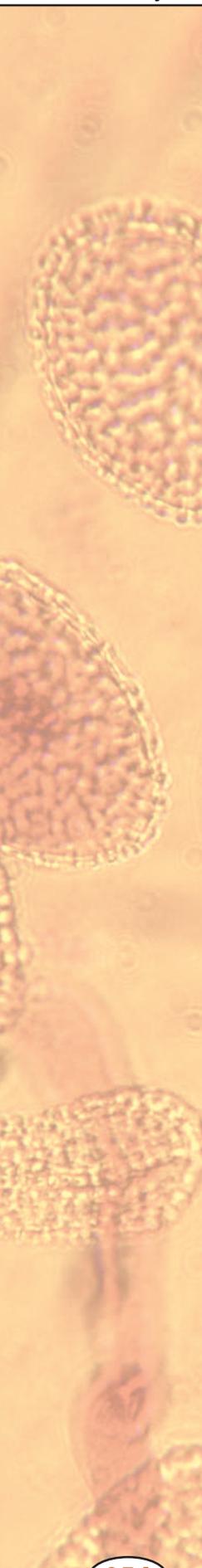
catalyze aid in the reaction of

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
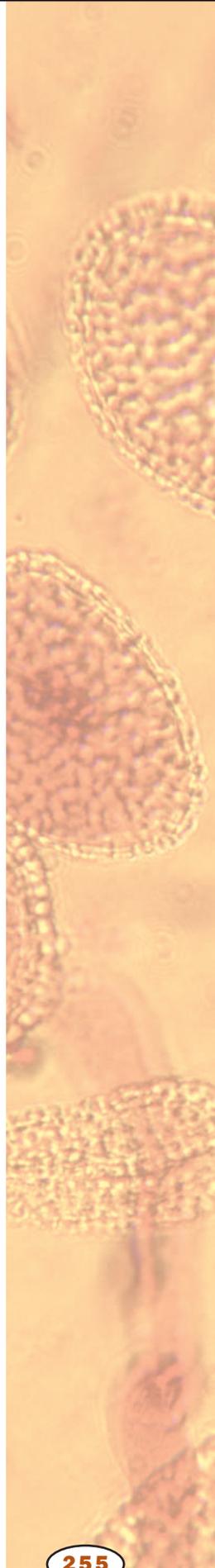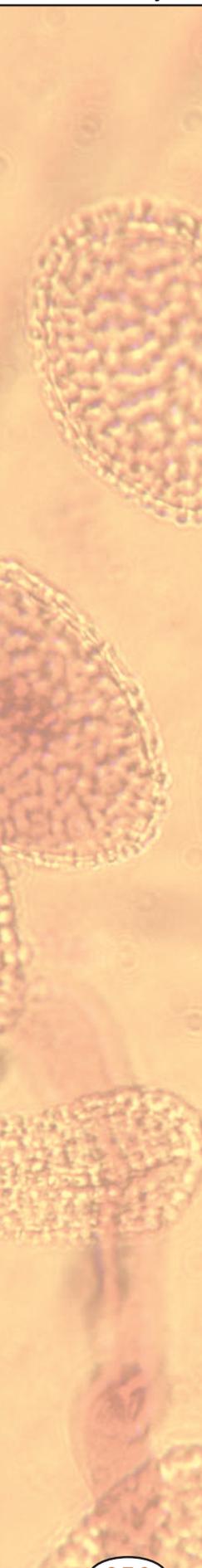
dimerizes forms a pair

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
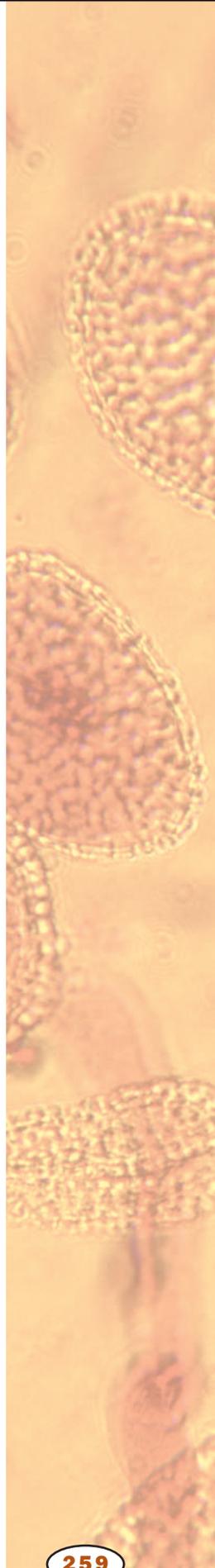
inducible able to be switched on

