biology

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VOLUME 1
A–D

Richard Robinson, Editor in Chief

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Preface

The scope of biology is so vast it can be dizzying. Upwards of 50 million species of living things exist on Earth. Within each species, the number of creatures can range from the alarming (only a handful of Yangtze River dolphins exist), to the worrisome (our own species numbers six billion and counting), to the astonishing (five hundred quadrillion individual wheat plants emerge and die every year). But numbers alone can't tell the tale, because life at every level is a process and a pattern, from the development of a single creature to the evolution of a whole species, and from the expression of a single gene to the nutrient cycling of an entire ecosystem. The human body contains about fifty trillion cells, every one of which draws on its store of thirty thousand genes to make the pattern of proteins that control it and make it unique. Within the human brain, one hundred billion neurons make one hundred trillion connections, which combine to make the pattern of thoughts, memories, and feelings that make each of us unique.

Central Ideas and Vital Details

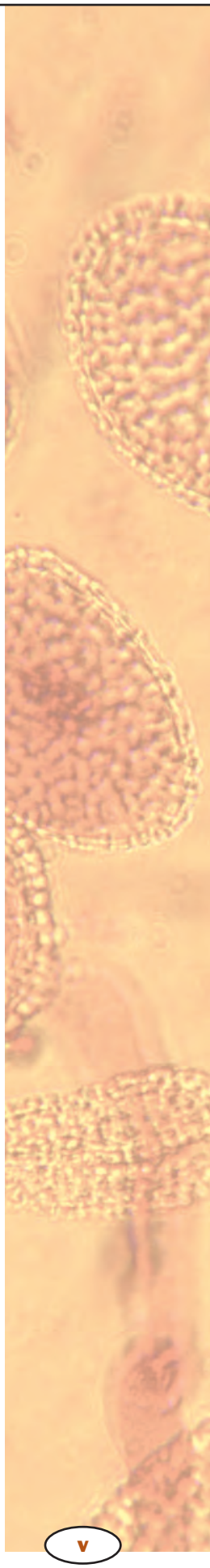
How can a single book, or even a four-volume encyclopedia, encompass so vast a subject? It can't. And in producing *Biology*, we didn't try to cover every topic from Aardvark to Zyzzyva. Instead, in our 432 entries we present as broad an introduction as possible to the many facets of biology, while concentrating in depth on a smaller number of central ideas and phenomena that are at the heart of all biological processes.

One of our major themes is molecular genetics, which in the last two decades has taken center stage in biology, along with its offspring, biotechnology. In these volumes, students will find detailed and accessible descriptions of the many aspects of these growing disciplines, from genes and chromosomes to cloning and the Human Genome Project. Genes exert their effects through proteins in cells, and we discuss both individual cell processes and the rapidly growing understanding of control mechanisms. Throughout, our emphasis is on clear explanation of the underlying principles, so that students can prepare to understand phenomena that may yet remain undiscovered.

✶**Explore further in DNA, Nucleus, and Clone**

Understanding of human physiology is central to medicine and health, and in *Biology*, we discuss almost every aspect of the human system, including bones, brains, and behavior. We devote special attention to several health issues especially important to students, including smoking, alcohol, and sexually transmitted diseases. Comparative animal physiology and plant physiology are also featured.

✶**Explore further in Development, Immune Response, and Smoking and Health**



✶Explore further in Eubacteria, Conifers, and Conservation

The world's biodiversity is being revealed even as it is increasingly threatened, and we survey both of these crucial aspects within our pages. Animal and plant diversity is discussed in many separate entries, and major entries are provided on archaea, eubacteria, fungi, and protists. Up-to-date classification systems are used throughout. We examine the major environmental challenges facing the world today, including global climate change, extinction, desertification, and the growing human population.

✶Explore further in Grasslands, Population Dynamics, and Sexual Selection

"The ecological theater and the evolutionary play" was how one notable biologist described the vital connection between these two major areas in biology. This interplay is explored in entries that range from physiological ecology to human evolution, and in environments from the Arctic tundra to the depths of the oceans. Finally, we examine the history of biology through major entries and capsule biographies, and we look at careers in biology at every level in every field.

Organization of the Material

To aid students and teachers in exploring this vast territory, *Biology* includes individual volume indexes as well as a cumulative index at the end of Volume 4. We also provide a glossary of more than 550 terms with definitions both in the page margin and collected at the end of each volume. Each entry contains suggestions for further reading. A topical index provides a guide to entries by subject, and useful references are provided as frontmatter, including a geologic time scale and tables of metric conversions.

Acknowledgments and Thanks

A work of this scope would be impossible without the dedication and hard work of many people. Our contributors are biologists who have devoted their careers to understanding the living world, and have now devoted many hours to explaining it carefully and clearly enough for a beginning audience. Hélène Potter of Macmillan Library Reference charted a challenging and inspiring course in launching this encyclopedia, and Linda Hubbard, Michelle Harper, Diane Sawinski, and Christine Slovey of the Gale Group provided a sure hand on the tiller during rough weather. Ricki Lewis offered invaluable editorial review when it mattered most.

The editorial advisors for this project have given their time and expertise unstintingly, often far beyond the call of duty. As will be clear from the list of authors, several of them are also gifted and generous authors. They have my deep gratitude for all their work on this encyclopedia. Sadly, Tom Frost, an aquatic ecologist of national stature, did not live to see the completion of this work. His loss was a blow to this project, and even more so to the world of ecology. But he has left his mark on *Biology*, and we dedicate this work to him.

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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

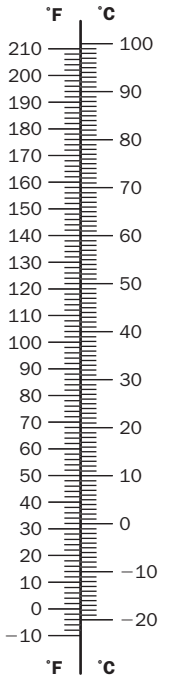
Definitions

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

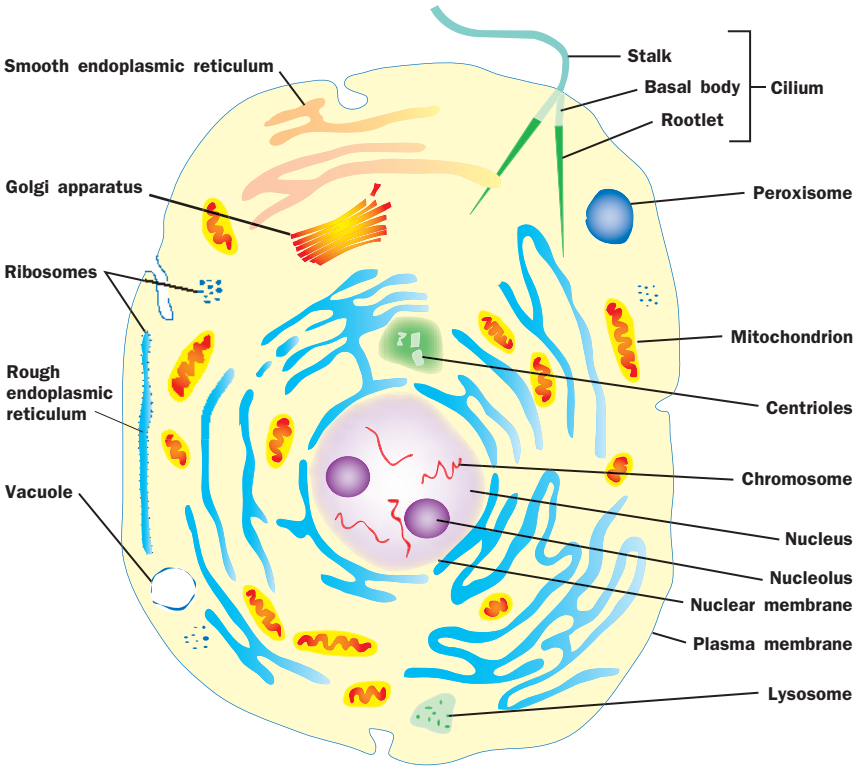


100°C = water boils
0°C = water freezes

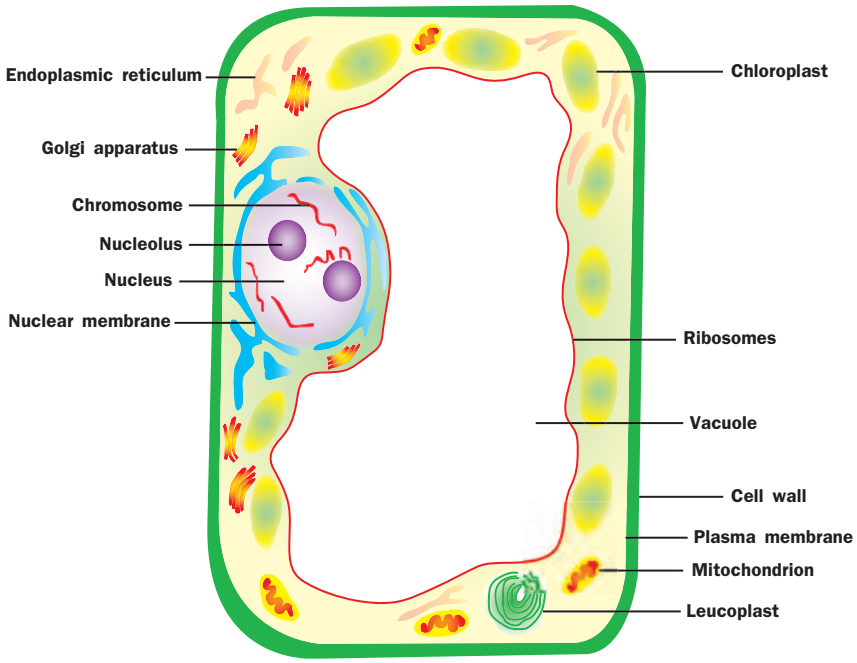
GEOLOGIC TIMESCALE

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

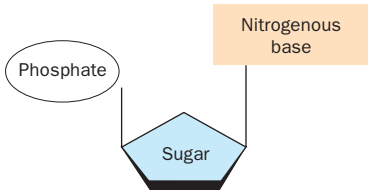


A TYPICAL PLANT CELL



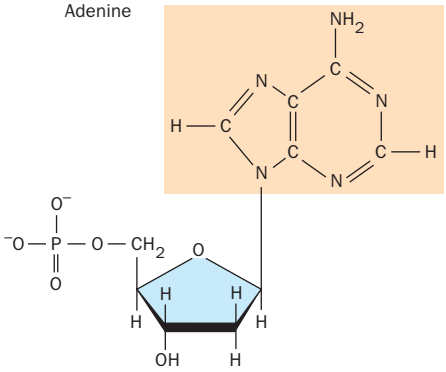
STRUCTURE OF DNA NUCLEOTIDES

Components of a nucleotide

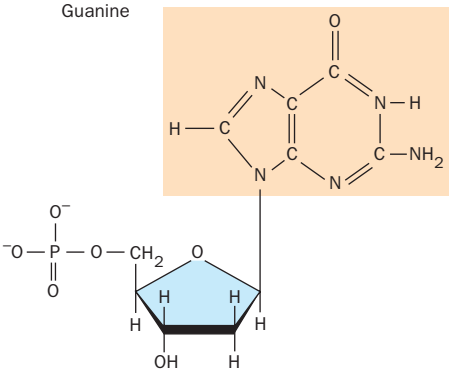


Purine-containing nucleotides

Adenine

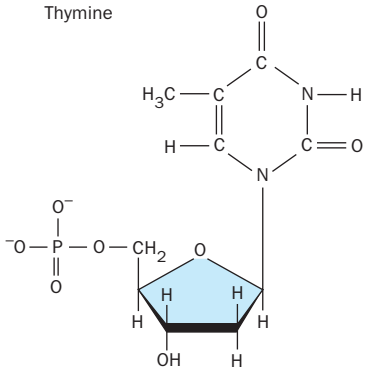


Guanine

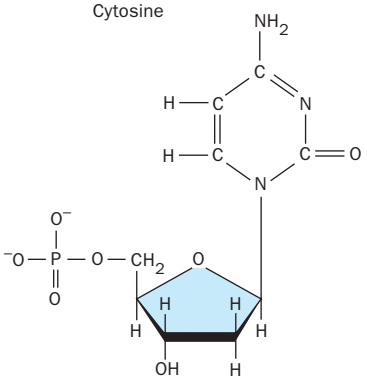


Pyrimidine-containing nucleotides

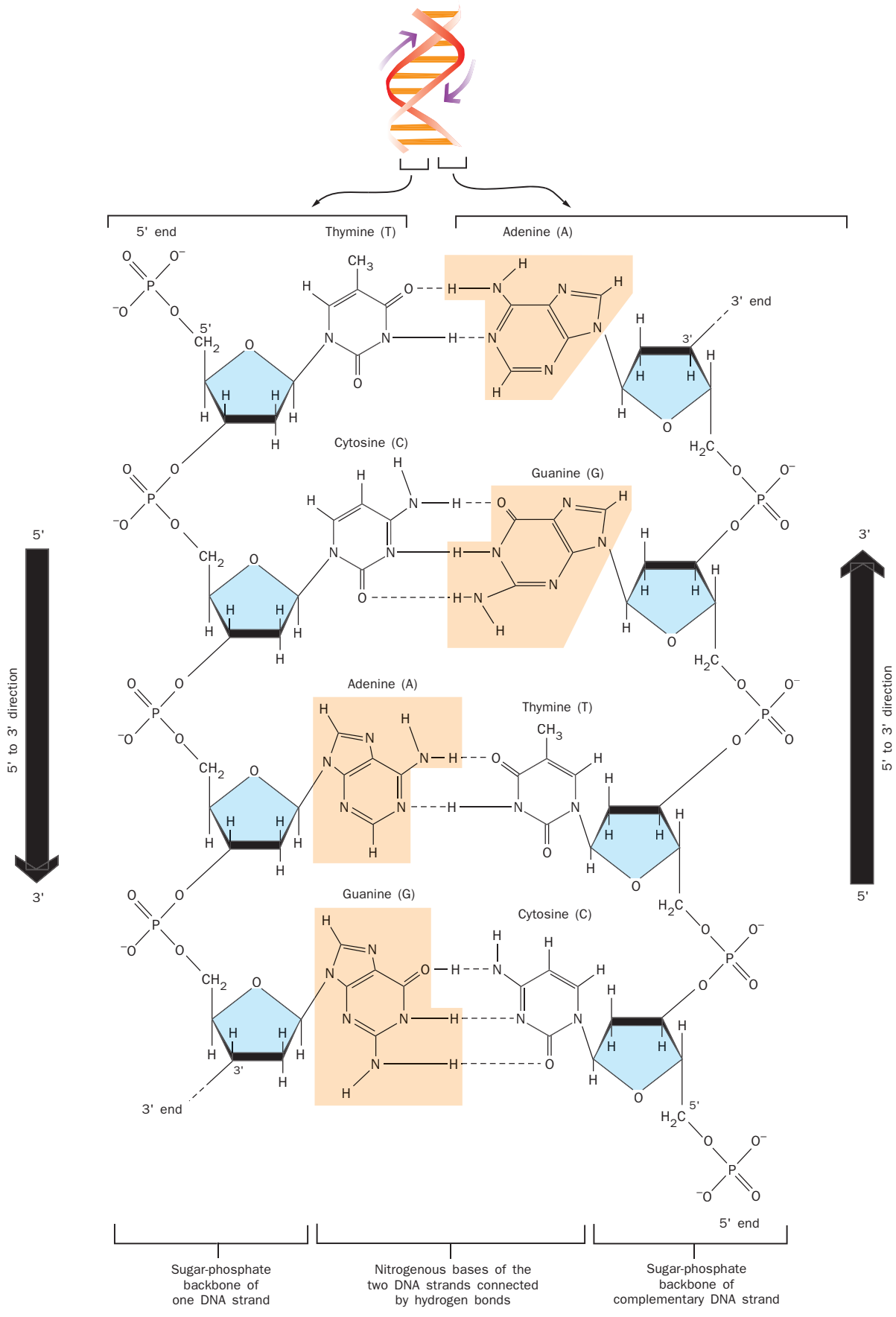
Thymine



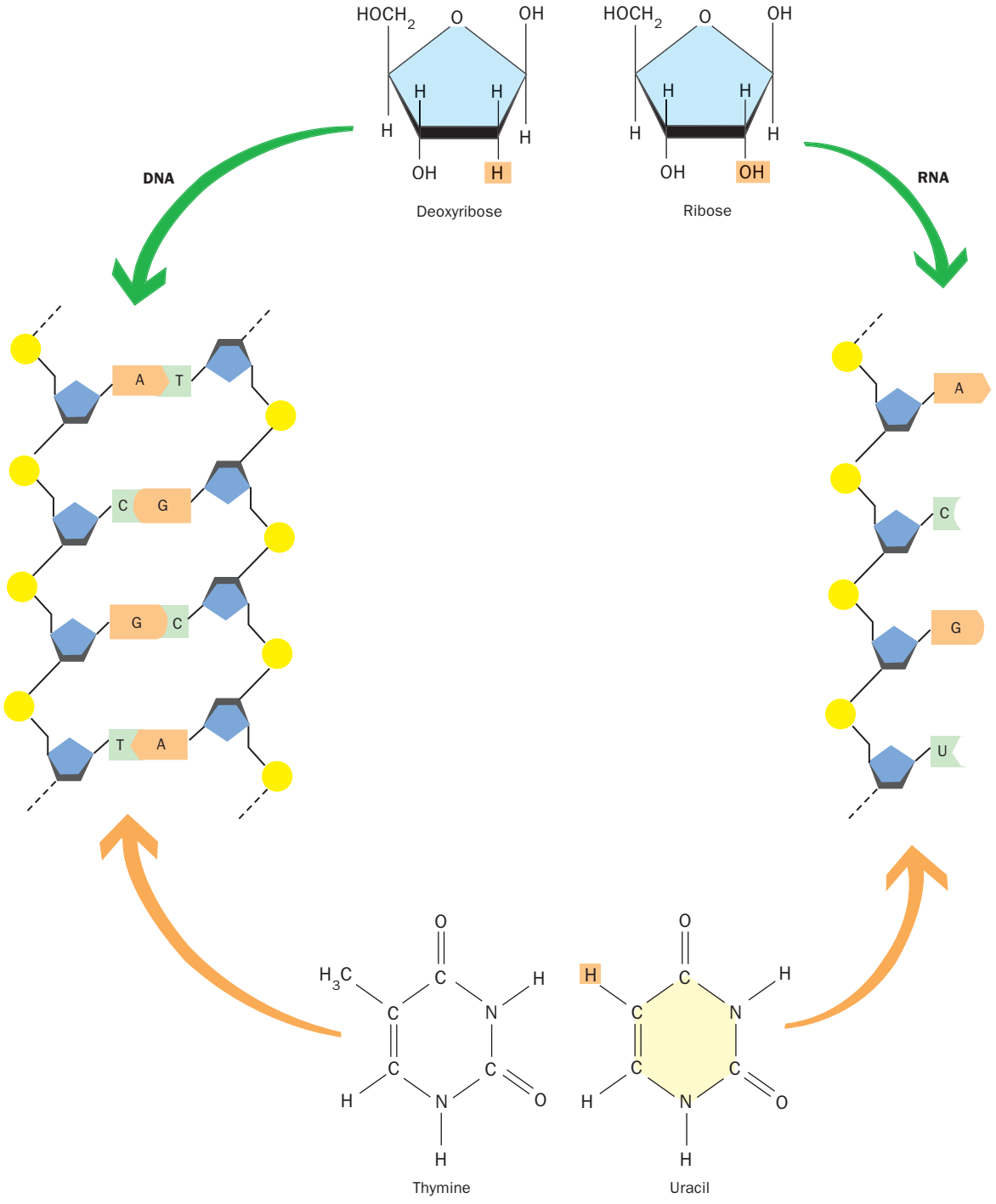
Cytosine



DNA NUCLEOTIDES PAIR UP ACROSS THE DOUBLE HELIX



COMPARISON OF DNA AND RNA



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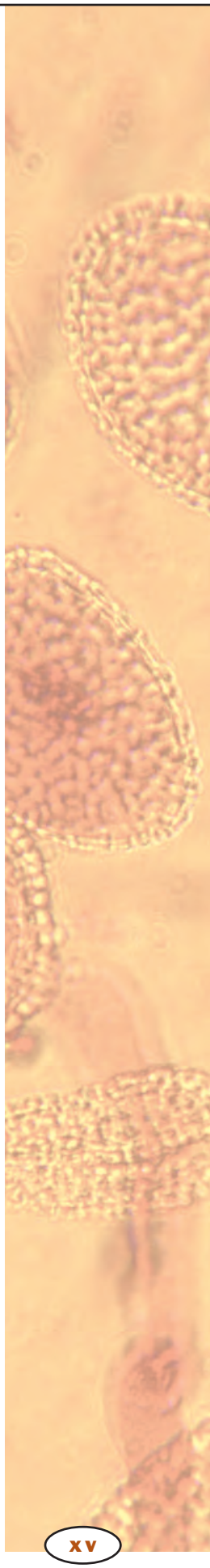

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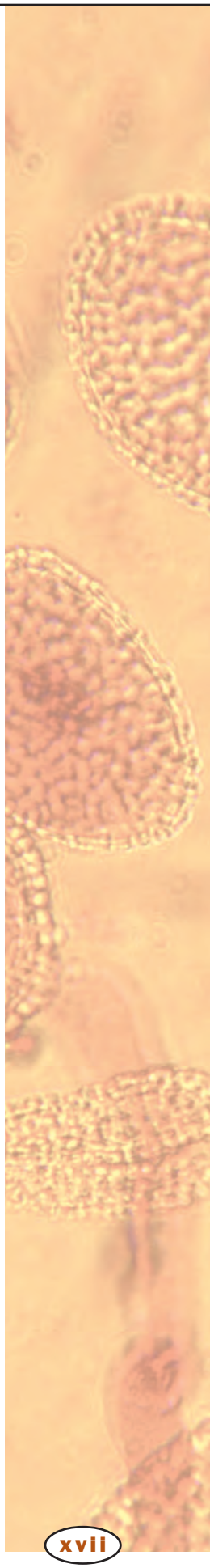

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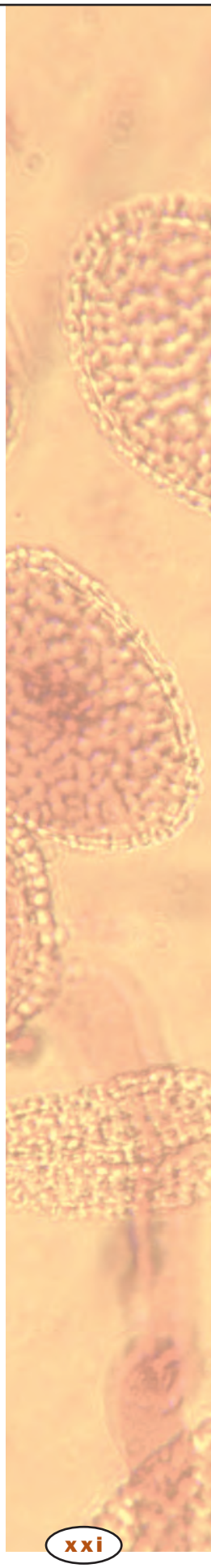

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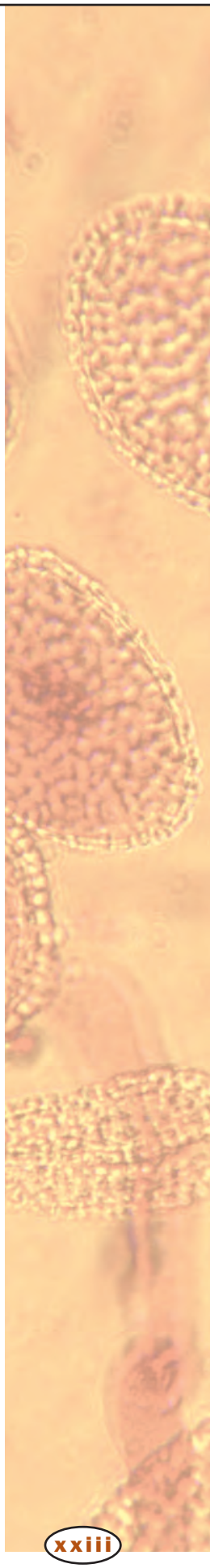

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biology

Active Transport

Active transport is the movement of molecules up their concentration **gradient**, using energy.

gradient difference in concentration between two places

Concentration Gradients

The concentration of most molecules inside a cell is different than the concentration of molecules in the surrounding environment. The plasma membrane separates the internal environment of the cell from the fluid bathing the cell and regulates the flow of molecules both into and out of the cell. The second law of thermodynamics states that molecules, whether in the gas or liquid state, will move spontaneously from an area of higher concentration to an area of lower concentration or down their concentration gradient.

A concentration gradient can be likened to water stored behind a dam. The water behind the dam will flow through the dam via any available channel to the other side. The energy from the water moving through the dam can be harnessed to make electricity. Water can also be pumped in the opposite direction from the river below the dam up to the reservoir behind the dam, with an expenditure of energy. Cellular membranes act somewhat like a dam. They block the movement of many types of molecules and have specific channels, transporters and pumps to provide pathways for the movement of certain molecules across the membrane.

When a molecule moves *down* its concentration gradient using one of these membrane channels or transporters, the process is called facilitated diffusion. In facilitated diffusion, no input of energy is needed to move the molecules. Instead, the potential energy of the concentration gradient powers the movement, just like water flowing out of a dam. For further diffusion, the channel or transporter does not determine in which direction the molecules will move, it only provides a pathway for the movement.

In cells, some molecules must be moved against their concentration gradient to increase their concentration inside or outside the cell. This process requires the input of energy and is known as active transport. As with facilitated diffusion, special transporters in the membrane are used to move the molecules across the membrane. The plasma membrane is not the only cellular membrane that requires active transport. All **organelles** surrounded by

organelle membrane-bound cell compartment

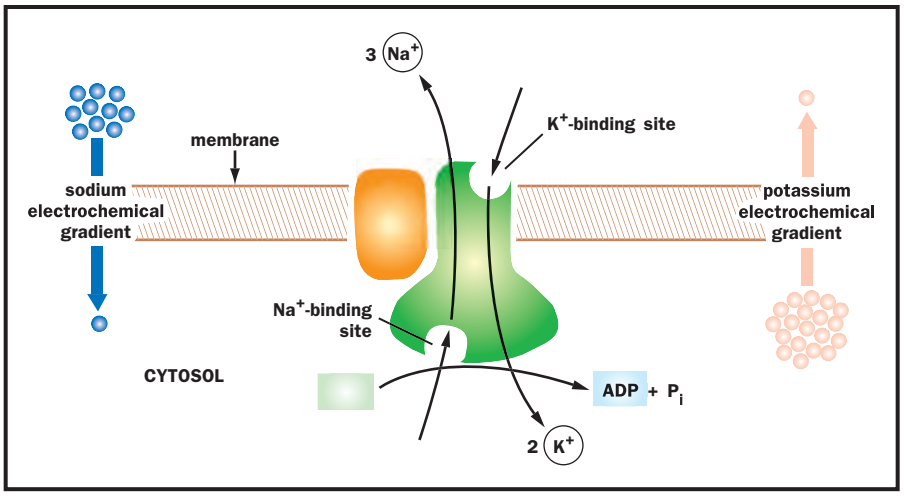

Diagram of carrier protein, which actively pumps Na^+ out of and K^+ into a cell. For every molecule of ATP hydrolyzed inside the cell, three Na^+ are pumped out and two K^+ are pumped in.

membranes must concentrate some molecules against their concentration gradients.

Types of Active Transporters

There are three types of active transporters in cells: (1) Coupled transporters link the "downhill" transport of one molecule to the "uphill" transport of a different molecule; (2) **ATP**-driven pumps use the energy stored in adenosine triphosphate (ATP) to move molecules across membranes; (3) Light-driven pumps use the energy from photons of light to move molecules across membranes. Light driven pumps are found mainly in certain types of bacterial cells.

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

Most of the energy expended by a cell in active transport is used to pump **ions** out of the cell across the plasma membrane. Because ions have an electrical charge, they do not easily cross membranes. This phenomenon allows large ion concentration differences to be built up across a membrane. Highly selective transporters are present in membranes that pump certain ions up their concentration gradients, but ignore other ions.

ion an electrically charged particle

The NA^+-K^+ Pump. One of the best understood active transport systems is the sodium-potassium pump, or NA^+-K^+ pump. This carrier **protein** is a coupled transporter that moves sodium ions out of the cell while simultaneously moving potassium ions into the cell. Because of the pump, the sodium ion concentration inside the cell is about ten to thirty times lower than the concentration of sodium ions in the fluid surrounding the cell. The concentration of potassium ions inside the cell is almost exactly the opposite, with a ten- to thirtyfold higher concentration of potassium ions inside the cell than outside.

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

Because the cell is pumping sodium from a region of lower concentration (inside) to a region of higher concentration (outside), the NA^+-K^+ pump must use energy to carry out its pumping activity, and this energy is supplied by ATP. For this reason, the NA^+-K^+ pump is also considered an **enzyme**. It belongs to a class of enzymes known as ATPases that use the energy stored in ATP to carry out another action. Other membrane transporters use the energy from ATP to pump ions like calcium, **amino acids**, and other electrically charged molecules either into or out of the cell.

enzyme protein that controls a reaction in a cell

amino acid a building block of protein

Ions carry a positive or negative electrical charge so that these gradients have two components: a concentration gradient and a voltage or electrical gradient. For instance, sodium ions are positively charged. The higher concentration of sodium ions outside of the cell than inside means that outside of the cell will have a positive charge and the inside of the cell will have a negative charge. This potential difference, or voltage, across the membrane can be used as an energy source to move other charged molecules. Positively charged molecules will be attracted towards the inside of the cell and negatively charged molecules will be attracted to the outside of the cell. It is, in fact, this electrical potential that causes positively charged potassium ions to enter the cell through the Na-K pump, even though they are moving up their concentration gradient.

The potential energy of the gradient can be used to produce ATP or to transport other molecules across membranes. One of the most important uses of the NA^+ gradient is to power the transport of **glucose** into the cell. The NA^+-glucose cotransporter moves sodium down its concentration gradient, and glucose up its gradient, as both move into the cell. SEE ALSO MEMBRANE TRANSPORT; NEURON; OXIDATIVE PHOSPHORYLATION; PHOTOSYNTHESIS

Stephen A. Adam

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

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Adaptation

To survive and reproduce, all living organisms must adjust to conditions imposed on them by their environments. An organism's environment includes everything impinging upon it, as well as everything that is affected by that organism. Conformity between an organism and its environment constitutes what biologists call adaptation.

Biotic and Abiotic Environments

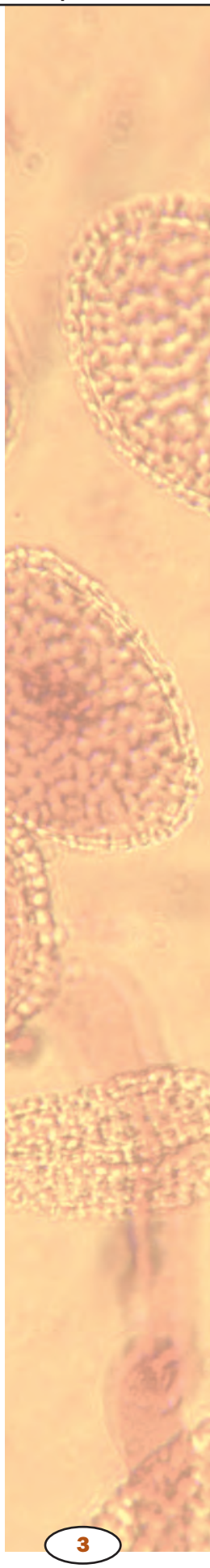
Plants and animals have adapted to their environments genetically and by means of physiological, behavioral, or developmental flexibility, including both instinctive behavior and learning. Adaptation has many dimensions in that most organisms must conform simultaneously to numerous different aspects of their environments. Adaptation involves coping not only with the physical **abiotic** environment (light, dark, temperature, water, wind), but also with the complex **biotic** environment (other organisms such as mates, competitors, **parasites**, predators, and escape tactics of prey). Conflicting demands of these various environmental components often require that an organism compromise in its adaptations to each.

abiotic nonliving

biotic living

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

Conformity to any given dimension requires a certain amount of energy that is then no longer available for other adaptations. The presence of predators, for example, may require that an animal be wary, which in turn is likely to reduce its feeding efficiency and hence its competitive ability.



A willow ptarmigan in winter color.

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

hormone molecule released by one cell to influence another

avian concerning birds

For a small bird, trees are an important part of its environment: They offer vital shade during the heat of a hot summer day, places to forage for insects, safety from ground-dwelling predators, and safe places to build nests and raise chicks. Blades of grass or hairs used to line a bird's nest are also important components of a bird's environment. During the dangerous night, a bird copes with **nocturnal** predators such as raccoons by sleeping perched on a small twig high above the ground. While gleaning tiny insects from tree leaves during the day, a bird remains alert for diurnal predators like hawks.

Many birds cope with changing seasonal conditions by migrating to warmer places at lower latitudes where there is more food. Over eons of time, natural selection has molded birds to make them effective at escaping from the predictable dire consequences of winter (a time of high mortality). Birds that did not successfully evade winter's icy clutches died without leaving any surviving offspring, whereas those that migrated survived to pass on their genes. Natural selection has endowed birds with a built-in biological clock, which they compare against day length, effectively giving them a built-in calendar. Changing day length affects a bird's pituitary gland, causing it to secrete **hormones** that control **avian** behavior. Short autumn days elicit a "wanderlust," ultimately leading to migratory behavior. Experiments with migrating birds in planetaria have shown that tiny bird brains have been hard-wired so that they contain a map of the stars. Indeed, natural selection "invented" celestial navigation.

Factors that Affect Adaptation

Organisms can conform to and cope with a highly predictable environment relatively easily, even when it changes in a regular way, as long as the changes are not too extreme. Adaptation to an unpredictable environment is usually more difficult; adapting to extremely erratic environments may even prove impossible. Many organisms have evolved dormant stages that allow them to survive unfavorable periods, both predictable and unpredictable. Brine shrimp in deserts and annual plants everywhere are good examples. Brine shrimp eggs survive for years in the salty crust of dry desert lakes; when a rare desert rain fills one of these lakes, the eggs hatch, the shrimp grow rapidly to adults, and they produce many eggs. Some plant seeds known to be many centuries old are still viable and have been germinated.

Very small undirected changes in the physical environment can sometimes improve the level of adaptation between an organism and its environment, but large changes are almost always detrimental. Changes in the environment that reduce overall adaptation are collectively termed the "deterioration of environment." Such changes cause directional selection resulting in accommodation to the new environment, or adaptation. Changes in biotic environments (such as the hunting efficiency of an organism's predator) are usually directed and typically reduce the level of adaptation.

Every individual is simultaneously a member of a population, a species, and a community; therefore, it must be adapted to cope with each and must be considered in that context. An individual's fitness—its ability to perpetuate itself as measured by its reproductive success—is greatly influenced by its status within its own population. An individual might be a resident or a vagrant, mated or unmated, or high or low in a pecking order, all factors

that strongly affect its fitness. Any given individual's fitness is also influenced by various **interspecific** associations of its species and especially by the particular community in which it finds itself embedded.

A willow ptarmigan in summer color.

interspecific between different species

"Arms Races"

Individuals and species must "track" their environments in ecological and evolutionary time, adapting and evolving as their environments change. Natural selection acting on natural enemies (prey, parasites, and predators) will always result in a deterioration of an organism's biotic environment, diminishing fitness. Every prey-predator or host-parasite interaction constitutes an escalating "arms race," in which moves alternate with countermoves.

Prey that are better able to escape from their predators, or hosts that can better resist infection by parasites, will enjoy a fitness advantage. But better predators and better parasites are also favored by natural selection themselves, assuring that the arms race will continue to escalate indefinitely. Indeed, most species are probably evolving rapidly just to maintain a given current level of adaptation in the face of a continually deteriorating environment. Still other interactions between species are mutually beneficial, resulting in increased fitness for both parties, such as between plants and their pollinators.

Any genetically based physiological, behavioral, or ecological trait that enables an organism to cope with, and to survive and reproduce in, its environment represents an adaptation. Some traits may not be adaptive but simply leftover vestiges of traits that once were adaptive. A given trait can also be "preadapted" if it was formerly adaptive under some prior set of conditions now gone but is later co-opted as the basis of a new adaptation under some new environmental conditions. For instance, it is likely that bird feathers were initially important for temperature regulation, rather than for flying. SEE ALSO COMMUNITY; CONVERGENT EVOLUTION; EVOLUTION; NATURAL SELECTION; PARASITIC DISEASES; PITUITARY GLAND; POPULATION DYNAMICS; PREDATION AND DEFENSE; SEXUAL SELECTION; SYMBIOSIS

Eric R. Pianka

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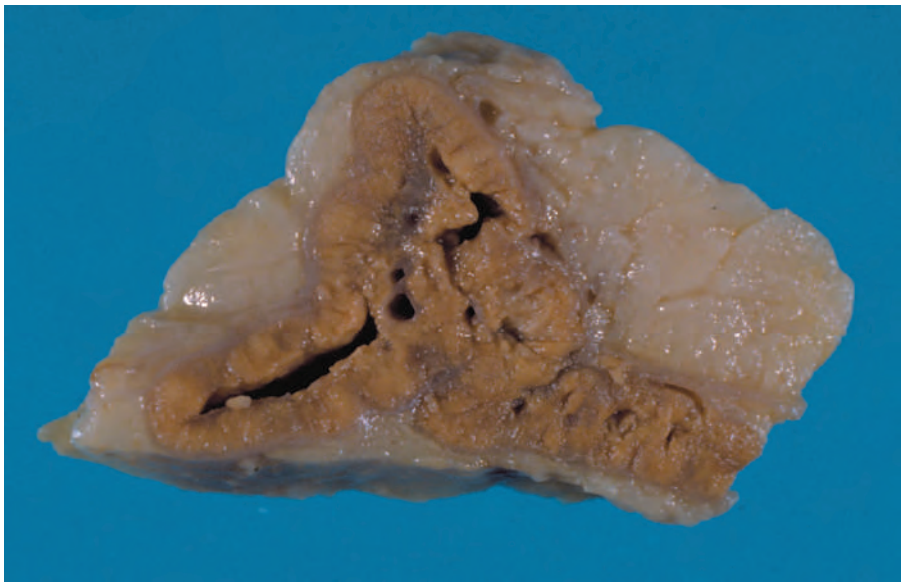
Adrenal Gland

The adrenal glands are located on the upper pole of each kidney. In fact, their name designates their location: the prefix *ad* means "adjacent," and *renal* refers to the kidney. In the human body, they are small yellowish glands that weigh about five grams (0.175 ounces) each.

The adrenal gland is actually two organs in one. The outer portion, called the adrenal cortex (*cortex* means "bark," as in the bark of a tree), is about nine-tenths of the gland's total weight. The inner part, called the adrenal medulla (*medulla* means "marrow," as found in the inside of a bone),



Cross section of a human adrenal gland.

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

hormone molecule released by one cell to influence another

is about one-tenth. They are both **endocrine** glands, meaning that they secrete chemical messengers called **hormones** into the bloodstream. However, the adrenal cortex and medulla are different in their embryological development, their tissue structure, the types of hormones they secrete, and the way they are regulated. So why is one located inside the other?

Adrenal Cortex

aggregate clump together

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

excrete deposit outside of

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

metabolism chemical reactions within a cell

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

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

The adrenal cortex develops from the mesoderm (middle layer) of the embryo. The tissue destined to become the adrenal cortex **aggregates** near the developing kidney and becomes organized into three zones. The outer zone is called the zona glomerulosa (meaning that the cells are arranged in little balls called glomeruli), the middle zone is the zona fasiculata (the cells are in parallel fascicles or bundles), and the zona reticularis (reticular means network) is innermost.

The hormones secreted from each zone all resemble the molecule cholesterol and are called **steroids**, but each zone secretes slightly different hormones. The zona glomerulosa secretes hormones that influence the kidneys to **excrete** or retain sodium and potassium, depending on the needs of the body. These hormones are called mineralocorticoids (sodium and potassium are **minerals**). The zona fasiculata secretes hormones called glucocorticoids that influence the **metabolism** of **carbohydrates**, including **glucose**. The glucocorticoids include hydrocortisone, corticosterone, and cortisone.

In addition to regulating metabolism, these steroids provide resistance to stress and suppress the inflammatory response and some allergic reactions. Steroids such as these are often rubbed onto inflamed and itchy skin to make it feel better. The zona reticularis secretes steroids that resemble the sex hormones secreted by the ovary in the female and testes in the male.

The adrenal cortex is regulated by the pituitary gland in the head. The pituitary gland secretes a hormone called adrenocorticotropic hormone (ACTH). *Tropic* (pronounced with a long o) is from a Greek word meaning

"nourishment," so ACTH simply refers to this hormone's ability to produce a change in the adrenal cortex. ACTH is necessary for cell growth and maintenance and stimulates glucocorticoid synthesis.

Adrenal Medulla

The adrenal medulla forms from ectoderm (outer layer) very near the embryonic spinal cord. From its beginnings, the adrenal medulla is part of the nervous system. These cells migrate into the middle of the developing adrenal cortex and form into a solid ball. The cells of the adrenal medulla secrete a class of hormones called catecholamines, adrenaline (or epinephrine) being the best known. Norepinephrine is also secreted.

In times of acute stress, the brain and spinal cord send a signal to the adrenal medulla, and it secretes adrenaline into the bloodstream. This causes the heart to beat faster, opens up the airways, and gets the body ready for physical activity. This "fight or flight" reaction is a survival mechanism, allowing people (and other animals) to escape from a dangerous situation. A person experiences the effects of the adrenal medulla when he or she gets scared or excited.

Why is the adrenal medulla inside the cortex? Steroids in the adrenal cortex activate the **enzyme** that puts the final atoms onto adrenaline. Therefore, the adrenal cortex helps the adrenal medulla to synthesize adrenaline, allowing the medulla to do its job. SEE ALSO ANABOLIC STEROIDS; ENDOCRINE SYSTEM; HOMEOSTASIS; HORMONES; PITUITARY GLAND; STRESS RESPONSE

Stephen W. Carmichael

enzyme protein that controls a reaction in a cell

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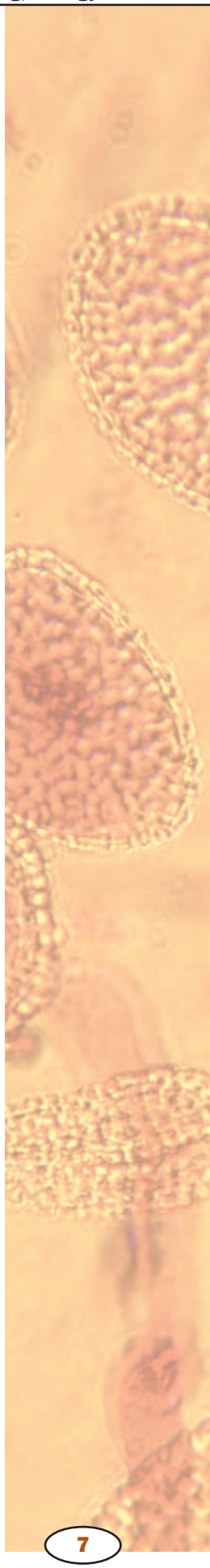
Aging, Biology of

Human life span, or longevity, has two components: mean longevity (also called life expectancy) and maximum longevity. Mean longevity is the average age at death of all members of a population. Throughout history, human life expectancy has increased. For example, life expectancy in the United States in the late eighteenth century was thirty-five years. By the last quarter of the twentieth century, it had increased to seventy-two years. The second component of life span, maximum longevity, is the age at which the most long-lived individuals of a population will die. This is difficult to determine in humans but is generally accepted to fall between 110 and 120 years.

The trend for life expectancy to get closer to maximum longevity has been attributed to improvements in nutrition, sanitation, and medical care. Maximum longevity, in actuality, appears to be independent of these environmental factors and is an absolute limit, probably determined by the action of genes. The genes that determine maximum longevity are believed to be responsible for repairing errors in the genetic information, repairing mistakes in the process of **protein** synthesis, and determining the time of death.

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



Improvements in nutrition, sanitation, and medical care have contributed to increased life expectancy.

Aging Changes that Occur in Humans

Some of the most easily observed age-related changes in humans are found in the skin and its derivatives. These include a loss of pigment in the hair, wrinkling of the skin, an increase in pigment in the skin, and thickening of the nails. Other observable changes are a decrease in size, due to loss of muscle and bone mass; a decrease in muscle strength; a decrease in mobility in the joints; and a variety of neurological changes, including diminished sensory function (vision, hearing, smell, and taste), increased response time, and diminished capacity for learning and memory. The latter have been attributed to a loss in brain mass, due at least in part to a loss of brain cells.

Less easily observed changes include a decrease in metabolic rate; diminished function of the kidneys, lungs, and pancreas; cardiovascular disease; diminished immune function; increased susceptibility to cancer; and a decrease (in males) or termination (in females) of reproductive function. All of these changes have been attributed to cellular events and processes that are described by various theories of aging.

Theories of Aging

It is widely accepted that the process of aging cannot be traced to a single cause. A number of theories have been proposed to explain the changes observed during aging. In order to be a valid candidate for an explanation of the aging process, the changes proposed by the theory must meet the following criteria: (1) they will commonly occur in all or most humans; (2) as an individual ages, these changes will become more pronounced; and (3) the changes will lead to cellular or organ dysfunction that ultimately cause failure of the organ or system. The following explanations are the most commonly accepted ones for the aging process.

Free Radicals. Free radicals are chemical particles that contain an unpaired electron and are extremely reactive. They are produced by **aerobic metabolism** and by radiation and other environmental agents. Their effects

aerobic with air, or requiring it

metabolism chemical reactions within a cell

are widespread. They alter or break down the structure of many other molecules in the cell and thus impair their functions. Free radicals react with proteins, which have **enzymatic**, structural, and control functions. They cause breaks in deoxyribonucleic acid (DNA) and thus alter the information necessary for synthesizing proteins. They cause **lipids** to stick together, which causes cell membranes to break down.

Their effects on **carbohydrates** are less well documented. Free radicals are most abundant in the cellular **organelles** called **mitochondria**, where **oxidative** reactions occur. Mitochondrial damage, including damage to mitochondrial DNA, has been proposed as a contributing factor to the aging process. The effects of free radicals are diminished by certain **enzymes** (superoxide dismutase and catalase) that interrupt the cycle of reactions that cause their damage. **Antioxidants** such as vitamins C and E also protect against free radical damage by quenching the reactions.

Crosslinkage of Proteins. In addition to the effects of free radicals, proteins can be altered by the spontaneous and uncontrolled joining of protein molecules to one another by **glucose**. The cumulative effect of this glycosylation is to cause the proteins to stick together. For example, the fibrous extracellular protein collagen, found in **connective tissue**, becomes stiff via this process, which contributes to the wrinkling of the skin and the loss of joint mobility.