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
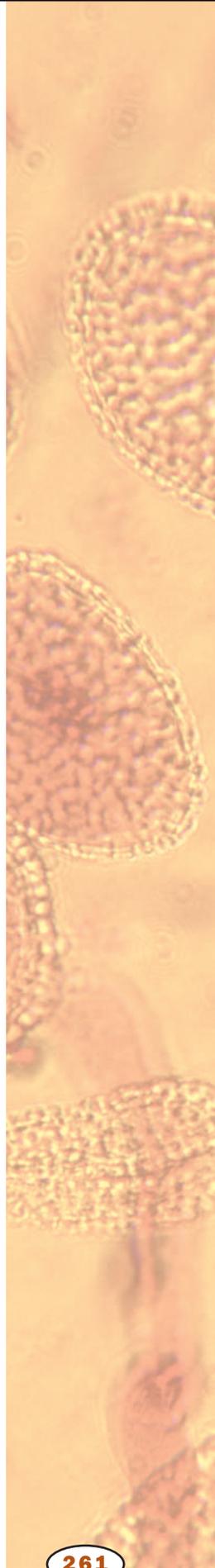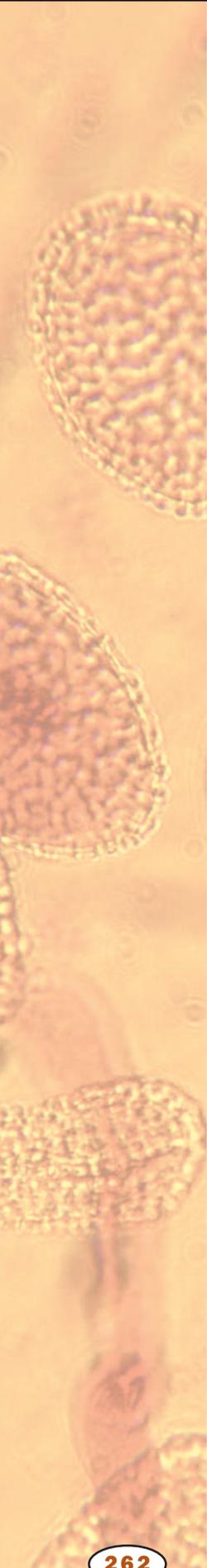
middle lamella layer of material between two plant cells that holds them together

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
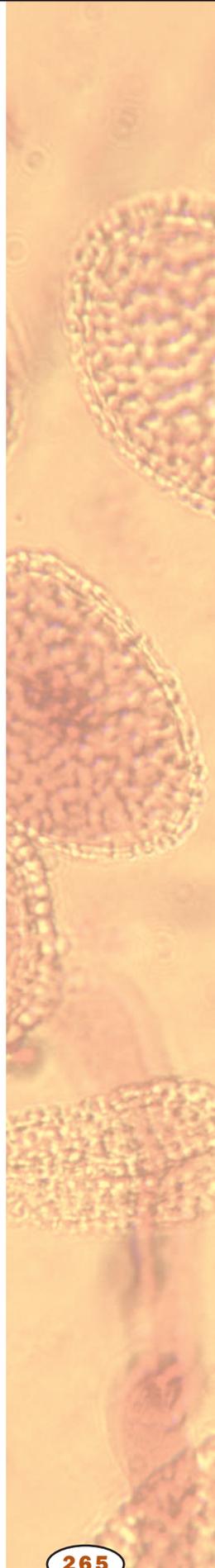
primer short nucleotide sequence that helps begin DNA replication

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
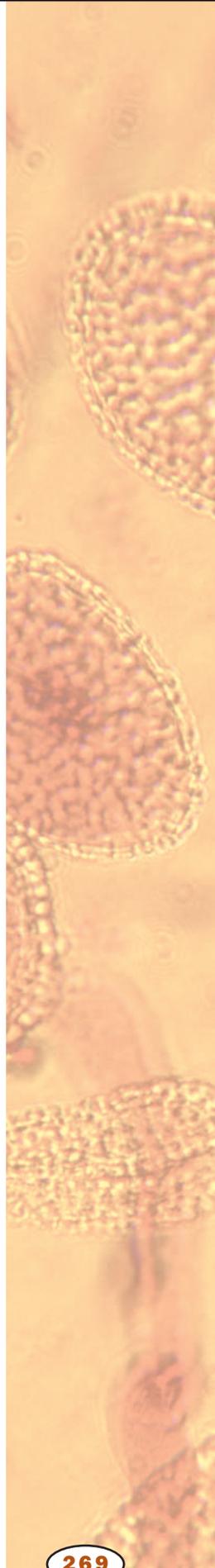
Topic Outline

AGRICULTURE AND ECONOMIC BOTANY

Agriculture
Agronomist
Beer-making, Botany of
Coffee, Botany of
Desertification
Ethnobotany
Forester
Grain
Grasses
History of Agriculture
Horticulturist
Hybridization-Plant
Landscape Ecology
Nitrogen Cycle
Nitrogen Fixation
Organic Agriculture
Plant Pathogens and Pests
Pollution and Bioremediation
Soil
Vavilov, Nikolay
Wine-making, Botany of