Events Affecting the Genetic Material. Mutations, or changes in the DNA, are common and can lead to changes in the structure and function of proteins. There are a number of mechanisms that can repair these changes, but it is possible that these mechanisms diminish in their effectiveness with age, since they are carried out by enzymatic proteins, which are themselves damaged by the aging process. Another suggestion is that there are specific genes responsible for the death of individual cells.

Also, it is known that cells in tissue culture will undergo only a certain number of cell divisions. In human cells, this limit is approximately fifty cell divisions. This so-called Hayflick limit (after the scientist who first described it) has been tentatively explained by the progressive shortening of the telomere, the section of each DNA molecule that is responsible for initiating replication of DNA. As the telomere becomes too short, an increasing number of mistakes occur in the replicated DNA.

The Effects of Hormones. These chemical messengers normally have well-regulated effects on body tissues. Abnormally high levels of some hormones (which may be caused by other changes described here) can change the sensitivity of tissues to the hormones, as well as stimulate the **secretion** of other hormones whose uncontrolled effects could be deleterious. Insulin, growth hormone, glucocorticoid hormones, and reproductive hormones have been suggested as candidates in this mechanism.

Changes in the Immune System. This major defense system of the body may experience two kinds of change, either one of which could contribute to the aging process. First, the immune system may gradually lose its ability to distinguish cells of the body from foreign cells, resulting in immune attack on the body itself. Second, the immune system appears to be less able to respond to microbes or foreign molecules, thus rendering the cells

enzymatic related to function of an enzyme

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

organelle membrane-bound cell compartment

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

oxidative characterized by oxidation, or loss of electrons

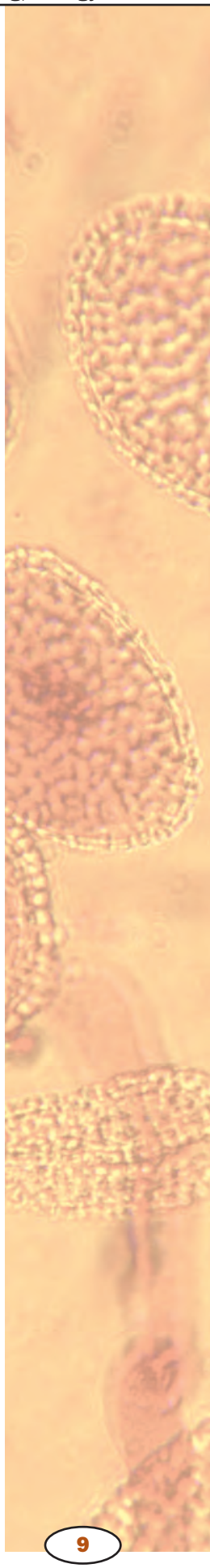
enzyme protein that controls a reaction in a cell

antioxidant substance that prevents damage from oxidation

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

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

secretion material released from the cell



of the body more susceptible to the effects of these noxious agents. SEE ALSO AUTOIMMUNE DISEASE; LIFE CYCLE, HUMAN; MITOCHONDRION; PEROXISOMES

Steven N. Trautwein

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Agriculture

ecosystem an ecological community and its environment

Agriculture is both an occupational practice and a subject to be studied. Farmers, horticulturists, and ranchers are examples of individuals who grow things for human use. Scientific researchers who experiment to improve plant and animal productivity; historians who examine the development of agrarian processes and the industry; and ecologists who study fields and fish ponds as managed **ecosystems** are examples of those who pursue agriculture as an area of academic interest. Decision making, leadership, research, and many other roles in modern agriculture require a college education in fields such as agronomy, animal husbandry, pathology, floriculture, agricultural economics, and mariculture.

Farming began early in the development of human society. The earliest ancestors of modern humans were scavengers, hunters, and gatherers. The search for food was an ongoing process, and the collected items were consumed shortly after being found. The abundance of food was very dependent on periodic variations in weather and natural disasters such as flood, fire, drought, and severe cold. The beginnings of agriculture rest with individuals who learned to plant seeds of edible crops or keep a small herd of goats or maintain a flock of chickens.

The transition to sustainability involved using the milk of the goats, or gathering eggs, rather than butchering animals as soon as possible for meat. Some cultures were ingenious in developing ways to obtain multiple sustainable resources from a single species. Examples of this are the cattle herded by the Masai of present-day Kenya and Tanzania, and reindeer managed by many indigenous peoples of northern Eurasia. These animals provide resources such as milk, meat from excess calves, and even blood as food, plus leather and bone for clothes, tools, and ornaments.

Globally, a variety of cultural patterns developed as family units grew into villages, villages into towns, and ultimately towns grew into the complex urban cultures present throughout the world today. With the concentration of humans into cities, the ability of the individual to produce food for a family unit declined to the point where as of the twenty-first century a large number of individuals are totally dependent on others for their nourishment. In some societies this involves a daily trip to the marketplace where

family farmers sell the products of their efforts. In many less-developed countries a great deal of the food consumed is still self-produced or obtained from small agricultural units in this manner. In more developed and industrialized countries, the local market has been extensively replaced by large chain stores that distribute packaged and processed foods that are produced by large commercial farms, ranches, and orchards. However, even in these highly developed areas, there are many who prefer locally grown foods and flock to farmers markets, **organic** food stores, and other small businesses.

Modern agriculture is now a big business, which is driven by ever-increasing scientific knowledge. The family farm found throughout America during the twentieth century is disappearing. These traditional, somewhat self-contained operations, where field crops were grown to produce grain, and gardens cultivated for vegetables, and a mixture of animals including cows, pigs, chickens, and sheep produced food and necessary materials such as leather and wool, are no longer economically practical. They have, in the industrialized world, given way to corporate farms that operate in much the same way as other large businesses. These agricultural units include not only the obvious specialized food-producing dairy farms, poultry operations, apple orchards, cattle ranches, and expansive wheat, corn, and soybean fields, but also such industries as catfish farms, shrimp nurseries, and oyster cultures. Agriculture also produces nonedible products such as tobacco and cotton, and grain for the production of methanol, a substitute for fossil fuels.

A wild rice plant growing in Ocala, Florida. For the earliest ancestors of modern humans, the search for food was an ongoing process.

organic a type of agriculture stressing soil fertility and avoidance of synthetic pesticides and fertilizers

The agricultural operations of the past depended greatly on the intuition and experience of the family unit concerning when to plant, how to recognize a disease in the herd, and the best time to harvest. This information was passed from generation to generation. Decisions are now based on research and development carried out by university and private industry scientists. At one time it was a matter of knowing which farmer in the township had the best bull and bartering with him or her to bring this fine specimen to one's herd of females. Today genetic research has resulted in the development of the best bull in the country, and a farmer can order frozen sperm from across the continent. In fact, in this new millennium, the commercial distribution of cloned embryos of individual livestock specimens with the best possible characteristics is at hand.

Genetic engineering has virtually unlimited potential for producing frost- and disease-resistant crops, high-yield animals, products with a longer shelf life and a better flavor, and a multitude of other advances. Biotechnology, which has the great promise of advancing agriculture, has potential deleterious effects. For example, it could result in the herbicide-resistant gene inserted in a grain variety being transferred through unintended hybridization into a natural population of a related "weedy" or deleterious species, allowing it to prosper out of control.

Not only has modern agriculture introduced additional science into the barnyard, it has also brought in the economists, the lawyers, the television commentators for agri-business shows, and a multitude of businesspeople who advertise and market the product. This is a far cry from a farmer selling his best calf at the end of the summer at the county fair.

Finally, there is another element of modern agriculture. When farms were spread out across the countryside interspersed with wood lots, or when cattle production involved letting the herd range over hundreds of acres

A herd of Holsteins eat silage from troughs on a Minnesota farm. Modern agriculture is now a big business, which is driven by ever increasing scientific knowledge.

during the summer, the local impact on the land and environment was relatively low (although the total impact was high, given the large number of acres devoted to agriculture). Modern, high-intensity agriculture with fields cultivated using tractors as large as elephants, fertilizers, pesticides, and irrigation systems is a potential threat to the environment. These techniques can place high demands on freshwater sources and have the potential for introducing toxic contaminants and excess nutrients into streams and rivers or promoting soil erosion. High-density animal production, such as hog farms in North Carolina, cattle feed lots in the Midwest, and turkey and dairy farms in the Shenandoah Valley, produce fecal contamination that can pollute waterways with bacteria and cause cultural **eutrophication** of aquatic ecosystems due to excess nutrients. Even the best planned containment of animal wastes can break down under the flood conditions of hurricanes and high rainfall years.

eutrophication process by which waters become enriched in dissolved nutrients that promote plant growth, which results in depletion of dissolved oxygen

The human population is growing at such a high rate that humans in less-developed countries will surely starve and die without pulses of progress such as the green revolution that produced high-quality rice for underdeveloped countries in the 1960s. Prevention of this situation is the hope of

industrial and biological technology advances that are sure to happen during the twenty-first century. However, this is a double-edged sword. Agricultural progress without due attention to environmental impacts has the potential for creating a world that will not be desirable to live in for the people supported by its products. SEE ALSO AGRONOMIST; GRAIN; HISTORY OF AGRICULTURE; HORTICULTURIST; ORGANIC AGRICULTURE

Dean Cocking

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Agronomist

An agronomist is a professional who practices, or does research in the area of, agronomy, which is the art and science of managing field crops and the soils beneath them. Agronomy emerged early in the twentieth century when this component of agriculture involving the growing of plants was separated from animal husbandry. It has continued to evolve as subcategories develop within the crop and soil sciences, such as the study of forage crops, tropical cropping systems, weed science, and turf science and management (the growth of grasses for golf courses and parks).

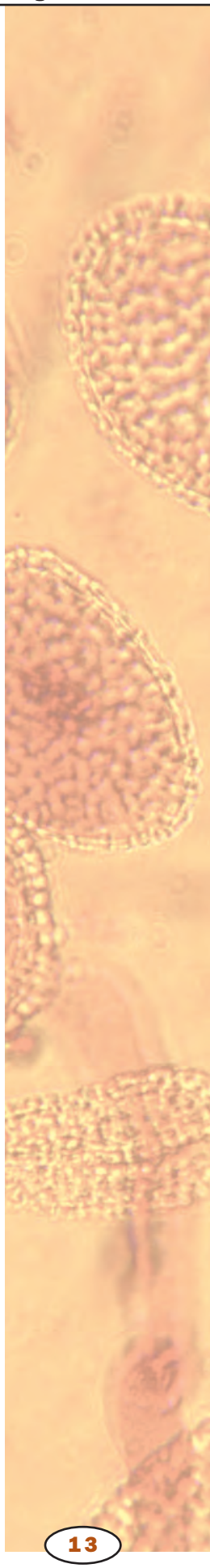
Seed science and technology, agro-forestry (the growth of timber in plantations), agricultural economics and engineering, and the nutrition, **physiology**, and ecology of crop plants are other interests of agronomists. They also often concentrate on soil conservation and the structural, chemical, and physical properties of soil that affect the growth of crops. Because of this extensive diversification, professionals working in these fields now often use the specialty to define their occupation rather than the broader designation of agronomist. All of these disciplines contribute toward increasing the productivity of farmlands, enhancing the quality of the agricultural product, and improving the economic efficiency of farming practices.

physiology branch of biology that deals with the functions and activities of living matter

Because farming cannot always occur under optimal plant growth conditions, many agronomists focus on the utilization of marginal habitats and problems occurring in the less-industrialized countries. These include conditions such as fields under frequent water deficiency, where dry-land farming practices can be utilized, and farming on nutrient-poor soils. Others seek to make plants grow under **saline** conditions; in extremely hot or cold environments; or in habitats with abbreviated growing seasons. Many of these challenges can be resolved through traditional plant breeding or the application of biotechnology.

saline of, relating to salt

These scientifically based aspects of the profession require undergraduate college study. In the United States, this is frequently at federally established land-grant universities. Many of these individuals become farm managers or owners, county agricultural agents, or work in industry or the



federal government. Students interested in these subjects need to follow a college preparatory track focusing on science, computer, and writing skills and, where possible, courses covering practices in business and agriculture. Internships or applied experience in agricultural operations can provide practical information that is very useful in making career decisions. Furthermore, the continually increasing emphasis on scientific research by agronomists provides opportunities for trained scientists to contribute to the growth of knowledge in agronomy. Masters degree and doctorate programs can be entered as a continuation of undergraduate applied study, or following liberal arts degrees, particularly in biology or geology with an emphasis on soil science. SEE ALSO BIOTECHNOLOGY; PLANT NUTRITION; SOIL

Dean Cocking

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AIDS

AIDS (acquired immunodeficiency syndrome) is defined as the stage of infection with HIV-1, or HIV (human immunodeficiency virus), in which an infected person's immune system has become so weak that he or she is at risk of developing other infections or cancers (or has already developed them) that can potentially lead to death. Though all people with AIDS are infected with HIV-1, not all people with HIV-1 infection have AIDS, nor will all of them develop AIDS.

HIV Pathogenesis

enzyme protein that controls a reaction in a cell

transcribe to create an RNA copy of a DNA gene

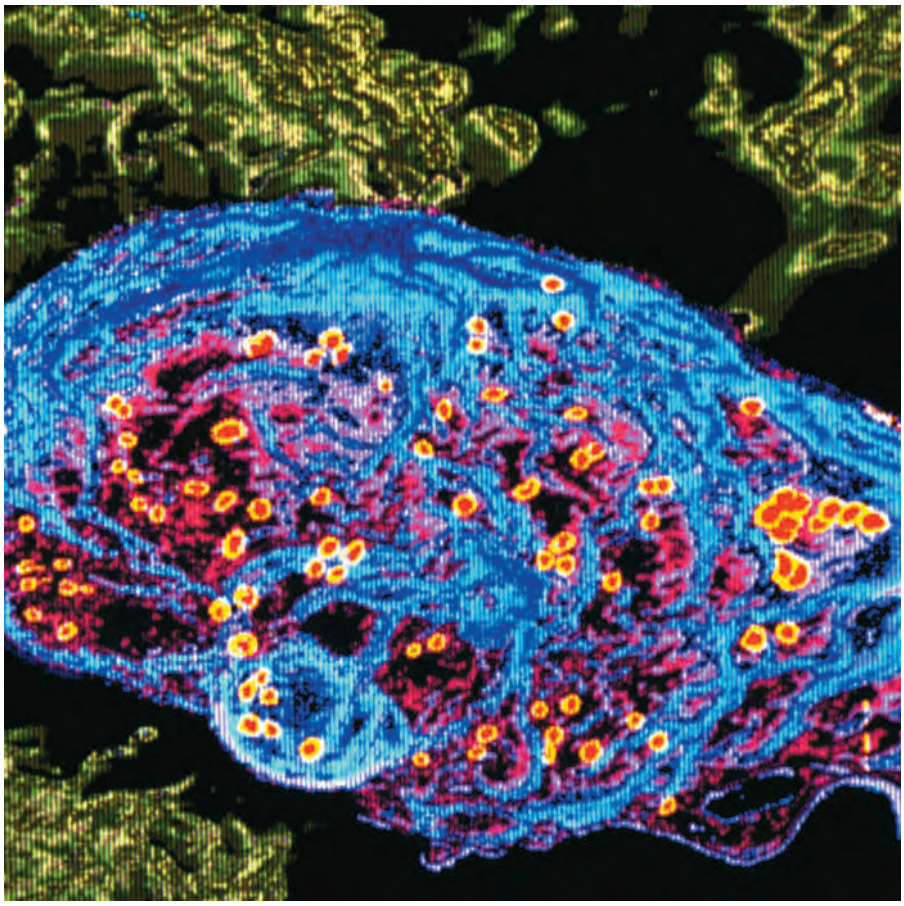
pathogenesis pathway leading to disease

T cell white blood cell that controls the immune response

The cause of AIDS is human immunodeficiency virus-1 (HIV-1), a member of a group of viruses called retroviruses. Retroviruses are enveloped ribonucleic acid (RNA) viruses that contain an **enzyme** (reverse transcriptase) that will **transcribe** viral RNA to deoxyribonucleic acid (DNA). In the case of HIV-1, this DNA (now called a DNA provirus) is then integrated into the infected person's DNA. When the infected person's DNA is then transcribed, or read by the cell's molecular machinery, the proviral DNA is also read, leading to the creation of new virus and release from the infected cell.

The **pathogenesis** of HIV-1 infection is complex. HIV-1 binds to cells that have specific types of molecular receptors on their surface, such as CD4 and chemokine receptors. Cells that have these receptors include CD4 lymphocytes, macrophages, and microglial cells in the brain. CD4 lymphocytes are a kind of helper **T cell**. Macrophages are immune cells that consume infected cells, and microglial cells perform certain immune functions in the brain. After the virus binds and enters the cell, it will replicate as discussed above. In the course of a day, as many as ten billion virus particles can be produced in an infected person.

CD4 lymphocytes are one of the main targets of HIV-1. These cells are essential in the functioning of the immune system. The CD4 lymphocytes are destroyed by direct viral killing, by other lymphocytes that destroy HIV-infected cells, and probably by other mechanisms. As the CD4 lymphocytes



A scanning electron micrograph of the AIDS virus attacking T4 lymphocytes.

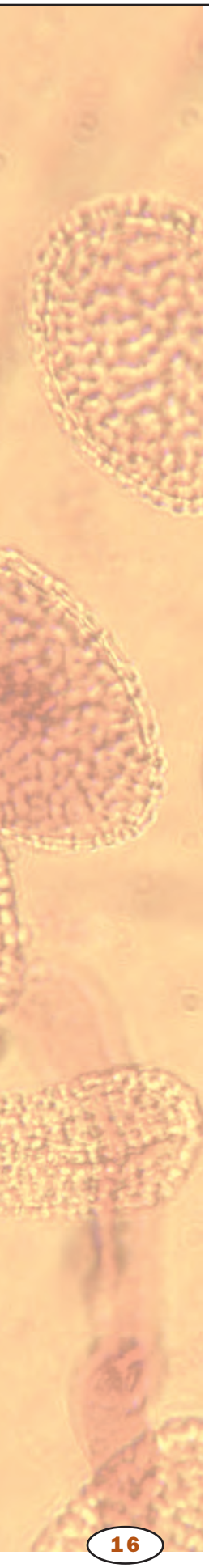
become depleted, the immune system's ability to fight off infections and certain types of cancers is lost. When the loss becomes severe enough, these infections and cancers can occur, and may kill the HIV-infected person. At this stage of depleted CD4 cells, medical professionals say that the infected person has full-blown AIDS.

Transmission

The epidemiology of HIV infection/AIDS has changed over the years. When the disease was first recognized in the early 1980s, men who had sex with men were by far the largest affected risk group, followed by intravenous drug users who were sharing needles, individuals who received HIV-infected blood, and hemophiliacs who received infected clotting factors. Women who had sexual contact with infected men were recognized as being at high risk of contracting HIV, and if they were pregnant, passing it on to their unborn children.

Though this disease was first recognized in the United States, cases soon appeared in many countries of the world. Particularly hard hit were countries in sub-Saharan Africa, the Caribbean, and Asia. At the turn of the twenty-first century, it is estimated that more than forty million people are infected worldwide and as many as one million in the United States alone.

Transmission of HIV-1 occurs through infected bodily fluids. Sexual contact by far is the most common mode of transmitting HIV. Anal sex is the most efficient sexual manner of transmitting the virus. Vaginal intercourse



poses the next highest risk, but more to the female than the male. In other words, it is much easier for an infected man to infect a woman through penile-vaginal intercourse than the other way around, especially if the man is circumcised and has no sores or ulcers on his penis. Since HIV is a blood-borne infection, those individuals engaging in intravenous drug use and sharing needles can easily transmit the virus in this manner. Prior to testing for the virus in the blood supply, there was a risk of acquiring HIV from transfusion of blood or a blood product, but this risk is now extremely small. Vertical transmission, or transmission from mother to child during pregnancy, occurs in about one-third of HIV-infected pregnant women who are not treated with anti-HIV medications.

Prevention

Prevention of HIV transmission is both a behavioral and medical problem. Abstinence from sexual behavior is promoted as the only sure way of preventing transmission of HIV. Though this of course is true, premarital and extramarital sexual behavior is common in most societies. Condoms provide an effective barrier to sexual transmission. Social, religious, political, and cultural issues, however, enter into the education of youth on the use of condoms, and lead to controversies over education about sexual behavior in general. With as many as one-third or more of HIV infections occurring during adolescence, aggressive and honest educational approaches must be implemented. One can only make an informed decision about one's behavior if one understands the consequences and has knowledge of how to prevent transmission.

Beyond all of this, there are the medical areas of transmission prevention. As mentioned above, HIV-infected pregnant women who are treated with anti-HIV medications can reduce their risk of transmitting the virus to their baby. Health care workers who are stuck with needles contaminated with blood from HIV-positive patients can reduce their risk of infection by using anti-HIV medications. Medical studies in the early twenty-first century are looking at the possibility of reducing the risk of HIV transmission following a sexual contact by treating the uninfected contact with anti-HIV medications. Vaccines against HIV are being researched in many parts of the world, but as of yet, have not been shown to be protective.

Treatment

reverse transcriptase enzyme that copies RNA into DNA

Treatment of HIV/AIDS is both complicated and expensive. The medications that are available inhibit the **reverse transcriptase** enzyme, and inhibit an enzyme that helps the virus mature into one that can infect other cells. By using a combination of at least three different medications that are active at these various sites, one can clear the blood stream completely of virus. Once this occurs, the patient's immune system often improves, and in some cases, returns to normal. If the patient takes medications as directed and the virus stays suppressed, there is a chance that the patient may never become ill. The virus, however, is still present in the lymph nodes and probably other tissues. If the patient stops taking medications or takes them erratically, the virus will return to the bloodstream. Once the virus is actively produced again, there is a high probability that it will

mutate to a form resistant to the medications that the patient was previously on. When this occurs, especially if the patient has been on more than one regimen of medicines, a virus resistant to all available medications can be selected for. At this point, little else can be done. One major concern about these individuals is that if they are still sexually active or continue to share needles, they will transmit resistant virus. This is being documented more frequently.

New medications are being studied that may be able to overcome this resistance problem by attacking different sites of viral production, or those that are not affected by mutations in the resistant virus. The problems here include the possibility that the patient could die before the new medicines are available; that if the patient is still alive, he or she will be unable to tolerate the side effects of the new medicines; and, finally, that the patient will be unable to afford the medicines. Anti-HIV or anti-retroviral medications are very expensive, costing over $10,000 per year in the United States. This, plus the costs of blood tests and doctor visits, makes treatment beyond the means of most of the infected people in the world.

HIV/AIDS is and will continue to be one of the greatest medical challenges medical professionals have ever faced. Prevention and education are the only means that public health professionals currently have to stem the tide of this ever-growing **epidemic**. SEE ALSO BIRTH CONTROL; RETROVIRUS; REVERSE TRANSCRIPTASE; SEXUALLY TRANSMITTED DISEASES; T CELLS; VIRAL DISEASES

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

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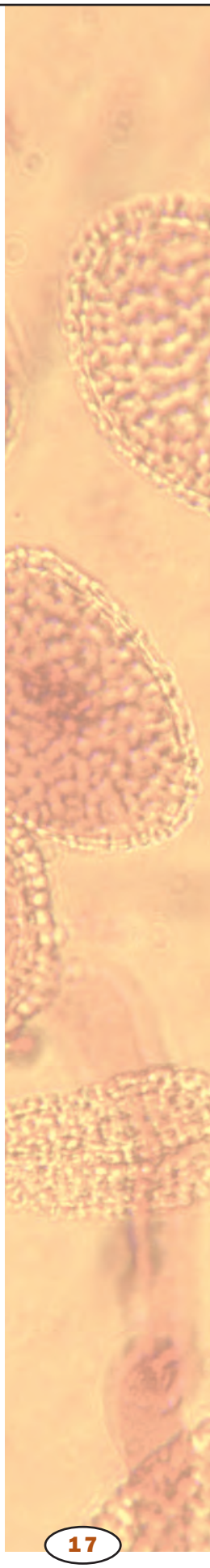
Alcohol and Health

Ethanol, C_2H_5OH, also known as ethyl alcohol or grain alcohol, is the only common alcohol that humans are able to digest. Alcohol is readily absorbed by the body when consumed in an **aqueous** solution. All common alcoholic drinks are aqueous solutions of ethanol.

aqueous watery or water-based

Alcohol absorption generally begins in the stomach, although most absorption takes place from the small intestine. Because alcohol is distributed to all body fluids (in proportion to the water content of that fluid), alcohol can be detected and quantitatively measured in the blood, urine, cerebrospinal fluid, and water vapor from the lungs. Drug testing for alcohol level relies on this fact.



A Santa Monica police officer administers a breathalyzer test to a man to determine the alcohol level in his bloodstream.

excrete deposit outside of

oxidation reaction characterized by loss of electrons, or reaction with oxygen

enzyme protein that controls a reaction in a cell

catalyze aid in the reaction of

Metabolism

Only about 2 percent of consumed alcohol is **excreted** unchanged by the lungs or kidneys. The rest is metabolized by the body through biological **oxidation** with the aid of the **enzymes** alcohol dehydrogenase and acetaldehyde dehydrogenase. These are induced enzymes (produced in response to need), and are found in larger quantities in heavy drinkers than in nondrinkers.

Alcohol dehydrogenase **catalyzes** the oxidation of ethyl alcohol to acetaldehyde. Acetaldehyde is moderately toxic and is believed to be a major cause of headaches and hangovers.

The second enzyme, acetaldehyde dehydrogenase, catalyzes the oxidation of acetaldehyde to acetate. A small amount of acetate enters the Krebs (cellular digestion) cycle, while other acetate molecules enter other energy-conversion pathways of the body. The remainder of the acetate is stored as long-chain fatty acids and is ultimately oxidized to form carbon dioxide and water.

Although some human variation exists, the body can metabolize only about one drink ($1\frac{1}{4}$ fluid ounces [0.036 liters]) per hour. Because the oxidation reactions are enzyme-catalyzed, little can be done to speed up the reactions.

Alcohol is processed by the liver. However, excessive quantities of alcohol cannot be processed during a single pass through the liver. Thus, alcohol can have a direct effect on other parts of the body. Most tissue effects are a part of an intricate, interrelated series of events.

Physiological Effects

Alcohol is a vasodilator (the blood vessels dilate or enlarge). Chronically dilated veins are often associated with liver disease, and the "enlarged red nose" of the chronic alcoholic is usually the result of permanently dilated blood vessels. **Dilation** of the veins of the **esophagus** can lead to hematemesis (vomiting blood). Late-stage alcoholics have been known to drown in their own blood because of ruptured esophageal blood vessels.

dilation expansion or swelling

esophagus tube connecting throat to stomach

Edema, the accumulation of tissue fluid, occurs with alcohol consumption because when the blood vessels expand, the **proteins** as well as the fluids within the capillaries leak into the **interstitial space**. This accumulation between the cells leads to tissue swelling. Because the fluid is not within the blood vessels, apparent dehydration exists. Jaundice (yellowing of the body tissues) is generally caused by excessive bilirubin (a normal body pigment) in the extracellular fluids, and may indicate liver disease.

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

interstitial space space between cells in a tissue

Alcohol is a **central nervous system** (CNS) depressant, meaning that with alcohol the central nervous system is operating at decreased efficiency. Alcohol is also a depressant of all major systems of the body. High quantities of alcohol function as an anesthetic. Alcohol also depresses the psychological inhibition and thus may appear to be a stimulant. Because of this apparent stimulation of certain behaviors, psychologists call alcohol a biphasic drug. The combination of CNS depression and inhibition release leads to the symptoms of drunkenness. Drunkenness, a term for which there is no precise definition, varies with body size, metabolic rate, individual absorption, and individual tolerance.

central nervous system brain and spinal cord

Chronic Alcoholism

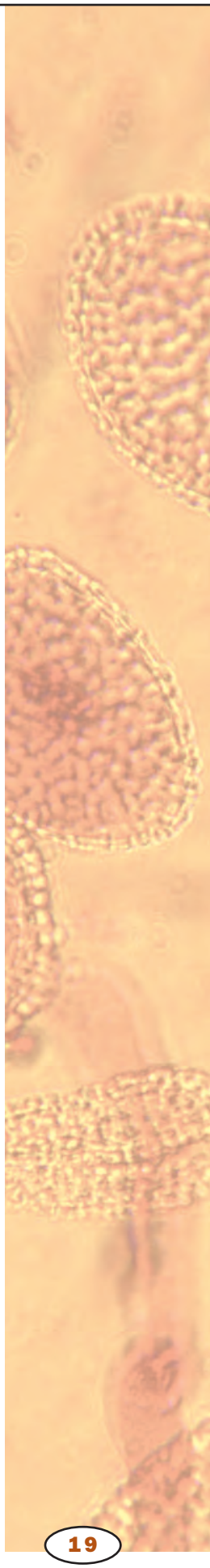
Prolonged use of alcohol can lead to compensatory mechanisms for the depressed normal nervous system activity. The nervous system tends to "work harder" to maintain equilibrium and therefore, upon withdrawal of alcohol, the nervous system may experience excessive excitement which may lead to convulsions, seizures, and ultimately delirium tremens (the DT's), a state of restlessness, disorientation, and **hallucinations**.

hallucination altered sensory experience

Mental impairment in chronic alcohol use is difficult to quantify because some impairment is reparable either by itself or by the construction of alternate nervous routes in the brain. Perhaps the most noticeable of the reparable impairments is personality loss.

Other physiological involvements include **sleep apnea**, decreased REM (restful) sleep, headaches, inhibition of testosterone synthesis, pancreatic inflammation, and electrolyte imbalance in the blood.

sleep apnea difficulty breathing while asleep



The major nutritional problem with alcohol is poor diet. Also, excessive alcohol ingestion often leads to gastrointestinal irritation, and this can lead to ulcers, colitis (inflamed colon), and other chronic ailments.

It is estimated that about 10 percent of the human population is addicted to alcohol. Probably no single cause of alcohol addiction exists. Certain genetic markers have been discovered, and the genetic component of alcoholism is well documented. Nevertheless, genetics alone does not explain all alcohol addiction. Psychological components to alcohol addiction have also been identified. For most alcohol addicts, the only treatment is total abstinence from alcohol and participation in a program such as Alcoholics Anonymous. The alcoholic's body does not "forget" alcohol, and the induced enzymes mentioned earlier remain ready to continue their metabolic actions if alcohol use resumes. SEE ALSO DIGESTIVE SYSTEM; DRUG TESTING; KREBS CYCLE; LIVER

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Algae

ecosystem an ecological community and its environment

Algae are a diverse group of all photosynthetic organisms that are not plants. Algae are important in marine, freshwater, and some terrestrial **ecosystems**. Seaweeds are large marine algae. The study of algae is called phycology.

phytoplankton microscopic floating creatures that photosynthesize

Algae may be unicellular, colonial, or multicellular. Some algae, like the diatoms, are microscopically small. Other algae, like kelp, are as big as trees. Some algae, the **phytoplankton**, drift in the water. Other algae, the epiphitic or benthic algae, grow attached to rocks, docks, plants, and other solid objects.

Classification

prokaryote single-celled organism without a nucleus

The major groups of eukaryotic algae are the green algae, diatoms, red algae, brown algae, and dinoflagellates. They are classified as protista. Another group, the blue-green algae, is the cyanobacteria. Some authorities do not consider the blue-green algae to be true algae because they are **prokaryotes**, not eukaryotes.

Green Algae. Green algae are the algae most closely related to plants. They have the same pigments (chlorophyll a and b and carotenoids), the same chemicals in their cell walls (cellulose), and the same storage product (starch) as plants. Green algae may be unicellular or form filaments, nets, sheets, spheres, or complex mosslike structures. There are both freshwater and marine species. Some species of green algae live on snow, or in symbiotic associations as lichens, or with sponges or other aquatic animals. Edible green algae include Chlorella and sea lettuce. There are at least seventeen thousand species of green algae.

Diatoms. Diatoms are often regarded as the most beautiful of the algae. Each diatom has a cell wall made of glass that is very finely etched with a species-specific pattern of dots and lines. The patterns on the diatom cell walls are so precise that they were used for years to test the optics of new microscopes. Diatoms are also the most abundant algae in the open ocean and responsible for about one-quarter of all the oxygen gas produced on the earth each year. Diatom populations often bloom in lakes in the spring, providing a major food for zooplankton, forming the base of the aquatic food chain. There are over one hundred thousand species of diatoms.

Red Algae. Red algae are almost exclusively marine and include many edible and economically important species, including nori and laver. Red algae are also the source of carageenan and **agar**, which are used as food thickeners and stabilizers. Red algae are mostly large, complex seaweeds. There are four thousand to six thousand species.

Brown Algae. Brown algae are almost exclusively marine and include the largest and most complex seaweeds. Kelp, for example, may be more than 60 meters (200 feet) tall, and forms dense underwater forests off the California coast. Other important brown algae include the rockweeds and Sargassum, for which the Sargasso Sea is named. There are about fifteen hundred species of brown algae.

Dinoflagellates. Dinoflagellates are unicellular algae with armor made of **cellulose** and flagella that cause them to spin as they swim. Dinoflagellates are found in both freshwater and marine ecosystems. Some species of dinoflagellates emit an eerie blue light when disturbed, called **bioluminescence**. Other dinoflagellates are toxic and responsible for red tides and outbreaks of shellfish poisoning. There are two thousand to four thousand species of dinoflagellates.

Algae on a pond. Algae are important in freshwater as well as in marine and some terrestrial ecosystems.

agar gel derived from algae

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

bioluminescence production of light by biochemical reactions

Life Cycles

Life cycles among the algae are incredibly varied. In fact, almost any type of life cycle one can imagine is displayed by some member of the algae. In an asexual life cycle, individuals reproduce by splitting. Some dinoflagellates reproduce primarily by asexual division. There are three types of sexual life cycles, which involve at some stage the fusion of **gametes**: gametic **meiosis**, zygotic meiosis, and sporic meiosis.

Gametic Meiosis. In the gametic meiosis life cycle (which is employed by humans), meiosis produces the gametes, so the only **haploid** cells in the life cycle are the gametes. The individual that one sees is made of **diploid** cells. Diatoms have gametic meiosis.

Zygotic Meiosis. In zygotic meiosis, the **zygote** undergoes meiosis, so the only cell that is diploid is the zygote. All the other cells in the organism are haploid. Many of the green algae, including sea lettuce, have zygotic meiosis.

Sporic Meiosis. In sporic meiosis, there are both haploid individuals and diploid individuals within the life cycle. Meiosis produces haploid spores, which then divide to produce an individual that is made entirely of haploid cells. This individual produces gametes by **mitosis**. Two gametes unite and form a diploid zygote. The zygote divides to produce an individual that is made entirely of diploid cells. This individual produces spores by meiosis

gamete reproductive cell, such as sperm or egg

meiosis cell division that forms eggs or sperm

haploid having single, non-paired chromosomes in the nucleus

diploid having pairs of chromosomes in the nucleus

zygote fertilized egg

mitosis separation of replicated chromosomes

to complete the cycle. Because the life cycle includes two generations of individuals, a haploid generation and a diploid generation, it is called "alternation of generations." Plants and many of the green, red, and brown algae have sporic meiosis.

In Japan, Korea, and China, the production of nori is a billion-dollar-a-year industry, but because the two generations in the nori life cycle look completely unlike each other it was not until the early twentieth century that the second generation was discovered. This discovery radically improved the ability of humans to grow nori, and there is a memorial park in Japan dedicated to the British scientist, Kathleen Drew Baker, who discovered it.

Economic and Ecological Importance

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

Algae are the base of the aquatic food chain. Humans also eat many types of algae. The marine algae nori and kelp have been harvested in China for over two thousand years. *Spirulina*, a blue-green algae that is rich in **protein** and vitamin B, is harvested from Lake Chad in Africa. The photosynthesis done by algae is very important to the biosphere because it reduces the amount of carbon dioxide and increases the amount of oxygen in the atmosphere.

Some types of algae can cause environmental problems such as red tides and fishy-tasting water. These problems are usually caused by the excessive release of nutrients from farms, sewage, and other human activities. The outbreak of the nerve-toxin-producing *Pfiesteria* (a dinoflagellate) on the Atlantic coast, for example, has been linked to overflowing sewage lagoons. SEE ALSO ALTERNATION OF GENERATIONS; CELL WALL; CHLOROPLAST; EVOLUTION OF PLANTS; LICHEN; LIFE CYCLES; LIMNOLOGIST; OCEAN ECOSYSTEMS: HARD BOTTOMS; OCEAN ECOSYSTEMS: OPEN OCEAN; OCEAN ECOSYSTEMS: SOFT BOTTOMS; PHOTOSYNTHESIS; PLANKTON; PLANT; PROTISTA

Virginia Card

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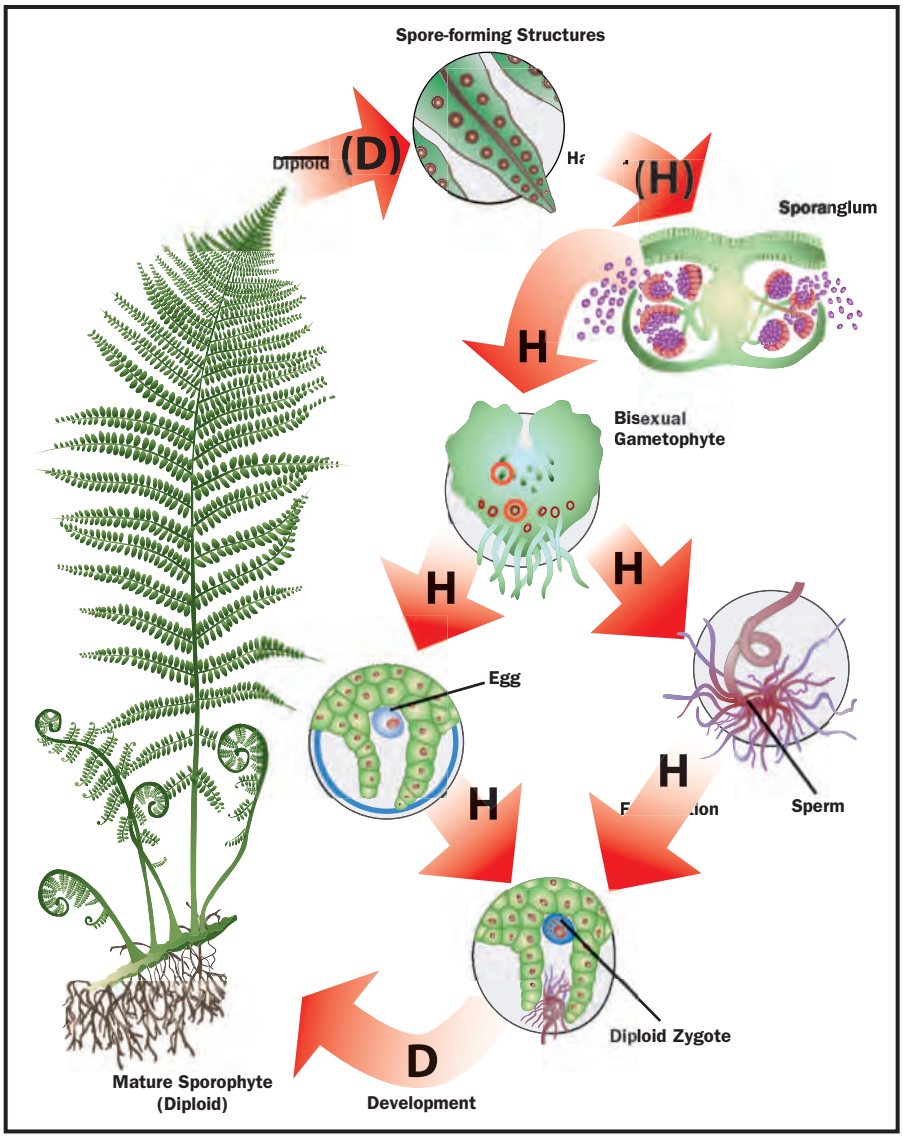
Alternation of Generations

diploid having pairs of chromosomes in the nucleus

meiosis cell division that forms eggs or sperm

haploid having single, non-paired chromosomes in the nucleus

For sexually reproducing multicellular organisms such as plants and animals, the life cycle requires that **diploid** cells divide by **meiosis** to create **haploid** cells. Haploid cells then fuse to recreate the diploid number and a new organism. Alternation of generations refers to the occurrence in the plant life cycle of both a multicellular diploid organism and a multicellular haploid organism, each giving rise to the other. This is in contrast to animals, in which the only multicellular phase is the diploid organism (such as the human man or woman), whereas the haploid phase is a single egg or sperm cell.



The fern is an example of alternation of generations, in which both a multicellular diploid organism and a multicellular haploid organism occur and give rise to the other.

Alternation of generations is easiest to understand by considering the fern. The large, leafy fern is the diploid organism. On the undersurface of its fronds or leaves, its cells undergo meiosis to create haploid cells. However, these cells do not immediately unite with others to recreate the diploid state. Instead, they are shed as spores and germinate into small haploid organisms. Because the diploid organism creates spores, it is called the sporophyte generation of the life cycle. Upon reaching maturity, the haploid organism creates haploid egg and sperm cells (gametes) by **mitosis**. Because the haploid organism creates **gametes**, it is called the **gametophyte** generation of the life cycle. The male gametes (sperm) are then released and swim to the female egg. Fusion of the gametes creates the new diploid sporophyte, completing the life cycle.

mitosis separation of replicated chromosomes

gamete reproductive cell, such as sperm or egg

gametophyte a haploid plant that makes gametes by mitosis

Whereas the fern gametophyte and sporophyte generations are completely independent, in some types of plants one generation lives on or in the other and depends on it for nutrition. In mosses, the familiar lush carpet of moss is the gametophyte, and its gametes require a moist environment for short-distance swimming before fusing. The sporophyte lives as a

ovule multicellular structure that develops into a seed after fertilization

fertilization union of sperm and egg

zygote fertilized egg

triploid possessing three sets of chromosomes

endosperm nutritive tissue within a seed

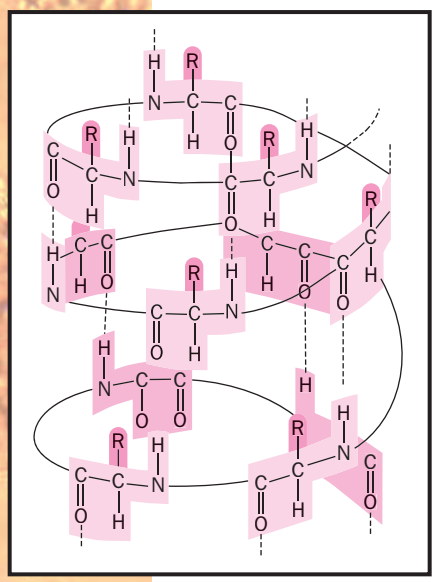
thin stalk attached to the gametophyte. Spores are released into the air and can travel on the slightest breezes to other habitats.

In contrast, in flowering plants (angiosperms), the sporophyte is the dominant form. The male gametophyte has been reduced to just three cells, two of which are sperm. These together form the pollen grain, which is formed from the anther, part of the sporophyte. Similarly, the female gametophyte has been reduced to just seven cells, one of which is the egg cell. These are retained inside the **ovule**, which is part of the sporophyte. In angiosperms, two **fertilization** events take place: one sperm fertilizes the egg to form the diploid **zygote** of the new individual, and the other sperm fertilizes the so-called polar nuclei to form the **triploid endosperm**, a nutritive tissue. Together with maternal sporophyte tissue, these make up the seed. SEE ALSO ANGIOSPERMS; BRYOPHYTES; LIFE CYCLES; MEIOSIS; POLLINATION AND FERTILIZATION; PTERIDOPHYTES; REPRODUCTION IN PLANTS

Richard Robinson

Amino Acid

Amino acids are molecules that have both an amino group (-NH_2) and a carboxylic acid group (-COOH), hence the name. The most common amino acids are the ***α*-amino acids**, the building blocks of **proteins**. These have the amino group, the carboxylic acid group, a hydrogen, and a characteristic side chain all attached to one carbon atom, designated the *α*-carbon. Each type of *α*-amino acid has a unique side chain that determines its properties and its role in proteins. The side chains (or "R" groups) can range from a hydrogen atom, as in glycine, to the more complicated side chains of tryptophan or arginine.



Amino acids link together to form alpha-helices and other fundamental structures, which interact to give proteins their ultimate three-dimensional shape.

α the Greek letter alpha

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

peptide bond bond between two amino acids

polypeptide chain of amino acids

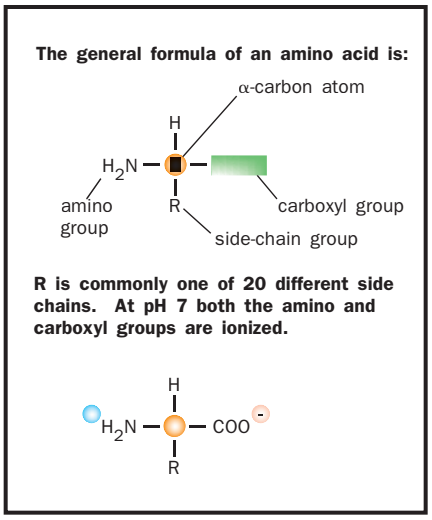
gene portion of DNA that codes for a protein or RNA molecule

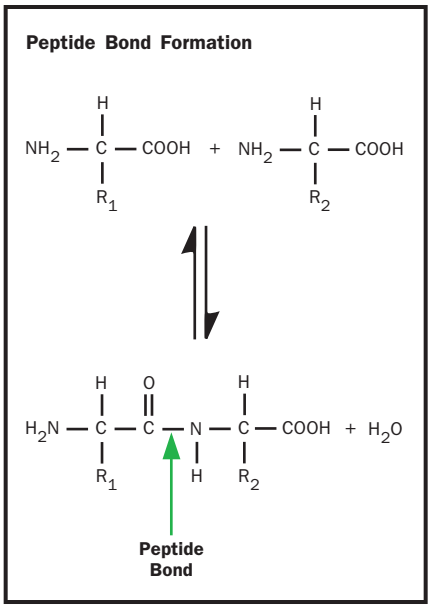
The *α*-carbon atom has four different groups attached to it arranged at the points of a tetrahedron. This arrangement is asymmetric and can occur in two different forms, or enantiomers, that are related to each other in the same way as an object and its image in a mirror. These two enantiomers are called L and D. Only L-amino acids occur in proteins made by living systems. D-amino acids and amino acids other than *α*-amino acids occur in biological systems but are not incorporated into proteins.

Many organisms can synthesize all of the amino acids they require from compounds present in the metabolic pathways they use for energy production. Humans, however, are not able to synthesize all of the necessary amino acids, and a number of them must be obtained from the diet.

The major use of amino acids is to construct proteins. A protein is a linear chain of amino acids linked together by **peptide bonds**. A peptide bond is formed when the amino group attached to the *α*-carbon of one amino acid is joined to the carboxyl group of a second amino acid with the elimination of water. The side chain of each amino acid residue protrudes from the **polypeptide** backbone. The sequence of amino acids in the chain is determined by the deoxyribonucleic acid (DNA) sequence of the **gene** that codes for that protein.

The three-dimensional structure and the properties of a specific protein, and therefore its biological role, are determined by the sequence of





amino acid side chains. In proteins, **acidic** amino acid side chains are negatively charged, and **basic** ones are positively charged. The **polar** and charged amino acids are hydrophilic, meaning they like to interact with water (or are water-loving). The nonpolar, **aromatic**, and sulfur-containing amino acid side chains prefer to interact with themselves or each other (they are hydrophobic, or water-avoiding).