ANIMAL ANATOMY AND PHYSIOLOGY

Amniote egg
Animalia
Circulatory Systems
Connective Tissue
Digestion
Epithelium
Excretory Systems
Gas Exchange
Growth
Life Cycles
Locomotion
Model Organisms in Physiology and Medicine
Muscle
Nervous Systems
Neuron
Organ

Osmoregulation
Physiological Ecology
Respiration
Scaling
Sex Determination
Skeletons
Social Behavior
Temperature Regulation
Vision
Zoology

ANIMAL BEHAVIOR

Behavior, Genetic Basis of
Behavior Patterns
Feeding Strategies
Field Studies in Animal Behavior
Migration and Animal Navigation
Mimicry, Camouflage, and Warning Coloration
Pheromone
Physiological Ecology
Population Dynamics
Predation and Defense
Sexual Selection
Symbiosis
Temperature Regulation
Wildlife Biologist

ANIMAL DIVERSITY

Amphibian
Animalia
Annelid
Arachnid
Arthropod
Biodiversity
Bird
Bony Fish
Cambrian Explosion
Cartilaginous Fish
Chordata
Cnidarian

Coral Reef
Crocodilian
Crustacean
Echinoderm
Endangered Species
Entomologist
Extinction, Mammals
Human Evolution
Insect
Mammal
Marsupial
Mollusk
Monotreme
Nematode
Parasitic Diseases
Platyhelminthes
Porifera
Primate
Reptile
Tuatara
Tunicate
Turtle
Zoology
Zoology Researcher

AQUATIC BIOLOGY

Algae
Amphibian
Bony Fish
Cartilaginous Fish
Cnidarian
Coral Reef
Crustacean
Echinoderm
Estuaries
Extreme Communities
Lakes and Ponds
Limnologist
Marine Biologist
Mollusk
Ocean Ecosystems: Hard Bottoms
Ocean Ecosystems: Open Ocean
Ocean Ecosystems: Soft Bottoms
Platyhelminthes
Porifera
Rivers and Streams
Water

BACTERIA AND ARCHAEA

Archaea
Bacterial Cell
Bacterial Diseases
Bacterial Genetics
Bacterial Viruses

Biotechnology
Cell Evolution
Cell Wall
Chloroplast
Clone
Control of Gene Expression
Cyanobacteria
Dubos, René
Ecosystem
Eubacteria
Microbiologist
Mitochondrion
Model Organisms: Cell Biology and Genetics
Plant Pathogens and Pests
Poisons
Recombinant DNA
Sexually Transmitted Diseases
Transgenic Techniques

BEHAVIOR

Behavior, Genetic Basis of
Behavior Patterns
Brain
Competition
Feeding Strategies
Field Studies in Animal Behavior
Flight
Learning
Locomotion
Migration and Animal Navigation
Mimicry, Camouflage, and Warning Coloration
Pheromone
Predation and Defense
Sexual Reproduction
Sexual Selection
Sleep
Social Behavior
Sociobiology

BIOCHEMISTRY

Amino Acid
Antibodies in Research
Biochemist
Biogeochemical Cycles
Carbohydrates
Carbon Cycle
DNA
DNA Sequencing
Drug Testing
Electrophoresis
Enzymes
Glycolysis and Fermentation
History of Biology: Biochemistry
Krebs Cycle

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

Replication
Retrovirus
Reverse Transcriptase
Transgenic Techniques
Transposon
Virus
Watson, James

HISTORY OF BIOLOGY

Buffon, Count (Georges-Louis Leclerc)
Carson, Rachel
Crick, Francis
Darwin, Charles
De Saussure, Nicolas
Dubos, René
Ecology, History of
Gray, Asa
Harvey, William
History of Agriculture
History of Biology: Biochemistry
History of Biology: Cell Theory and Cell
    Structure
History of Biology: Inheritance
History of Evolutionary Thought
History of Medicine
History of Plant Physiology
Ingenhousz, Jan
Lamarck, Jean-Baptiste
Leakey Family
Leeuwenhoek, Anton
Linnaeus, Carolus
McClintock, Barbara
Mendel, Gregor
Pasteur, Louis
Pauling, Linus
Porter, Keith
Taxonomy, History of
Torrey, John
Van Helmont, J. B.
Vavilov, Nikolay
Vesalius, Andreas
Von Humboldt, Alexander
Watson, James

IMMUNE SYSTEM

AIDS
Antibodies in Research
Antibody
Autoimmune Disease
Immune Response
Lymphatic System
Nonspecific Defense
Stress Response
T Cells

Transplant Medicine
Vaccines

INHERITANCE

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
Radiation Hybrid Mapping
Replication
Transgenic Techniques

INTERACTIONS, POPULATIONS, AND COMMUNITIES

Behavior Patterns
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