A protein folds so that nonpolar side chains tend to be buried within the protein while polar and charged side chains tend to be exposed to the water around the protein. The biological function of a protein is generally highly dependent on its three-dimensional structure. SEE ALSO ENZYMES; PROTEIN STRUCTURE

Wayne F. Anderson

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

basic having an excess of OH^- ions and a high pH

polar partially charged, and usually soluble in water

aromatic compound including a double-bonded carbon ring

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Amniote Egg

The amniotic egg was an evolutionary invention that allowed the first reptiles to colonize dry land more than 300 million years ago. Fishes and amphibians must lay their eggs in water and therefore cannot live far from water. But thanks to the amniotic egg, reptiles can lay their eggs nearly anywhere on dry land.

The amniotic egg of reptiles and birds is surrounded by a tough outer shell that protects the egg from predators, **pathogens**, damage, and drying. Oxygen passes through tiny pores in the shell, so the embryo doesn't suffocate. Inside the shell are four sacs. The first sac inside the shell is the chorion, which carries oxygen from the shell to the embryo and waste carbon dioxide from the embryo to the shell. Within the chorion is the

pathogen disease-causing organism

amnion, the membrane for which the amniotic egg is named. The amnion keeps the embryo from drying out, so it's critical to living on land. A third sac, the allantois, stores wastes from the embryo and also fuses with the chorion to form the chorioallantoic membrane, which carries oxygen and carbon dioxide to and from the embryo, just like a lung. A fourth membrane, the yolk sac, holds and digests nutritious yolk for the developing embryo.

Together, the shell and membranes create a safe watery environment in which an embryo can develop from a few cells to an animal with eyes and ears, brain, and heart. Because reptiles, birds, and mammals all have amniotic eggs, they are called amniotes.

The duck-billed platypus and some other mammals also lay eggs. But most mammals have evolved amniotic eggs that develop inside the mother's womb, or uterus, and so lack a shell. In humans and other mammals, the chorion fuses with the lining of the mother's uterus to form an organ called the placenta. The placenta transports oxygen and carbon dioxide to and from the embryo and delivers nutrients from the mother's blood. SEE ALSO BIRD; EVOLUTION; FETAL DEVELOPMENT, HUMAN; MAMMAL; REPTILE

Jennie Dusheck

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Amphibian

The class Amphibia consists worldwide of nearly 4,700 species, contained in three major orders: Caudata (salamanders), Gymnophiona (caecilians), and Anura (frogs and toads). Salamanders are composed of about 415 species worldwide, and are typically characterized by their long tails and four limbs of nearly equal size. They first appeared in the fossil record over 190 million years ago in the late Triassic.

The caecilians consist of about 165 species. They have a mostly pantropical distribution, and are characterized by their elongated, annulated (ringed) bodies and lack of legs, resembling worms. These amphibians first appeared in the fossil record nearly 190 million years ago in the early Jurassic.

By far the most successful of the three orders with about 4,100 species worldwide, frogs and toads are characterized by lack of a true tail and by generally having comparatively enlarged hind limbs. The order Anura first surfaced in the fossil record about 230 million years ago in the early Triassic.

cutaneous respiration gas exchange through the skin

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

Amphibians have relatively moist, scaleless skin and rely heavily on **cutaneous respiration** and/or the presence of a buccopharyngeal pump (a muscular pump in the throat) to force air into their mouth and lungs, features not found in other classes of terrestrial vertebrates. In addition, most amphibians produce eggs that develop and hatch outside their bodies laying gelatinous, unshelled eggs in water or moist places. Many undergo a larval aquatic existence before **metamorphosis** into adults (unlike other classes

A strawberry poison arrow frog in Costa Rica.

of terrestrial vertebrates). In a few species, the female retains the eggs in her body where they are nourished directly by her before she gives birth to her young, or they develop by absorbing their own yolk (a phenomenon also known to occur in at least one species of sea snake, class Reptilia).

Some populations of amphibians have disappeared or begun to decline, and this has raised concern among biologists worldwide. It is unknown if this phenomenon is uniformly widespread across all continents, or is occurring only in selected areas. SEE ALSO CROCODILIANS; REPTILE; TUATARA; TURTLE

Joseph T. Collins

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Anabolic Steroids

Anabolic steroids are synthetic chemicals that mimic the effects of the male sex **hormone** testosterone. Some athletes seeking increased muscular strength and size abuse anabolic steroids. They may reach their goal of increased strength in the short term but risk serious medical complications in the long term.

"Anabolic" denotes the ability to induce **protein** synthesis, particularly in muscle cells. As a result, **isometric** muscle strength increases. These steroids are also androgenic, which means that they cause changes characteristic of males, such as growth of facial hair, loss of scalp hair, deepening of the voice, skin oiliness, and aggressive behavior.

hormone molecule released by one cell to influence another

requires energy

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

isometric relating to contraction without movement

Anabolic steroids increase muscular strength and size, but put their abusers at risk for serious medical complications.

A female taking anabolic steroids experiences irregular menstrual periods and atrophy of the breasts and uterus, and develops the male-associated characteristics. A male may develop an enlarged prostate and atrophy of the testicles.

Steroid abuse stunts height, increases weight, dampens immunity, and can damage the kidneys, liver, and heart. Blood vessels may become blocked with fatty plaque. The liver may develop tumors, and infertility is common. Psychiatric symptoms include depression, delusions, and violent tendencies, sometimes called "'roid rage."

Athletes call anabolic steroids 'roids, juice, pump, or hype. Some of the one hundred varieties are oxymetholone, oxandrolone, and stanozolol (taken orally) and nandrolone and boldenone (taken by injection). Abusers may take one huge dose seeking instant strength, slowly build up the dose (pyramiding), or "stack" different types of steroids. Whatever the delivery route, the message to the body is the same: there's too much testosterone; halt normal production.

Despite the well-known side effects of anabolic steroids, use among athletes is widespread, perhaps because of the example set by professional baseball, basketball, and hockey players who use them. However, the National Football League, International Olympic Committee, and National Collegiate Athletic Association ban their use. Still, about 30 percent of college and professional athletes use anabolic steroids, as do 10 to 20 percent of high school athletes. Among U.S. bodybuilders, studies show that steroid use exceeds 80 percent.

Olympic athletes have often been punished for steroid use. After Canadian Ben Johnson flew past his competitors in the 100-meter run in the 1988 summer Olympics, officials rescinded his gold medal when a urine test revealed stanozolol in Johnson's system. His natural testosterone level was only 15 percent of a normal male's. Shot-putters, discus throwers, wrestlers, and swimmers have also been known to use anabolic steroids. In 2000, a urine test on U.S. shot-putter C. J. Hunter revealed one thousand times the allowable limit of nandrolone.

anemia lack of oxygen-carrying capacity in the blood

Anabolic steroids do have legitimate medical uses. They were first synthesized in the 1930s to treat underdeveloped testes and resulting testosterone deficiency. In the 1950s, they were used to treat **anemia** and muscle-wasting disorders and to bulk up patients whose muscles had atrophied from extended bed rest. In the 1960s, anabolic steroids were used to treat some forms of dwarfism. Today anabolic steroids are being studied for their ability to alleviate the extreme body wasting associated with acquired immunodeficiency syndrome (AIDS). Their most common use, however, remains among athletes seeking a quick competitive edge. SEE ALSO ENDOCRINE SYSTEM; HORMONES; MALE REPRODUCTIVE SYSTEM; MUSCLE

Ricki Lewis

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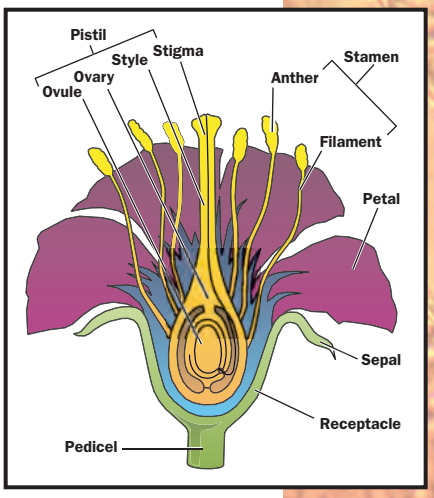
Anatomy of Plants

Plants are the primary producers in Earth's **ecosystem**. Plants are autotrophic, meaning that they produce their own food (via photosynthesis), and as a result ultimately produce food for the ecosystem's consumers (such as humans). Understanding plant function is the key to enhancing crop production, preserving plant biodiversity, producing medicines, and much more. However, in order to understand plant function, one must understand plant form.

ecosystem an ecological community and its environment

General Anatomical Organization of Plants

Like animals, plant bodies are made up of a variety of cell types that are organized into tissues. Tissues are organized into organs, and organs function together within systems. Within this hierarchy of structure, emergent properties arise at each level. An emergent property is a characteristic or function that can be found at one level that is not present at lower levels. For example, an individual cell of a leaf cannot perform all of the functions of the leaf, but the cells of the leaf collectively perform the function of a leaf. Therefore, the function of each lower level is best understood in the context of the system in which it exists. For this reason, this article begins by exploring the gross anatomical features of a plant and proceeds to examine the anatomy in progressive detail.



Structure of angiosperm flowers. Redrawn from Van de Graaff et al., 1994.

Plants are made up of two organ systems: the shoot system and the root system. For terrestrial plants the shoot system is above ground and consists of a number of organs. These include stems, leaves, and flowers. On the other hand, the root system is most often underground and consists of organs such as roots, underground stems (tubers), and rhizomes.

Each of these organs performs a different function. Stems are support structures and mediate the growth of the plant. Shoot tips contain actively dividing regions called meristems, which produce auxin, a **hormone** that regulates the growth and shape of the plant. Leaves are the primary sites of photosynthesis, so they are the food production centers of the plant. Flowers are reproductive structures, where eggs and sperm (pollen) are produced and where pollination and **fertilization** occur. Roots, tubers, and rhizomes are the main system for nutrient and water acquisition and storage. All of these organs are made up of cells that can be categorized into three major tissue types: dermal, ground, and vascular tissue.

hormone molecule released by one cell to influence another

fertilization union of sperm and egg

Dermal Tissue

Dermal tissue makes up the outer layers of the plant and contains epidermal cells that secrete and are coated with a waxy layer. This waxy coating, the cuticle, prevents excessive water loss from the plant. While the dermal tissue primarily serves a protective role, it also has a variety of other specialized functions depending on the particular organ where it is located.

In leaves, dermal tissue contains specialized cells called **guard cells** that make up structures called **stomata**. Stomata facilitate the exchange of gases in the leaf. Carbon dioxide (CO_2) diffuses into the leaf through the stomata for use in photosynthesis, and oxygen (O_2), the waste product of photosynthesis, diffuses out of the leaf through stomata. Stomata are also crucial for water transport through the **xylem**. Stomatal opening results in the evap-

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

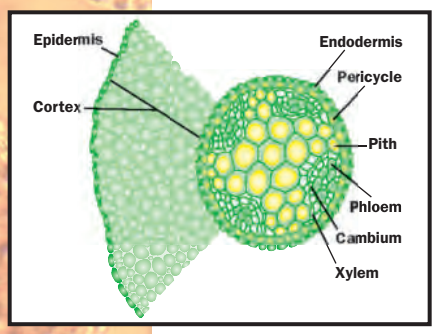
oration of water from the air spaces of the leaf. This creates negative water pressure that pulls on the column of water in the xylem. The evaporation of water from the stomata is the main driving force for water transport through the water. In roots, epidermal cells have a specialized structure that facilitates water and nutrient absorption, the main function of the root. Some of the root epidermal cells have long membranous extensions called root hairs that increase the absorptive surface area of the root. Root epidermis also interacts with symbiotic fungi that form **mycorrhizae**, which increase nutrient absorption.

mycorrhizae symbioses between soil fungus and plant root to maximize absorption

Ground Tissue

Many different functions are performed by ground tissue including photosynthesis, storage, and support. Ground tissue makes up the majority of the plant structure and is composed of three cell types: parenchyma, collenchyma, and sclerenchyma cells.

Parenchyma cells are the least specialized cells in a plant. These cells are responsible for the production and storage of nutrients. Photosynthesis occurs in the chloroplasts of parenchyma cells in leaves. Parenchyma cells in stems, roots, and fruits have structures that store starch. Most developing plant cells are structurally similar to parenchyma cells. During their differentiation, they become specialized in form and function and lose the potential to divide. Mature parenchyma cells do not usually divide, but they retain the ability to divide and differentiate into different cell and tissue types in the event of an injury to the plant.



Transverse section of tissues of a dicot root. Redrawn from Van de Graaff et al., 1994.

Collenchyma and sclerenchyma cells provide structural support for the plant. Collenchyma cells have thick, yet pliable, cell walls. These cells give structural support to newly formed portions of a plant without restricting growth. Collenchyma cells are stacked end on end and are oriented in strands just beneath the epidermis of the young structure. The relatively soft cell wall allows the collenchyma cells to elongate as the structure grows.

On the other hand, sclerenchyma cells provide support to mature plant structures. Like collenchyma cells, they have very thick cell walls. However, the cell walls of sclerenchyma cells contain **lignin**, a molecule that makes the cell wall hard. This provides strength to the cell wall, but restricts the ability of the cells to elongate and grow. Since a sclerenchyma cell functions solely to provide structural support, many sclerenchyma cells are actually dead at functional maturity. The cell membrane, **protoplasm** (cytoplasm) and **organelles** are gone, leaving only the rigid cell wall that serves as a scaffolding system for that structure.

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

protoplasm fluid portion of a plant cell within the cell wall

organelle membrane-bound cell compartment

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

Vascular Tissue

Vascular tissues make up the organs that transport water, **minerals**, and food throughout the plant. Vascular tissue can be divided into two functional units. Xylem transports water and minerals from root to shoot. **phloem** transports nutrients (such as sugar and **amino acids**) from leaves and other production sites to roots, flowers, stems, and other tissues that need them. The cells that make up vascular tissue are unique in their structure. Their specialized characteristics allow them to transport material through the plant efficiently while providing structural support to the plant.

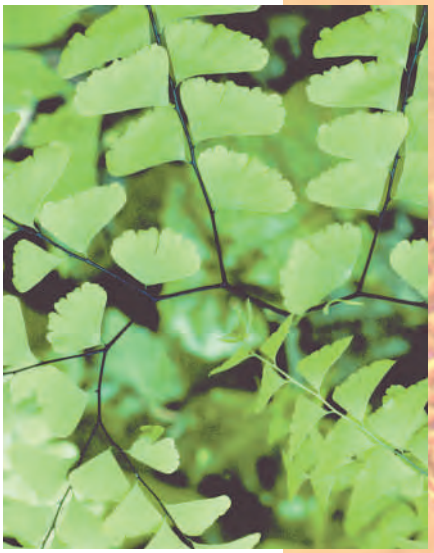
phloem plant tissue that conducts sugars from leaves to roots and other tissues

amino acid a building block of protein

Xylem tissue contains two types of cells: tracheids and vessel elements. Like sclerenchyma, both of these cell types are dead at functional maturity and therefore lack protoplasm. Tracheids are long, thin cells that have tapered ends. They overlap on another, and water passes from tracheid to tracheid via small pores. Vessel elements are shorter and are stacked end to end, forming more of a tube structure. Water flows in the tube by passing through perforated end walls between cells.

Phloem tissue is made up of two different types of cells: sieve tube members and companion cells. Sieve tube members are the main conducting cells, and are named for the sievelike areas along their cell walls through which the phloem sap moves from cell to cell. Unlike cells of the xylem, sieve tube members are alive at functional maturity, but do not have nuclei. For this reason, companion cells are closely associated with sieve tube members. These cells do have nuclei and serve to support the sieve tube members. The **cytoplasm** of sieve tube members and companion cells is connected through numerous pores called plasmodesmata. These pores allow the companion cells to regulate the content and activity of the sieve tube member's cytoplasm. Moreover, the companion cells help to load the sieve tube members with sugar and the other metabolic products that they transport throughout the plant. SEE ALSO ALGAE; ANGIOSPERMS; BRYOPHYTES; CELL WALL; CONIFERS; FRUITS; GYMNOSPERMS; LEAVES; MERISTEMS; MYCORRHIZAE; PTERIDOPHYTES; ROOTS; SHOOTS; TRANSLOCATION; WATER MOVEMENT IN PLANTS

Susan T. Rouse



A photograph of a maidenhair fern, showing its shoot system of stems and leaves.

cytoplasm material in a cell, excluding the nucleus

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Angiosperms

The angiosperms, or flowering plants, are the largest and most species-rich **phylum** of plants, with more than 250,000 species estimated.

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

Defining Characteristics

The term "angiosperm" derives from two Greek words: *angeion*, meaning "vessel," and *sperma*, meaning "seed." The angiosperms are those plants whose seeds develop within a surrounding layer of plant tissue, called the carpel, with seeds attached around the margins. This arrangement is easily seen by slicing into a tomato, for example. Collectively, carpels together with the style and stigma are termed the ovary, and these plus associated structures develop into the mature fruit. The enclosed seeds and the presence of carpels distinguish angiosperms from their closest living relatives, the **gymnosperms**, in which the seed is not enclosed within a fruit, but rather sits exposed to the environment. Some defining characteristics of angiosperms include flowers, carpels, and the presence of endosperm, a nutritive substance found in seeds, produced via a second **fertilization** event.

gymnosperms "naked seed" plants, including conifers

fertilization union of sperm and egg

An iris. Angiosperms, or flowering plants, are quite diverse in morphology, growth form, and habitat.

However, some current studies suggest that endosperm is not unique to angiosperms.

Angiosperm flowers are generically characterized by having four whorls, or sets of organs: **sepals**, petals, stamens, and carpels. The carpels may be united or fused to form a compound **pistil**, and the number of stigma lobes may then be indicative of the number of carpels. The pistil also includes the stigma, on which pollen lands, and style, the tube leading to the egg. Stamens are separated into anthers, which produce pollen, and filaments. The mature ovary (part of the pistil containing the seeds) is termed a "fruit." Sepals and petals may be showy and colorful to attract pollinators, or may be quite reduced in wind-pollinated plants, such as grasses. Likewise, fruits may assume a wide variety of forms associated with mode of dispersal, such as fleshy fruits (for example, berries) dispersed by animals, and dry, winged fruits adapted for wind dispersal, such as the samaras of maple trees, which twirl like helicopters as they fall.

Evolution and the Angiosperms

The angiosperms are a relatively recent group of land plants, and are thought to have originated in the early Cretaceous, only 130 million years ago. The angiosperms increased dramatically in abundance during the Cretaceous. This sudden, dramatic appearance of large numbers of very diverse flowering plant species in the fossil record was referred to by English naturalist Charles Darwin as an "abominable mystery." It is postulated that coevolution with animal pollinators, especially insects, may have contributed to the explosion and abundance of angiosperm species which characterize the modern earth's flora. However, even today, it is not clear what group of nonflowering plants the angiosperms are most closely related to, or what the relationships of the early **lineages** of flowering plants are to one another. This is in part due to the extremely fast evolution of this group of plants, over a relatively short period of time, and the extinction of many closely related lineages of seed plants, some of which may be more closely related to the modern angiosperms than extant seed plant lineages.

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

pistil female reproductive organ of a flower

lineage ancestral line

Most contemporary studies, which are based on **phylogenetic** analysis of deoxyribonucleic acid (DNA) sequence data from as many as six different genes, suggest that the closest relatives of the angiosperms are the gymnosperms, which include cycads, *Ginkgo*, conifers (the group that contains the pines, spruces, firs, and relatives), and Gnetales (a group containing three ancient genera: *Ephedra*, the Mormon tea; *Welwitschia*, a bizarre plant of southwest African deserts; and *Gnetum*, a genus of mostly tropical vines). The origins of angiosperms are not well understood and remain problematic, in part because many seed plant lineages have already gone extinct. However, studies indicate that the earliest lineage of flowering plants, or **basal** angiosperms, may include the family Amborellaceae (with the single living species *Amborella trichopoda*, a shrub from the South Pacific island of New Caledonia). Other early diverging lineages of angiosperms include Nympheales, the water lilies; Illiciales, or star anise; a group called the magnoliids, which includes magnolias, laurels, and black pepper; and the very large group called the **monocots**. A final lineage, the **eudicots**, contains all other flowering plants and comprises the bulk (approximately three-quarters) of the flowering plant species.

phylogenetic related to phylogeny, the evolutionary development of a species

basal lowest level

monocot any of various flowering plants, such as grasses and orchids, that have a single cotyledon in the seed

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

Monocots, Dicots, and Eudicots

The angiosperms have historically been divided into two groups: the monocotyledons (monocots) and the dicotyledons (dicots). These terms derive from the number of seed leaves, or **cotyledons**, the plants have upon germination. Dicots have recently been shown not to be an evolutionarily natural group.

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

The monocots do form an evolutionarily natural, or **monophyletic**, group, and include familiar plants such as lilies, grasses, and palm trees. The monocots are characterized by having a single cotyledon, an **adventitious** root system, stems with scattered vascular bundles, absence of woody growth, leaves with parallel venation, flower parts usually in sets of threes, and monoaperturate pollen (that is, pollen with one large, groovelike aperture).

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

adventitious growing from a nonstandard location

The dicots have historically included all those plants with two cotyledons, tap root systems, stems with vascular bundles in a ring, leaf venation forming a netlike pattern, and flower parts in fours or fives. Current studies indicate that the dicots do not form an evolutionarily monophyletic group, but instead include several different lineages, some of which are more closely related to the monocots.

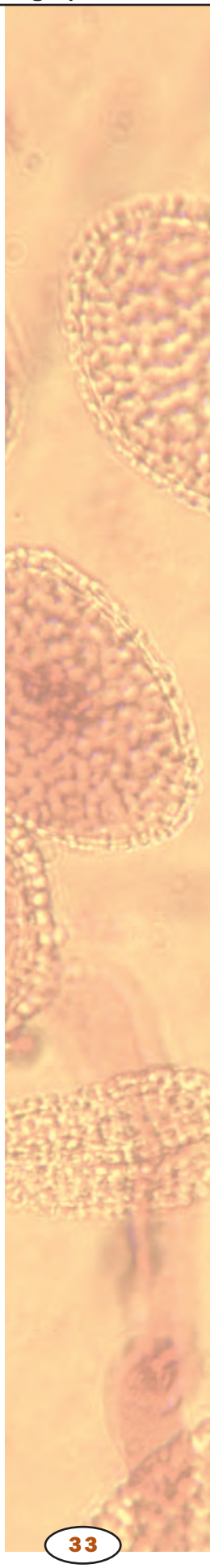
Two groups that are well supported in contemporary studies are the eudicots ("true dicots"), characterized by having triaperturate pollen (that is, pollen with three long, groovelike apertures), and the noneudicots, which are characterized by having inaperturate pollen; that is, pollen lacking apertures. Noneudicot, basal angiosperms include the monocots, the laurels and avocados, the magnolias, black pepper, *Amborella*, water lilies and Illiciaceae (the star anise family). Evolutionary relationships among these noneudicot groups are not well understood. The eudicots include many familiar plants, including most trees, and include two major groups of flowering plants, the asterids (including the composite family, and the economically important Solanaceae, the potato family) and the rosids (including the rose family and the economically important legume family).

Diversity and Symbioses

Some of the most species-rich families of flowering plants include the monocot species of Orchidaceae, the orchids (19,500 species), the Poaceae or grass family (8,700), the Cyperaceae or sedge family (4,500), and the eudicot families of Euphorbiaceae or spurge family (6,900), the Fabaceae or legume family (18,000), the Rosaceae or rose family (3,000), Brassicaceae or mustard family (4,130), Rubiaceae or coffee family (9,000), the Lamiaceae or mint family (6,970), the Apiaceae or carrot family (4,250), and the Asteraceae or composite family (23,000).

The angiosperms are of great ecological importance and are principal components of nearly all of the major land habitats. Correspondingly, flowering plants are quite diverse in **morphology**, growth form, and habitat, and range from the minute aquatic plants in the duckweed family (genus *Lemna*) to the massive forest trees, such as oak and maple. Angiosperm flowers can be quite reduced, as in the grasses, where the most visible floral parts are the stamens and stigmas, to quite elaborate floral structures exhibiting fusion of parts and development of complex shapes, such as those evolved to attract insect pollinators in the orchids, mints, and snapdragons.

morphology related to shape and form



symbionts organisms living in close association with another organism

An important aspect of angiosperm evolution is their well-documented relationships with other organisms such as animal pollinators, mycorrhizal (fungal) root associations, and even bacteria. Indeed, one of the most successful families of flowering plants, in terms of number of species, are the orchids, which have very specialized relationships with both pollinators and mycorrhizal interactions. Another highly successful family, the legume family, has evolved symbiotic relationships with nitrogen-fixing bacterial **symbionts**. Some flowering plants, such as the acacias of the legume family, obtain protection from herbivores via symbiotic relationships with ants. Through agriculture, humans have developed their own complex relationship with angiosperms. It is these relationships with other organisms that is the hallmark of angiosperms, and as such have contributed to the success of the flowering plants in the modern earth's flora. SEE ALSO CONIFERS; FRUITS; GYMNOSPERMS; MONOCOTS; NITROGEN FIXATION; POLLINATION AND FERTILIZATION; ROOTS; SYMBIOSIS

Molly Nepokroeff and Elizabeth A. Zimmer

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Animalia

eukaryotic of, relating to a cell with a nucleus

The kingdom Animalia, or Metazoa, includes all animals. Animals are multicellular, **eukaryotic** organisms, which are heterotrophic, meaning they obtain nutrition from organic sources. Most animals obtain nutrition by ingesting other organisms or decomposing organic material.

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

Animal cells are characterized by their lack of a rigid cell wall exhibited by fungi and plants. Instead, animal cells are held together by structural **proteins** such as collagen. All animals, except for the sponges, are made up of cells organized into tissues that are specialized for some function. As a result, most animals are capable of complex behavioral responses and rapid movement.

diploid having pairs of chromosomes in the nucleus

motile able to move

zygote fertilized egg

Most animals are **diploid**, meaning they have two copies of all genetic information for most of their life cycle. Most animals reproduce sexually with differentiated sex cells. These cells (large, nonmotile eggs and small, **motile** sperm) fuse to form a new diploid individual called a **zygote**. The zygote undergoes a series of cell divisions, called cleavage, to form a hollow, multicellular ball known as a blastula. The blastula then folds in on itself to form a gastrula, a double-walled structure with an opening to the outside called the blastopore. Some animals (including all mammals) develop and mature directly into adults but the development of most animals includes larval stages. Larvae are immature forms that are morphologically distinct from adults. The process of **metamorphosis** transforms larvae into

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

A jellyfish is a radially symmetric animal with internal organs that are visible through its transparent, gelatinous body.

their adult form. A familiar example is the metamorphosis of a tadpole into a frog.

Although taxonomists disagree about the identity of major animal groups and the relationships among them, most agree that Animalia is monophyletic. This means that all animals can trace their descent to a single common ancestor. There are approximately thirty-two living animal groups, or phyla, each with a distinctive body plan and biological properties.

All of these are the survivors of the one hundred or so animal phyla that evolved during the Cambrian explosion. This incredible diversity of animal body plans and lifestyles arose in the relatively short period of 40 million years, between 565 and 525 million years ago. All of today's remarkably diverse animal forms are variations on the basic body plans that evolved during the Cambrian.

The most primitive animal group is the phylum Porifera, the sponges. The remaining animal groups can be divided into radial and **bilaterally symmetric** animals. **Radially symmetric** animals are the cnidarians, including jellyfish, corals, and anemones, and ctenophores, or comb jellies.

bilaterally symmetric symmetric, or similar, across a central line

radially symmetric symmetric, or similar, about a central point (a wheel is radially symmetric)

Bilaterally symmetric animals (which include all vertebrates) are further divided based on types of body cavities and variations on the pattern of gastrula formation during development. Flatworms, phylum Platyhelminthes, have no body cavity. Ten phyla of animals, including **nematodes** and rotifers, have a primitive type of body cavity.

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

protostome "mouth first"; referring to the early development of the oral pore during gut tube formation

deuterostome "mouth second"; referring to the early development of the anal pore during gut tube formation

All other animals have a true body cavity and are divided into two major groups. **Protostomes** include Mollusca (clams, snails, and octopi), Annelida (segmented worms), Arthropoda (spiders, crustaceans, and insects), and several minor phyla. **Deuterostomes** include Echinodermata (sea stars and sea urchins), two proto-chordate phyla, and Chordata (tunicates, lancelets, sharks, fish, amphibians, snakes and lizards, birds, and mammals).

SEE ALSO ANNELID; ARTHROPOD; CAMBRIAN EXPLOSION; CELL; CHORDATA; CNIDARIAN; ECHINODERM; MOLLUSK; NEMATODE; PLATYHELMINTHES; PORIFERA; PROTEIN STRUCTURE; TUNICATE

Tanya A. Dewey

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Annelid

Annelids, or true-segmented worms, are members of the animal phylum Annelida, the most complex of all wormlike groups of organisms. Annelids are commonly found in terrestrial, as well as marine, brackish, estuarine, and freshwater **ecosystems** worldwide. Most annelids are free-living, although several species have parasitic, mutualistic, or commensal relationships with other animals, and many species are commonly associated with aquatic and terrestrial plants.

ecosystem an ecological community and its environment

Six major classes comprise this phylum: Polychaeta (polychaete, or many-bristled worms; primarily marine; more than 15,000 species [spp.]); Oligochaeta (oligochaete worms; freshwater, terrestrial, marine; more than 8,000 spp.), Hirudinea (leeches; freshwater, terrestrial, marine; more than 700 spp.), Branchiobdellida (crayfish worms; freshwater, live on crayfishes; more than 100 spp.), Aphanoneura (suction-feeding worms; freshwater; more than 30 spp.), and Acanthobdellida (bristle leech; parasitic on Arctic marine fishes; 1 sp.). As with any group of organisms, the **phylogenetic** relationships of the diverse groups within annelids, and of the phylum to others within the animal kingdom, is the subject of continuing debate. The marine invertebrate groups Echiura and Sipunculida recently were aligned with the annelids.

phylogenetic related to phylogeny, the evolutionary development of a species

bilaterally symmetric symmetric, or similar, across a central line

All annelids are **bilaterally symmetrical**, with an elongated, cylindrical body shape divided both externally and internally by a regular, linear series of segments. The highly developed digestive, circulatory, nervous, and excretory systems within the body cavity, or coelom, reflect external segmentation and generally are repeated serially; this is called metameric segmentation, and distinguishes annelids from all other wormlike groups. Annelids range in size from less than 0.7 millimeters (0.019 inch) to over 3

meters (9.8 feet) in length. The number of segments is relatively fixed in some groups (Branchiobdellida, Hirudinea), but indeterminate in others. External form of annelids is diverse, even within each group; the polychaetes may have distinct body regions, with limblike parapodia, chaetae (hairs), tentacles, and antennae, while others may appear similar to an earthworm, with few if any external **appendages**. Most oligochaete species have chaetae arranged in bundles on each segment. Several aquatic oligochaetes and many polychaetes have gills.

appendage attached organ or structure

Leeches are usually flattened, with a posterior sucker and **anterior** suckerlike mouth; several species have jaws, others have an extendable proboscis. The branchiobdellidans have a posterior sucker and an anterior end with several fused segments and distinct teeth. Chaetae are absent in leeches and branchiobdellidans. The single species of Acanthobdellida is shaped like an elongate leech, with a few hooked chaetae located ventrally on a few anterior segments. Annelids are hermaphroditic; reproduction is commonly sexual, but many species reproduce asexually by budding or fragmentation. Annelids are important components of their respective habitats, whether it be the bottom of freshwater or marine environments, or the soil. The feeding habits of many species are important in the decomposition of **organic** matter and recycling of nutrients in terrestrial and aquatic environments. Many annelids feed on algae, insects, carrion, and other worms, and several leech species consume the blood of turtles, birds, fishes, and mammals. SEE ALSO NEMATODE; PLATYHELMINTHES

anterior toward the front

organic composed of carbon, or derived from living organisms

Mark J. Wetzel

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Antibodies in Research

Antibodies are **proteins** made by B cells, part of the body's immune system. The normal function of antibodies is to latch onto foreign substances (antigens) and flag them for destruction, thus helping to fight infection. This ability to bind to specific molecules makes them ideal probes in cell research, where they are used to latch onto, and thus help isolate and identify, molecules of interest in and on cells. Antibodies have become one of the most important tools for studying protein function in cells.

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

To see how antibodies are used, consider the challenge of determining where actin is located in a nerve cell. Actin is a protein that forms part of the **cytoskeleton**, giving internal structure to the cell much like the human skeleton does. First, purified actin is used to trigger an immune reaction in a rabbit. The B cells that make the anti-actin antibodies are then isolated

cytoskeleton internal scaffolding in a cell, composed of protein

An enzyme-linked immunosorbent assay (ELISA) plate, an immunologic test that can be used to indicate pregnancy or HIV infection by detecting very small quantities of antigens and antibodies (HTLV-III viral antibodies, in this case).

and fused with tumor cells. Unlike B cells, tumor cells will grow forever in the lab, and thus can supply large amounts of anti-actin antibodies indefinitely. These can be harvested from the cells in large quantities. The resulting antibodies are called "monoclonal" antibodies, because they derive from identical (cloned) cells.

Next, in order to make the antibodies visible once inside the cell, a fluorescent molecule is attached to them. They are then injected into the cell using a very fine glass needle. Once an antibody encounters actin, it attaches to it. The cell can then be examined under the light microscope, where the fluorescent molecules will light up, revealing the location of the actin. Of course it is not just actin that can be found this way; any protein to which we can make an antibody can be located in the cell.

Several modifications and extensions of this basic procedure are possible. To mark more than one protein at a time, a set of different antibodies is used, each marked with a differently colored fluorescent tag. In this way, for instance, the spatial relations between actin and other cytoskeleton proteins can be visualized. Instead of fluorescent tags, antibodies can be attached to gold particles, which will show up under the electron microscope. Outside of cells, antibodies attached to glass beads can grab proteins out of a homogenized cell puree, allowing the protein to be isolated for further study. In one widely used technique called western blotting, fluorescently tagged antibodies are used to locate proteins of interest that have been separated in **electrophoresis** gels.

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

enzyme protein that controls a reaction in a cell

Antibodies are also used in a test, or assay, called the **enzyme**-linked immunosorbent assay (ELISA). This is the assay used in the home pregnancy test, which detects the presence of human chorionic gonadotropin (HCG), produced by human embryos. The test kit contains an antibody to HCG, which traps HCG if it is present in a woman's urine. Next, a second antibody to HCG is added, which will bind to the HCG if it is trapped. This antibody is linked to an enzyme called peroxidase. Chemicals are then

added which the peroxidase will cause to react, making a color change. The color change will only occur if the enzyme is present, and the enzyme will only be present if the HCG is present. Therefore, a color change indicates pregnancy. An ELISA test is also used to screen for HIV (human immunodeficiency virus) infection. In this case, the test kit contains HIV proteins, which bind to anti-HIV antibodies in the patient's blood.

It is the specificity of the antibody-antigen reaction, combined with the ability to link one or the other to fluorescent tags, enzymes, or other markers, that makes antibodies such versatile tools in both basic and clinical research. SEE ALSO ANTIBODY; CLONE; CYTOSKELETON; ELECTROPHORESIS; FEMALE REPRODUCTIVE SYSTEM

Richard Robinson

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YALOW, ROSALYN SUSSMAN (1921–)

U.S. biologist who developed a technique, called "radioimmunoassay," for detecting and measuring tiny amounts of biological substances using radioactive antibodies. Her technique led to enormous numbers of medical breakthroughs, but most notably it opened up the entire field of endocrinology, the study of hormones. Dr. Yalow was awarded the 1977 Nobel Prize in medicine for her research.

Antibody

In 1890 scientists transferred blood from animals with diphtheria to animals never exposed to the disease. The second group of animals became resistant (or immune) to diphtheria. Over the next decade, investigators such as Emil von Behring, Shibasabura Kitasato, Karl Landsteiner, and Paul Ehrlich studied this phenomenon and discovered that this transfer of immunity occurred because of **proteins** called antibodies. This type of immunity was called humoral immunity. The word "humoral" refers to body fluids, and antibodies are found in the liquid part of the blood. Antibodies are an extremely important part of the body's defense against infection.

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

Antibodies are also called gamma globulins and **immunoglobulins** (abbreviated "Ig"). Vertebrate animals make antibodies, but invertebrate animals do not. They are made by white blood cells called B lymphocytes (or B cells). Antibodies are capable of attaching to foreign invaders, targeting them for destruction. They can do this because of their structure.

immunoglobulin an immune protein, also called an antibody

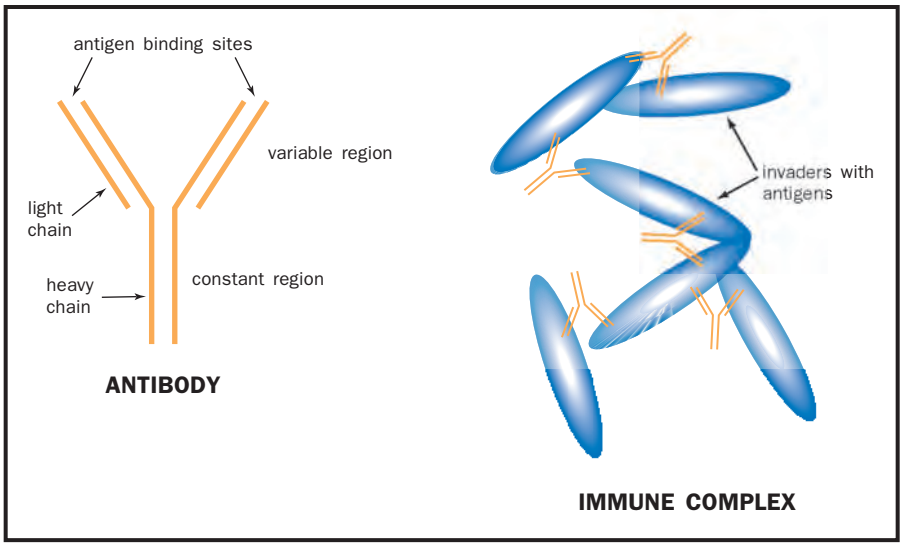
Structure

Antibodies are Y-shaped molecules. At the end of each arm of the Y is a pocket called an antigen binding site. An antigen is a piece of a foreign invader that starts an immune response. An antigen fits inside the antigen binding site of an antibody because the structures match, like a key in a lock. Each antibody has antigen binding sites different from other antibodies. Consequently, each antibody recognizes a different piece of a foreign invader. This explains how the immune system specifically identifies a wide variety of foreign invaders.

Each antibody is composed of four chains of **amino acids**. There are two light chains and two heavy chains. The arms of the antibody contain both light and heavy chains. They are called the *variable regions* because this is where antigen binding sites are located. The **genes** that determine the variable region's structure undergo a series of rearrangements as a B cell

amino acid a building block of protein

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



matures. Millions of possible antibodies can be produced by this rearrangement. However, once the genes are rearranged, the B cell is committed to making only one type of antibody.

The base of the Y contains only heavy chains and is called the *constant region*. The constant region determines the antibody's class. Mammals make five main classes of antibodies. Each class works differently to protect the body from disease.

Classes of Antibodies

IgM and IgD are two classes of antibodies. They are found on the surface of mature B cells. If a B cell encounters an invader with antigens that match its antibodies (like a key in a lock), the antigen is brought inside and then displayed on the surface, akin to waiving the enemy's captured flag. This alerts other immune cells that it is ready to be activated. If the B cell gets the appropriate signals from **T cells**, it becomes activated, dividing rapidly and secreting antibodies into the surrounding fluid. B cells that release antibodies are also called plasma cells. The first class of antibodies secreted by B cells is IgM. Like all antibodies, IgM travels through the body's fluids, binding to antigens to eliminate the invader. IgM antibodies are often found in groups of five, forming a structure called a pentamer.

T cell white blood cell that controls the immune response

The B cell may then switch the class of antibodies it is secreting to more effectively remove the invader. It will most likely start producing the IgG class of antibodies. Unlike other antibodies, IgG can be transferred across the placenta from mother to fetus.

B cells may also produce IgA antibodies. Because IgA is found in **secretions** such as milk, tears, saliva, sweat, and mucus, it represents an important first line of defense against invaders trying to enter the body. IgA antibodies are often found in groups of two, forming a structure called a dimer.

secretions materials released from the cell

Finally, B cells may produce IgE antibodies. IgE provides protection against parasitic infections. IgE binds to white blood cells called mast cells and basophils. When an antigen is encountered, IgE signals these cells to

release chemicals that cause inflammation. This process is responsible for the symptoms of many allergies.

The binding of antibodies to antigens protects the body in several ways. The invader may simply be neutralized, unable to infect healthy cells. Secondly, large numbers of antibodies can bind large numbers of antigens, forming an immune complex. Immune complexes are large and precipitate out of solution, increasing the chance that white blood cells called phagocytes will destroy them. In fact, any antigen with an attached antibody is likely to be phagocytosed. This is because phagocytes can bind to antibodies, allowing phagocytes to more easily recognize the antigen. Finally, blood proteins called complement can destroy the membranes of foreign cells. Complement proteins do this more easily when antibodies are attached to the target. **Phagocytosis** and complement proteins are both examples of nonspecific immunity.

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

As the research since the late 1800s has shown, interactions between specific antibodies and nonspecific defenses give the immune system a powerful tool to eliminate invaders. SEE ALSO AUTOIMMUNE DISEASE; IMMUNE RESPONSE; NONSPECIFIC DEFENSE; T CELL

John M. Ripper

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Antisense Nucleotides

Antisense nucleotides are either ribonucleic acid (RNA) or deoxyribonucleic acid (DNA) molecules that are **complementary** to a messenger RNA (mRNA) molecule. Because these molecules are complementary to given mRNA, they will bind to the RNA and form a free double-stranded molecule or double-stranded region of a **chromosome**. The double-stranded molecules are not able to interact with **ribosomes** and, as a result, a particular **protein** is unable to be made. Inhibiting the production of a given protein may be important in the control and treatment of many diseases such as cancer.

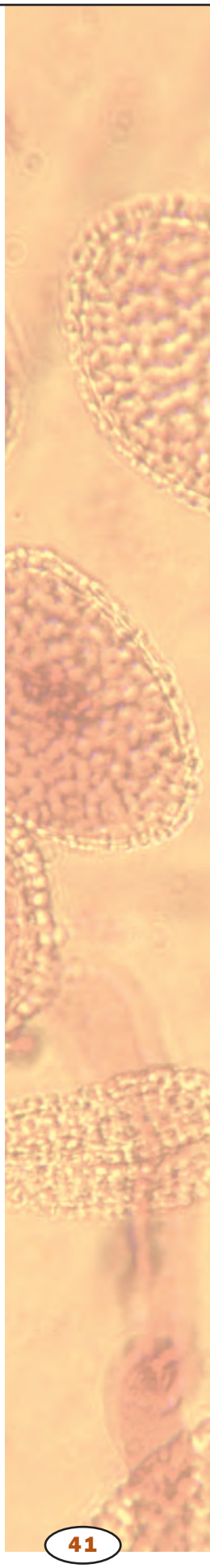
complementary matching opposite

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

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

Two approaches to antisense nucleotides have been tried: (1) direct introduction of antisense nucleotides into cells and (2) synthesis of antisense nucleotides within the cell. In the first approach, short antisense oligonucleotides are introduced directly into cells in hopes that they will interact with the appropriate mRNA. Scientists are using different nucleotides that are complementary to different regions of the mRNA—beginning, middle, or end—in an attempt to determine the most effective sequence.



enzyme protein that controls a reaction in a cell

Unfortunately, **enzymes** within cells often degrade these short oligonucleotides before they can interact with the target mRNA. Replacing the phosphate linkages in the nucleotides with sulfur or other linkages seems to prevent degradation.

The second approach involves using a vector (a vehicle for transferring genetic material) containing the entire gene to transfer DNA into the cells. This DNA will theoretically integrate into the chromosome, duplicate at each cell division, and remain within the cells. These vectors are constructed so that the control sequences for **transcription** are on the DNA strand opposite to the one that is usually used for transcription. Therefore, when inducers are added, the cells make the antisense RNA, which then binds to mRNA from the normal gene. In many cases, the amount of an undesirable protein is reduced.

transcription messenger RNA formation from a DNA sequence

The use of antisense nucleotides is in its infancy, but the results have been promising in reducing certain types of cancer in animals. The procedure has the potential of becoming widely used in the future to treat a variety of diseases, provided that it has low risks associated with it. SEE ALSO DNA; GENE; HYBRIDIZATION; RNA

William R. Wellnitz

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Arachnid

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

exoskeleton external skeleton

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

enzyme protein that controls a reaction in a cell

Spiders, mites, ticks, and scorpions make up the class Arachnida. Arachnids are members of the **phylum** Arthropoda, which also includes crustaceans (such as crabs and shrimp), insects, and other animals with an **exoskeleton** and jointed legs. Although arachnids vary in form and behavior, they share certain characteristics. All arachnids have two body segments, eight legs, and no antennae or wings. Unlike many insects, arachnids do not go through **metamorphosis** but hatch from eggs as miniature adults. Most arachnids are carnivores, often delivering digestive **enzymes** to their victims externally (by squirting it onto or injecting it into the dead or paralyzed prey), and then sucking in the liquefied food. Most arachnids have poor vision and rely mostly on sensing chemicals and vibrations. The jumping spiders, an exception, have excellent vision.

The most common arachnids are mites (order Acari) and spiders (order Araneae). Although mites outdo spiders in sheer numbers, and likely also in numbers of species, mites are all very small (often microscopic) and hard to observe. They usually parasitize plants or animals, and are very abundant in most terrestrial environments. Spiders, although less widely distributed, are found on all continents except Antarctica, and in almost all habitats except the ocean. (Sea spiders are neither true spiders nor arachnids.) Because of their greater physical size, spiders have been studied more, and have played more of a role in human society throughout history.

Newly hatched green lynx spiders.

The most interesting, distinctive, and useful adaptation of the spiders is their silk. Spiders secrete silk (a kind of **protein**) using organs on their abdomens called spinnerets. Spiders put the silk to a multitude of uses: building webs, covering egg sacs, lining their burrows, constructing safety tethers, even making "parachutes" for the dispersal of young spiders on a windy day. Some jumping spiders have even been observed attaching a thread to a wall like a bungee cord and then jumping into the air to catch an insect in flight.

SEE ALSO ARTHROPOD; CRUSTACEAN; INSECT

Robbie Hart

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

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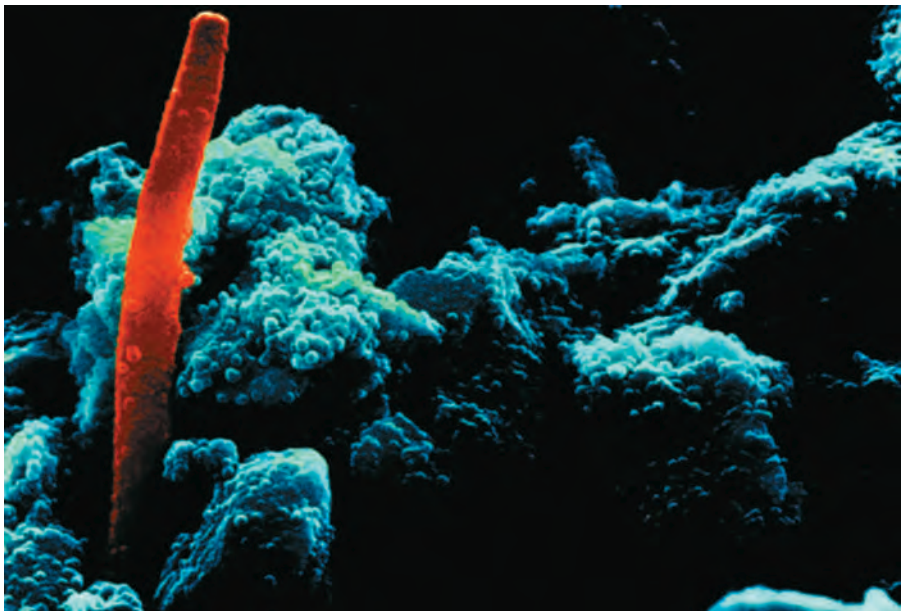
Archaea

Much of human knowledge of the diversity of life has been based on what can be seen. Early attempts at classifying life considered just plants and animals, with fungi part of the plant kingdom. Once microscopes revealed microbial life, biologists could distinguish the bacteria and cyanobacteria, whose cells lack nuclei, from the more complex Protista, single-celled organisms that have nuclei and other **organelles**. However, lumping together

organelle membrane-bound cell compartment



A scanning electron micrograph of a ten-million-year-old Archaea.

prokaryote single-celled organism without a nucleus

all unicellular organisms lacking nuclei—the **prokaryotes**—as bacteria proved inaccurate too.

It took a different way of looking at life to recognize that a group of prokaryotes, the Archaea, actually represent a third major form of life, necessitating invention of a term to supercede kingdom, the domain. The three domains of life are the Bacteria, the Archaea, and the Eukarya. Evidence obtained so far indicates that the Bacteria and Archaea diverged from a common ancestor about 3.7 billion years ago, and somewhat later the Archaea diverged from the **lineage** that would become the Eukarya. Carl Woese, a microbiologist at the University of Illinois, identified the Archaea and proposed the three-domain system of classifying life in 1977.

lineage ancestral line

Considering Different Characteristics

superficial on the surface; not deep

Traditionally, microbial classifications were based on **superficial** similarities, such as shape, habitat, or method of acquiring energy. This approach did not necessarily group organisms that are the most recently descended from shared ancestors. That is, traditional classification considered similarities, but not evolutionary relationships. For example, *Thermus aquaticus* and *Thermoplasma volcanium* both are thermophiles, thriving in hot springs, but the former is a bacterium, and the latter an archaeon. They are not closely related at all, but live in similar surroundings.

In the early 1970s, Woese and others began comparing nucleic acid sequences to discover the evolutionary relationships among microorganisms. Woese focused on ribosomal ribonucleic acid (rRNA) because these are very important molecules that are therefore unlikely to have changed much over evolutionary time. The more alike the rRNA sequences were between two microbes, the more recently they shared an ancestor. Because nucleic acid sequencing had not yet been invented, Woese used an indirect method to compare rRNA sequences. He cut rRNA molecules into pieces with **enzymes**, then visualized the pieces in size order using a technique called autoradiography.

enzyme protein that controls a reaction in a cell

Different patterns of rRNA pieces characterized the prokaryotes known at the time (bacteria), and the eukaryotes. At the suggestion of a colleague, Woese ventured beyond probing the rRNAs of common laboratory strains of bacteria and analyzed a microbe that a graduate student had collected from a nearby septic system. These microorganisms were methanogens; they produced methane (swamp gas) from hydrogen and carbon dioxide in the environment. Surprisingly, the rRNA pattern for the septic system microbe lacked some of the pieces that had been identified in more than forty types of bacteria, and had some mysterious spots of its own.

Woese found other methanogens that didn't fit the expected **prokaryotic** pattern or rRNA fragments. By 1977, he and his colleagues published a landmark paper that described ten species of methanogens that "appear to be only distantly related to typical bacteria" (Woese 1977, p. 5088). Even though further publications continued to make the case for two types of prokaryotes, the idea of domains in general, and of the newly distinguished archaea in particular, took a long time to gain acceptance. Confusion arose over the initial naming of the "new" organisms as "archaebacteria." They are not bacteria; they are archaea.

prokaryotic without a nucleus

Describing Archaea

Since 1977, microbiologists have identified and described several more members of domain Archaea. An initial misnomer was that these microbes are only found in what scientists call extreme environments, such as hot springs and deep-sea hydrothermal vents. Continued research showed that this is not the case. Archaea have been found in rice paddies, soils, swamps, freshwater, and throughout the oceans.

As more microbiologists came to accept the idea that archaea are not bacteria, more distinctions emerged. Archaean transfer RNA (tRNA) molecules differ in sequence from their bacterial or eukaryotic counterparts. Archaean cell walls lack the **peptidoglycans** that are part of bacterial cell walls, yet archaean cell membranes include **lipid** molecules not seen in other types of organisms. Archaea make methane using different enzymes than do bacterial methanogens.

peptidoglycans amino acid chains with linked sugars

lipid fat or waxlike molecule, insoluble in water

Archaeans are sensitive to different antibiotic drugs than are bacteria, indicating a basic difference in cell structure. However, archaea also share characteristics with members of the other two domains. They have some of the same surface molecules as bacteria and transport **ions** in much the same way. But archaea have **proteins** associated with their DNA that resemble the **histone** proteins of eukaryotes and synthesize proteins in a way similar to that of eukaryotes. Also like eukaryotes, archaean **genomes** have more genes interrupted with **intron** sequences, and more repeated sequences, than do bacterial genomes.

ion an electrically charged particle

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

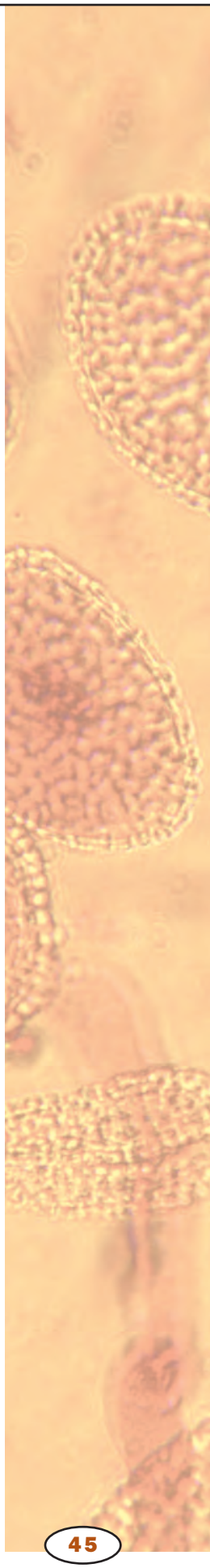
histone protein around which DNA wraps to form chromosomes

genome total genetic material in a cell or organism

intron untranslated portion of a gene that interrupts coding regions

Comparing Genomes

Genome studies confirm that the archaea mix characteristics of the other two domains of life, and much more. A team from The Institute of Genomic Research (TIGR), which included Carl Woese, published the first genome sequence of an archaeon in 1996. The researchers collected samples of *Methanococcus jannaschii* from a "white smoker" chimney 2,600 meters (over 8,500 feet) deep in the Pacific Ocean, an environment that lacks



oxygen and has extremely high temperature (near 85 degrees Celsius [185 degrees Fahrenheit]) and pressure (exceeding 200 atmospheres). Of *M. jannaschii*'s 1,738 protein-encoding genes, more than half are unknown in other organisms. Analysis of its genes revealed that its **metabolism**, cell surface, and ion transport mechanisms resemble those of bacteria, yet its DNA replication and protein synthesis mechanisms are more like those of eukaryotes.

metabolism chemical reactions within a cell

Two years later, TIGR sequenced a second archaeon, *Archaeoglobus fulgidus*. Now researchers could compare archaea. Although *A. fulgidus* resembles *M. jannaschii* in DNA replication, protein synthesis, and **biosynthetic** pathways, it differs markedly in how it senses the environment, moves substances into and out of cells, and regulates metabolism. One quarter of *A. fulgidus*' genes encode proteins that are uncharacterized, but two-thirds of them are also found in *M. jannaschii*. Half of *A. fulgidus*' proteins are known in other organisms. However, one-quarter of its genes are not known, even in *M. jannaschii*. *A. fulgidus* is a thermophilic anaerobe like *J. jannaschii*, but also leads a very different lifestyle in that it metabolizes sulfur. In 1999, TIGR introduced the genome sequence of another archaeon, *Aeropyrum pernix* K1. It differs from the other two in that it lives in the presence of oxygen, but it also has many unique genes.

biosynthetic forming a complex molecule from simpler ones

Compared to other types of organisms, biologists know very little about the archaea. However, the diversity seen among the few known types indicate that not only are the members of this third domain of life quite distinctive from members of the others, but they also differ from each other. SEE ALSO BACTERIAL CELL; CELL WALL; EUBACTERIA; EXTREME COMMUNITIES; KINGDOM; RNA; TAXONOMY, HISTORY OF

Ricki Lewis

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Arthropod

Arthropods are a **phylum** within the animal kingdom. They include four classes: Chelicerates (such as spiders, mites, ticks, scorpions, and horseshoe crabs), the extinct Trilobites, Crustaceans (such as lobsters, crabs, and shrimp), and Uniramians (millipedes, centipedes, and the most numerous group of all, the insects). The defining features of arthropods are their exoskeletons (hard outer coverings), segmented bodies, and jointed **appendages**, from which they derive their name (*arthro* means "joint," *pod* means "foot").

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

appendage attached organ or structure

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

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

The exoskeleton, secreted by the outer tissue layer, is composed of **protein** and a nitrogenous carbohydrate called **chitin**, which in crustaceans is fortified with calcium carbonate crystals. To grow, most arthropods either

shed (molt) the exoskeleton periodically or grow as soft-bodied larvae before undergoing **metamorphosis** into the adult, hard-bodied form. Some arthropods (such as millipedes) have legs on nearly every segment. However, most arthropods have evolved reduced numbers of legs, with many other appendages taking on highly specialized roles. Examples include the antennae and hardened mouth parts on head segments, and egg-clasping ovipositors on rear segments.

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

Arthropods are the most numerous of all animal phyla, both in numbers of species and numbers of individuals, primarily due to insect diversity and numbers. There are at least one million recorded species of arthropods, with the actual number probably ten or even twenty times that amount. SEE ALSO ARACHNID; CRUSTACEAN; INSECT

Richard Robinson

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Autoimmune Disease

In order for the immune system to protect the body against attack by foreign organisms, it must be able to distinguish between the body's own **proteins** (autoantigens) and proteins from foreign cells (foreign **antigens**). When the immune system turns against autoantigens, thus attacking its own tissues, the resulting condition is an autoimmune disease.

Common autoimmune diseases include:

- glomerulonephritis, which compromises the filtering ability of the kidney tubules
- Graves' disease, which stimulates the thyroid to overproduce thyroid hormone
- rheumatoid arthritis, which destroys joint tissue
- myasthenia gravis, which interferes with nerve-muscle communication
- multiple sclerosis, which destroys the fatty myelin coating of nerves
- systemic lupus erythematosus, which attacks deoxyribonucleic acid (DNA), causing widespread damage in kidneys, heart, lungs, and skin
- juvenile onset (Type I) diabetes mellitus, which destroys the insulin-producing beta cells of the pancreas, resulting in inability to regulate blood sugar properly.

A digitally enhanced X ray of the left hand of a sufferer of rheumatoid arthritis, an autoimmune disease that destroys joint tissue.

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

antigen foreign substance that provokes an immune response

T cell white blood cell that controls the immune response

Theories of Autoimmunity

The cells involved in immune reactions are B lymphocytes (B cells), which develop in the bone marrow, and T lymphocytes (**T cells**), which develop in the thymus. Each lymphocyte carries a recognition site for a specific antigen and becomes activated when that antigen is encountered. During development, most of the lymphocytes that could recognize and destroy widely

occurring autoantigens are deleted. Tissues bearing these autoantigens are generally safe from subsequent attack by the immune system unless either the autoantigen mutates or the immune system confuses the autoantigen with a foreign antigen. However, some tissue-specific autoantigens are unavailable when lymphocytes are developing in the bone marrow or thymus, and so lymphocytes with receptors for those autoantigens remain viable, posing the threat of tissue destruction in autoimmune diseases.

It is not yet clear why these lingering, self-reactive lymphocytes do not trigger autoimmunity more often, or why autoimmunity occurs when it does. However, there is strong suspicion that infection may play an important role in genetically susceptible individuals. An infection causes the production of inflammatory chemicals. If these are present at the same time that a lymphocyte is presented with its autoantigen by an antigen-presenting cell, the combination could activate self-reactive lymphocytes that were not deleted during development. Destruction of body tissues bearing those autoantigens would follow.

In another possible process, termed "molecular mimicry," a foreign protein bears such similarity to an autoantigen that B cell antibodies or cytotoxic T cells specific for that foreign antigen cross-react with autoantigens, causing tissue destruction. Alternatively, the combination of a foreign antigen with a self-protein can form a new complex capable of activating appropriate T or **B lymphocytes** to destroy tissues containing the complex.

B lymphocyte white blood cell that makes antibodies

SEE ALSO ANTIBODY; BLOOD SUGAR REGULATION; IMMUNE RESPONSE; T CELLS

Patricia L. Dementi

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Bacterial Cell

Hundreds of thousands of bacterial species exist on Earth. They can be found in very diverse environments ranging from cold to hot and **alkaline** to acid. They live in soil, in water, and on rocks. They exist deep in the earth, high on mountains, and in deep-sea vents. They grow on and in other bacteria, worms, insects, plants, animals, and people.

Bacteria are **prokaryotes**. Prokaryotic cells possess simpler structures than **eukaryotic cells**, since they do not have a **nucleus**, other membrane bound **organelles**, or a **cytoskeleton**. Bacterial cells have two major compartments, the **cytoplasm** and cell envelope, and may also have exterior **appendages**, such as flagella or pili. There are two major types of prokaryotes: bacteria and archaea. Archaea (also called archaebacteria) are often found in extreme environments, and while they are clearly prokaryotic, they have evolved separately from bacteria. **Mitochondria** and chloroplasts are two membrane-bound organelles carried within eukaryotic cells that are thought to have been derived from free-living prokaryotic organisms that became irreversibly engulfed by ancestral eukaryotes.

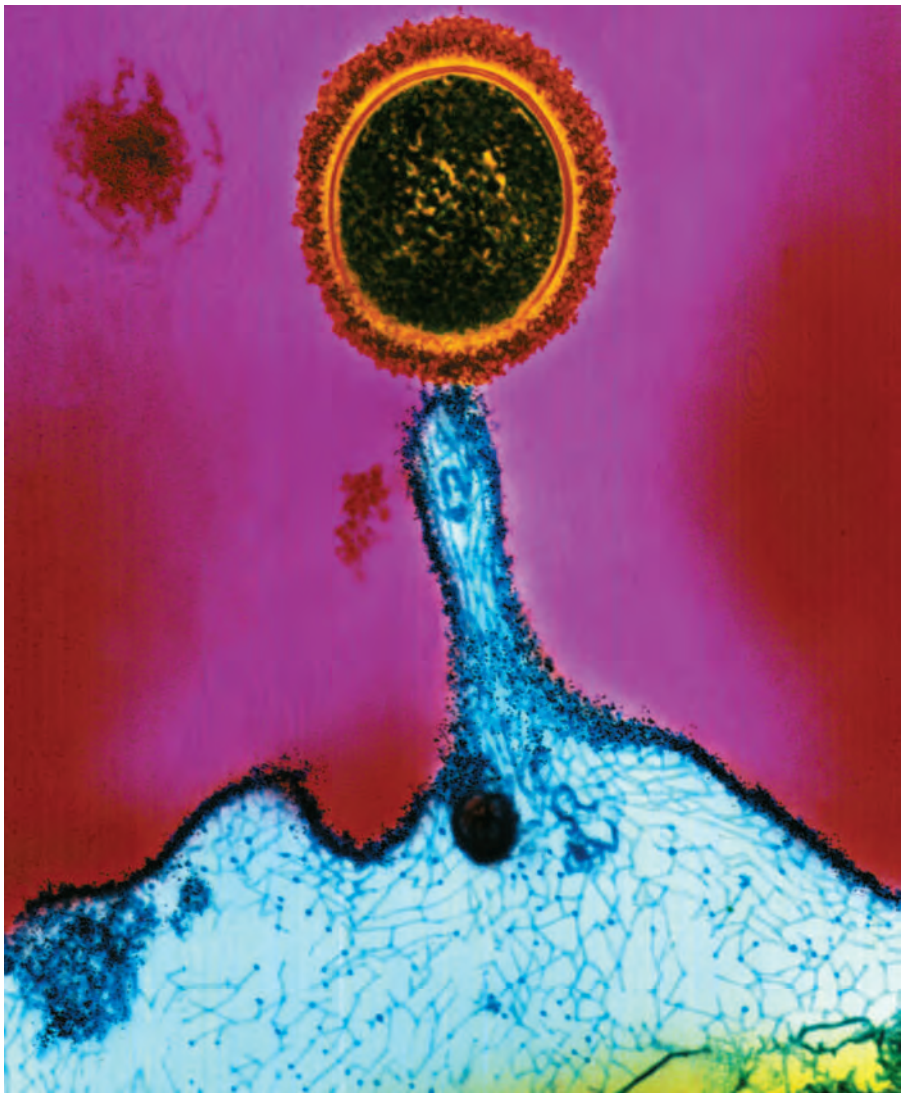
alkaline chemically basic, with an excess of OH- ions

prokaryote single-celled organism without a nucleus

eukaryotic cell a cell with a nucleus

nucleus membrane-bound portion of cell containing the chromosomes

organelle membrane-bound cell compartment



A colored transmission electron micrograph of Streptococcus bacteria attached to a human tonsil cell.

Growth and Reproduction

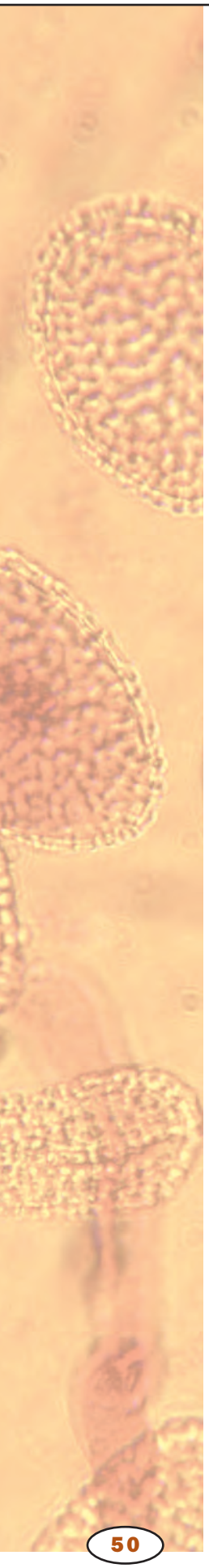
Bacterial cells grow by a process called binary fission: One cell doubles in size and splits in half to produce two identical daughter cells. These daughter cells can then double in size again to produce four sibling cells and these to produce eight, and so on. The time it takes for a bacterial cell to grow and divide in two is called the doubling time. When nutrients are plentiful, the doubling time of some bacterial species can be as short as twenty minutes. However, most bacterial species show a doubling time between one and four hours. A single bacterial cell with a one-hour doubling time will produce over 1 million offspring within twenty hours. If left unchecked, a single *E. coli* bacterium replicating once every twenty minutes could replicate to equal the mass of Earth in twenty-four hours. The enormous increase in cell numbers that accompanies this exponential growth provides these simple unicellular organisms with an incredible growth advantage over other unicellular or multicellular organisms. Luckily, there are always limits to bacterial growth.

cytoskeleton internal scaffolding in a cell, composed of protein

cytoplasm material in a cell, excluding the nucleus

appendage attached organ or structure

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



genome total genetic material in a cell or organism

transcriptional of, relating to messenger RNA formation from a DNA sequence

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

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

bilayer composed of two layers

amino acid a building block of protein

peptidoglycan polymer that is composed of polysaccharide and peptide chains

lipid fat or waxlike molecule, insoluble in water

polymer molecule composed of many similar parts

The cytoplasm of a bacterial cell contains the deoxyribonucleic acid (DNA) molecules that make up the bacterial **genome** (or nucleoid), the **transcriptional** machinery that copies DNA into ribonucleic acid (RNA), and the **ribosomes** that translate the messenger RNA information into **protein** sequence. Since there is no nucleus, all of these processes occur simultaneously. The rapid growth rate of the bacterial cell requires constant DNA replication and ways to segregate the two new **chromosomes** into the two daughter cells without tangling them.

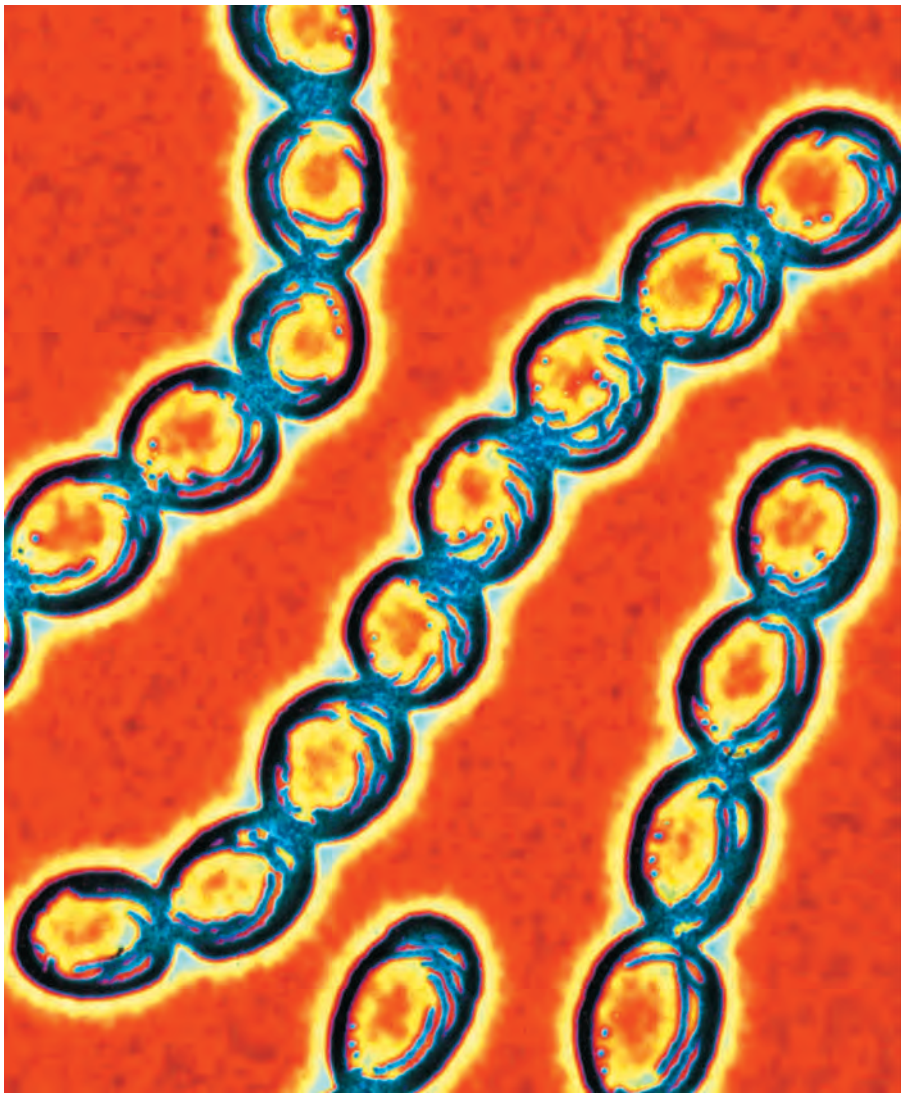
Structure and Diversity

Bacterial cells express a variety of shapes and sizes. The smallest bacteria are the *Mycoplasmas*, which range from about 0.1 to 0.25 micrometers in diameter, while the gigantic *Epulopiscium fishelsoni* is 250 micrometers long and visible to the naked eye. Some bacteria have a coccal (spherical) shape. Others are shaped as bacilli (rods), vibrio (curved rods), or spirochetes (spirals).

Bacterial cells are often classified by the structure of their cell envelope. All bacteria have a **bilayer** membrane that surrounds the cytoplasm. Integral membrane proteins within the cytoplasmic membrane are required to transport nutrients (sugars and **amino acids**) into the cell for growth. Most bacteria have a cell wall that is made up of **peptidoglycan**. The exceptions are the *Mycoplasma* species, which only have a cytoplasmic membrane that is unique in the prokaryotic world due to the presence of the **lipid** cholesterol. The peptidoglycan molecule is made up of chains of sugars (glycans) that are attached to one another by peptide (amino acid) cross-links. This is a naturally occurring **polymer**, similar to chemicals that make up plastics and synthetic fabrics. Peptidoglycan it is only found in bacterial cells. The beta-lactam antibiotics (penicillin, ampicillin, amoxicillin) act to prevent the peptide cross-links from forming, which makes them active in preventing the growth of a diverse number of bacteria.

Most bacteria are classified by how they react to a defined series of colored dyes (the Gram stain). The Gram stain is the basis of one major classification scheme for bacteria. Gram-positive bacteria have a thick cell wall with many peptide cross-links that allow a dark purple color to remain after the Gram stain procedure. The Gram-positive cell wall acts as a molecular barrier to prevent access to the cytoplasmic membrane and to keep large, harmful molecules from damaging the cell. In contrast, Gram-negative bacteria have a thin layer of peptidoglycan that makes up their cell wall that is surrounded by a second bilayer membrane called the outer membrane. The purple dye used in the Gram stain does not penetrate the outer membrane, and these cells do not stain purple. Gram-negative cells are instead identified by a pink color contributed by a different chemical stain during the Gram stain procedure. The Gram-negative outer membrane functions to protect the cytoplasmic membrane. The outer membrane contains porin proteins that form holes in the outer membrane to allow small molecules (sugars, peptides, salts) to enter the area between the two membranes (the periplasm).

The Gram-negative outer membrane is made up of a molecule called lipopolysaccharide (LPS). LPS has a unique chemical structure that is only found in Gram-negative bacteria and is recognized by the mammalian im-



A colored transmission electron micrograph of *Streptococcus pyogenes* bacteria.

mune system as a microbial product (endotoxin). Since LPS in the blood stream can be fatal to mammals, all products that are used clinically within the bloodstream (such as insulin) must be endotoxin-free to prevent septic shock. Gram-positive bacteria express lipoteichoic acids in their cell walls that act similar to LPS on the mammalian immune system.

Most bacterial species express other molecules and structures outside of their cell envelope that are important for interactions with the environment. **Polysaccharide** postmortem capsules prevent **desiccation** of environmental microbes and allow **pathogens** to resist **phagocytosis** by mammalian white blood cells. Most bacterial species have flagella, which allow the bacteria cells to move around in **aqueous** environments. Most Gram-negative bacteria express hairlike appendages called pili or fimbriae that allow them to adhere to other bacteria, bacterial viruses, eukaryotic cells, or other physical surfaces. Both Gram-negative and Gram-positive bacteria can express afimbrial **adhesions** that also allow adherence to a variety of molecules or surfaces. These exterior appendages help bacteria get to where they want to go, and then keep them there to facilitate growth.

polysaccharide carbohydrate composed of many individual units of sugar

desiccation drying out

pathogen disease-causing organism

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

aqueous watery or water-based

adhesion attachment; sticking to the surface of

Beneficial Bacteria

Most bacteria do not directly influence humans. However, a small number of bacterial species can cause human or animal diseases and are a major focus of scientific study. Other bacteria can be beneficial to humans by contributing to human nutrition and protecting the body from pathogens. The *E. coli* bacteria in our colons are an example. Bacterial cells such as *E. coli* are widely used in laboratories as factories to produce commercially or medically important proteins through the use of genetic engineering or recombinant DNA technologies. Other bacteria are important for agriculture since they take nitrogen from the air and replace it in the soil (nitrogen fixation). Bacteria are used to clean up oil spills and toxic chemicals in the environment. There are as many beneficial bacteria as there are destructive germs.

SEE ALSO ARCHAEA; BACTERIAL GENETICS; BACTERIAL VIRUSES; CELL WALL; EUBACTERIA; NITROGEN FIXATION; RECOMBINANT DNA; REPLICATION; TRANSCRIPTION

Hank Seifert

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Bacterial Diseases

Bacteria get a bad reputation for causing disease when, in reality, very few species of bacteria infect humans. The ones that do, however, are the ones most often written about in magazines and newspapers. These bacteria inhabit the human body because of the constant source of nourishment, moist environment, relatively stable **pH** and body temperature, and extensive surface area.

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

Contamination with bacteria from the environment can lead to colonization, taking up residence on or in the human body. The mixed collection of bacteria that are adapted to the body and reside in it for extended periods of time are called normal flora. Some bacteria inhabit the body only as transients, soon destroyed by human (host) defense mechanisms or removed by cleaning. Bacteria that evade host defenses and cause infection are described as virulent. Under certain circumstances, such as an imbalance in normal flora or lowered host resistance, even normal flora can cause infection.

Infection may proceed to disease if host defenses do not arrest the infection before tissue damage occurs. Bacterial disease can have several outcomes. The immune system may arrest the infection and stop progression of the disease. In other cases, the body may be unable to repair damaged tissues and permanent dysfunction or even death may result. For this reason, treatments are designed to stop the infection before permanent damage has occurred.

Most bacterial diseases are treated with antibiotics to kill the organisms. In recent years, more and more bacteria have become resistant to the avail-

WILLIAM, ANNA WESSELS (1863–1954)

Physician and bacteriologist who isolated a strain of the bacterium that causes diphtheria, from which she made an antitoxin that could be used to treat the disease. She also discovered a way to diagnose rabies in a few minutes instead of a few days, thus saving many more lives.

able antibiotics. This has forced the scientific community to examine the use of antibacterial agents in soaps and cleansers, the use of antibiotics in animal feeds, and the inappropriate prescription of antibiotics. Patients who terminate the treatment prematurely because they feel better, even though the infection is not yet eliminated, compound the problem of antibiotic resistance. All of these situations lead to the killing off of susceptible bacteria while leaving the resistant ones to multiply. The best "medicine" is still prevention of infection. SEE ALSO DISEASE; EUBACTERIA

Jackie Butler

KOCH, ROBERT (1843–1910)

German physician who discovered the three bacteria that cause the deadly diseases tuberculosis, cholera, and anthrax, and who won the 1905 Nobel Prize in medicine. His most enduring work was a set of guidelines, called Koch's postulates, for telling which pathogens (bacteria or viruses) cause which diseases.

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Bacterial Genetics

There are hundreds of thousands of bacterial species in existence on Earth. They grow relatively quickly, and most reproduce by binary fission, the production of two identical daughter cells from one mother cell. Therefore, each replication cycle doubles the number of cells in a bacterial population. The bacterial **chromosome** is a long circle of deoxyribonucleic acid (DNA) that is attached to the membrane of the cell. During replication, the chromosome is copied, and the two copies are divided into the two daughter cells. Transfer of genetic information from the mother cell to offspring is called vertical transmission.

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

Beneficial mutations that develop in one bacterial cell can also be passed to related bacteria of different **lineages** through the process of horizontal transmission. There are three main forms of horizontal transmission used to spread genes between members of the same or different species: conjugation (bacteria-to-bacteria transfer), transduction (viral-mediated transfer), and transformation (free DNA transfer). These forms of genetic transfer can move **plasmid**, bacteriophage, or genomic DNA sequences. A plasmid is a small circle of DNA separate from the chromosome; a bacteriophage is a virus that reproduces in bacteria by injecting its DNA; the **genome** is the total DNA of the bacterial organism.

lineage ancestral line

plasmid small ring of DNA found in many bacteria

genome total genetic material in a cell or organism

After transfer, the DNA molecules can exist in two forms, either as DNA molecules separate from the bacterial chromosome (an episome), or can become part of the bacterial chromosome. The study of basic mechanisms used by bacteria to exchange genes allowed scientists to develop many of the essential tools of modern molecular biology.

Conjugation

Bacterial conjugation refers to the transfer of DNA between bacterial cells that requires cell-to-cell contact. Joshua Lederberg and Edward Tatum first

A laboratory technician performing an Analytical Profile Index (API) test on bacteria.

described conjugation in 1946 when they discovered the F factor (an episome) that can move between *Escherichia coli* cells. The F factor is one of the most well studied conjugative plasmids (plasmids are circular episomes) and is the most well studied conjugative system. There are many different conjugal plasmids carried by members of most bacterial species. Conjugal plasmids that carry antibiotic resistance genes are called R factors. The F factor and R factors usually exist as episomes and each carries functions that allow it to replicate its DNA and thus be inherited by the daughter cells after binary fission. However, conjugative plasmids also express transfer functions that allow the movement of DNA from a donor to a recipient cell; this is the process of conjugation.

The steps of bacterial conjugation are: mating pair formation, conjugal DNA synthesis, DNA transfer, and maturation. The main structure of the F factor that allows mating pair formation is the F pilus or sex pilus (a long thin fiber that extends from the bacterial cell surface). There are one to three pili expressed on an *E. coli* cell that carries the F factor, and one pilus will specifically interact with several molecules on the recipient cell surface (attachment). About twenty genes on the F factor are required to produce

a functional pilus, but the structure is mainly made up of one **protein**, pilin. To bring the donor and recipient cell into close proximity, the F pilus retracts into the donor cell by removing pilin protein **monomers** from the base of the pilus to draw the bacterial cells together.

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

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

Once a stable mating pair is formed, a specialized form of DNA replication starts. Conjugal DNA synthesis produces a single-stranded copy of the F factor DNA (as opposed to a double-stranded DNA that is formed by normal replication). This DNA strand is transferred into the recipient cell. Once in the recipient cell, the single-stranded copy of the F plasmid DNA is copied to make a double-stranded DNA molecule, which then forms a mature circular plasmid. At the end of conjugation the mating pair is broken and both the donor and the recipient cells carry an identical episomal copy of the F factor. All of the approximately one hundred genes carried on the F factor can now be expressed by the recipient cell and will be inherited by its offspring.

In addition to transferring itself, the F factor can also transfer chromosomal genes between a donor and recipient cell. The F factor can be found inserted (integrated) into the bacterial chromosome at many locations in a small fraction of bacterial cells. An integrated F factor is replicated along with the rest of the chromosome and inherited by offspring along with the rest of the chromosome. When a mating pair is formed between the donor cell carrying an integrated F factor and a recipient cell, DNA transfer occurs as it does for the episomal F factor, but now the chromosomal sequences adjacent to the integrated F factor are transferred into the recipient. Since these DNA sequences encode bacterial genes, they can recombine with the same genes in the recipient. If the donor gene has minor changes in DNA sequence from the recipient gene, the different sequence can be incorporated into the recipient gene and inherited by the recipient cell's offspring. Donor cells that have an integrated copy of the F factor are called Hfr strains (High frequency of recombination).

Transduction

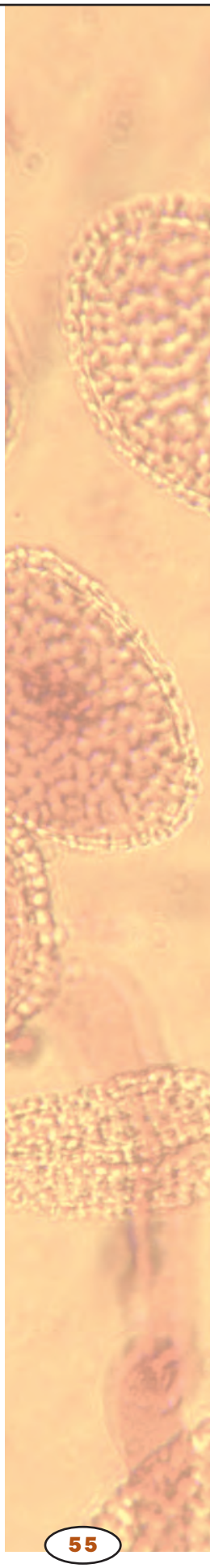
The second way that DNA is transferred between bacterial cells is through a **phage** particle in the process of transduction. Joshua Lederberg and Norton Zinder first discovered transduction in 1956. When phage inject their DNA into a recipient cell, a process occurs that produces new bacteriophage particles and kills the host cell (lytic growth). Some phage do not always kill the host cell (temperate phage), but instead can be inherited by daughter host cells. Therefore acquisition of a so-called temperate "prophage" by a recipient cell is a form of transduction. Many phage also have the ability to transfer chromosomal or plasmid genes between bacterial cells. During generalized transduction any gene can be transferred from a donor cell to a recipient cell. Generalized transducing phage are produced when a phage packages bacterial genes into its capsid (protein envelope) instead of its own DNA. When a phage particle carrying bacterial chromosomal genes attaches to a recipient cell, the DNA is injected into the **cytoplasm** where it can recombine with a **homologous** DNA sequences.

phage short for bacteriophage

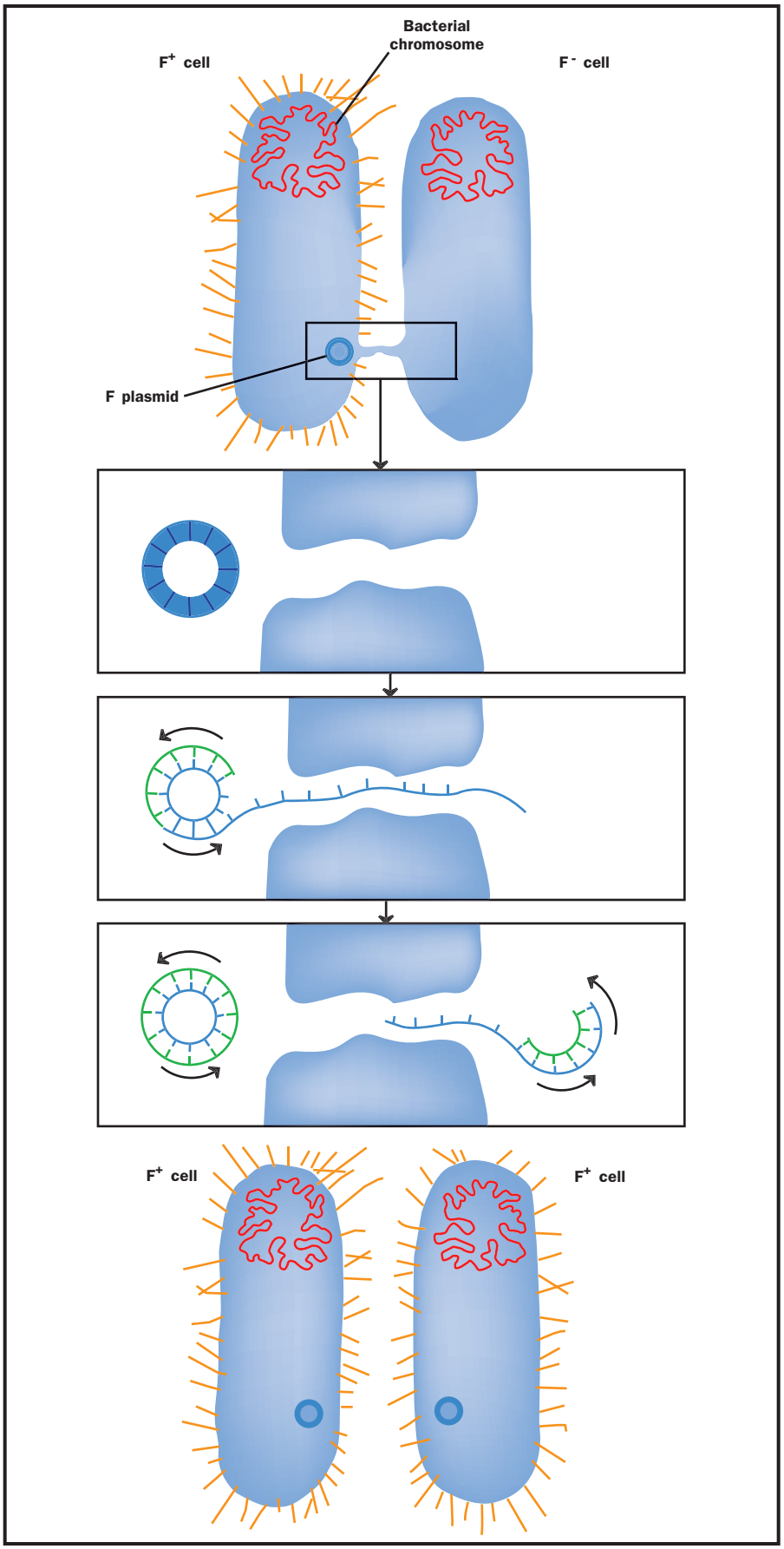
cytoplasm material in a cell, excluding the nucleus

homologous similar in structure

Some bacteriophage can pick up a subset of chromosomal genes and transfer them to other bacteria. This process is called specialized transduc-



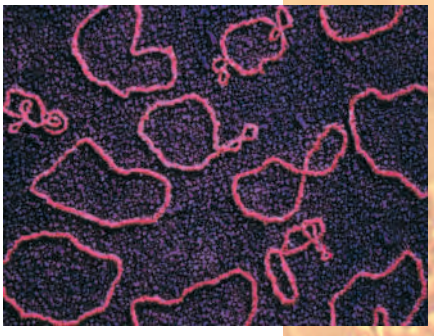
Bacterial conjugation. The bacterium on the left passes a copy of the F plasmid to the bacterium on the right, converting it from an F^- cell to an F^+ cell.



tion since only a limited set of chromosomal genes can be transferred between bacterial cells.

Transformation

The third main way that bacteria exchange DNA is called DNA transformation. Some bacteria have evolved systems that transport free DNA from the outside of the bacterial cell into the cytoplasm. These bacterial are called "naturally competent" for DNA transformation. Natural DNA transformation of *Streptococcus pneumonaiae* provided the first proof that DNA encoded the genetic material in experiments by Oswald Avery and colleagues. Some other naturally competent bacteria include *Bacillus subtilis*, *Haemophilus influenzae*, and *Neisseria gonorrhoeae*. Other bacterial species such as *E. coli* are not naturally competent for DNA transformation. Scientists have devised many ways to physically or chemically force noncompetant bacteria to take up DNA. These methods of artificial DNA transformation form the basis of plasmid cloning in molecular biology.



A scanning electron micrograph of bacterial DNA plasmids.

Most naturally competent bacteria regulate transformation competence so that they only take up DNA into their cells when there is a high density of cells in the environment. The ability to sense how many other cells are in an area is called quorum sensing. Bacteria that are naturally competent for DNA transformation express ten to twenty proteins that form a structure that spans the bacterial cell envelope. In some bacteria this structure also is required to form a particular type of pilus different than the F factor pilus. Other bacteria express similar structures that are involved in secreting proteins into the exterior **medium** (Type II secretion). Therefore, it appears that DNA transformation and protein secretion have evolved together.

medium nutrient source

During natural DNA transformation, doubled-stranded DNA is bound to the recipient cell surface by a protein receptor. One strand of the DNA is transported through the cell envelope, where it can recombine with similar sequences present in the recipient cell. If the DNA taken up is not homologous to genes already present in the cell, the DNA is usually broken down and the **nucleotides** released are used to synthesize new DNA during normal replication. This observation has led to the speculation that DNA transformation competence may have originally evolved to allow the acquisition of nucleic acids for food.

nucleotide the building block of RNA or DNA

The source of DNA for transformation is thought to be DNA released from other cells in the same population. Most naturally competent bacteria spontaneously break apart by expressing **enzymes** that break the cell wall. Autolysis will release the genomic DNA into the environment where it will be available for DNA transformation. Of course, this results in the death of some cells in the population, but usually not large numbers of cells. It appears that losing a few cells from the population is counterbalanced by having the possibility of gaining new traits by DNA transformation. SEE ALSO BACTERIAL CELL; BACTERIAL VIRUSES; CLONE; RECOMBINANT DNA

enzyme protein that controls a reaction in a cell

Hank Seifert

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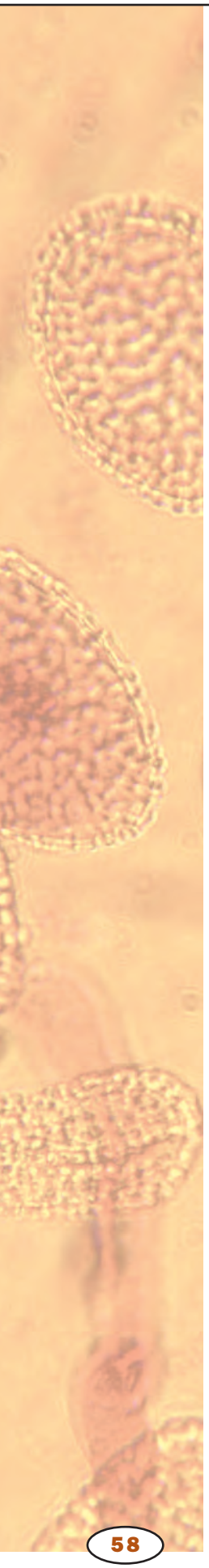


Bacterial Viruses

There are viruses that infect all types of cells: animal cells, plant cells, and unicellular organisms. Those that infect bacteria are called bacteriophage or just phage (*phage* means "to eat"). Bacteriophage exist as inert particles when they are outside of bacterial cells. They possess complex **protein** coats with defined structure and may also have tail structures. The protein coat, or capsid, surrounds the deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) molecules that make up the bacteriophage **genome**. Phage genomes can be single stranded or double stranded, and are either circular or linear. Different bacteriophage can encode as few as four proteins or as many as one hundred in their genome.

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

genome total genetic material in a cell or organism

Phage are similar to animal and plant viruses in that they are not alive, since they cannot replicate themselves or conduct metabolic processes. All phage require bacterial cells for reproduction, but each phage type exhibits a defined host range. Some phage are very specific for one or two closely related bacterial species, while others can infect and replicate in a variety of bacterial cells. The host cell functions required for bacteriophage reproduction define host range. These include attachment to specific molecules on the bacterial cell surface, injection of the bacteriophage DNA into the bacterial cell **cytoplasm**, avoidance of host cell defenses, proper expression and regulation of bacteriophage **genes**, production and assembly of the capsid, replication of the phage nucleic acid (DNA or RNA), packaging the nucleic acid into the capsid, and exit from the bacterial cell.

cytoplasm material in a cell, excluding the nucleus

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

The bacteriophage that infect the bacterium *Escherichia coli* can be used to illustrate many of the properties of different bacteriophage. One of the most well-studied bacteriophage is bacteriophage **λ**. The λ genome exists as a linear, doubled-stranded DNA molecule in the bacteriophage particle. There are 48,514 **base pairs** of DNA that encode about 50 genes that define the λ genome. λ phage bind to a receptor on the *E. coli* cell surface that includes a protein involved in transporting the sugar molecule, maltose. (It is common for viruses to use cellular molecules designed for another function for their own ends.)

λ the Greek letter lambda

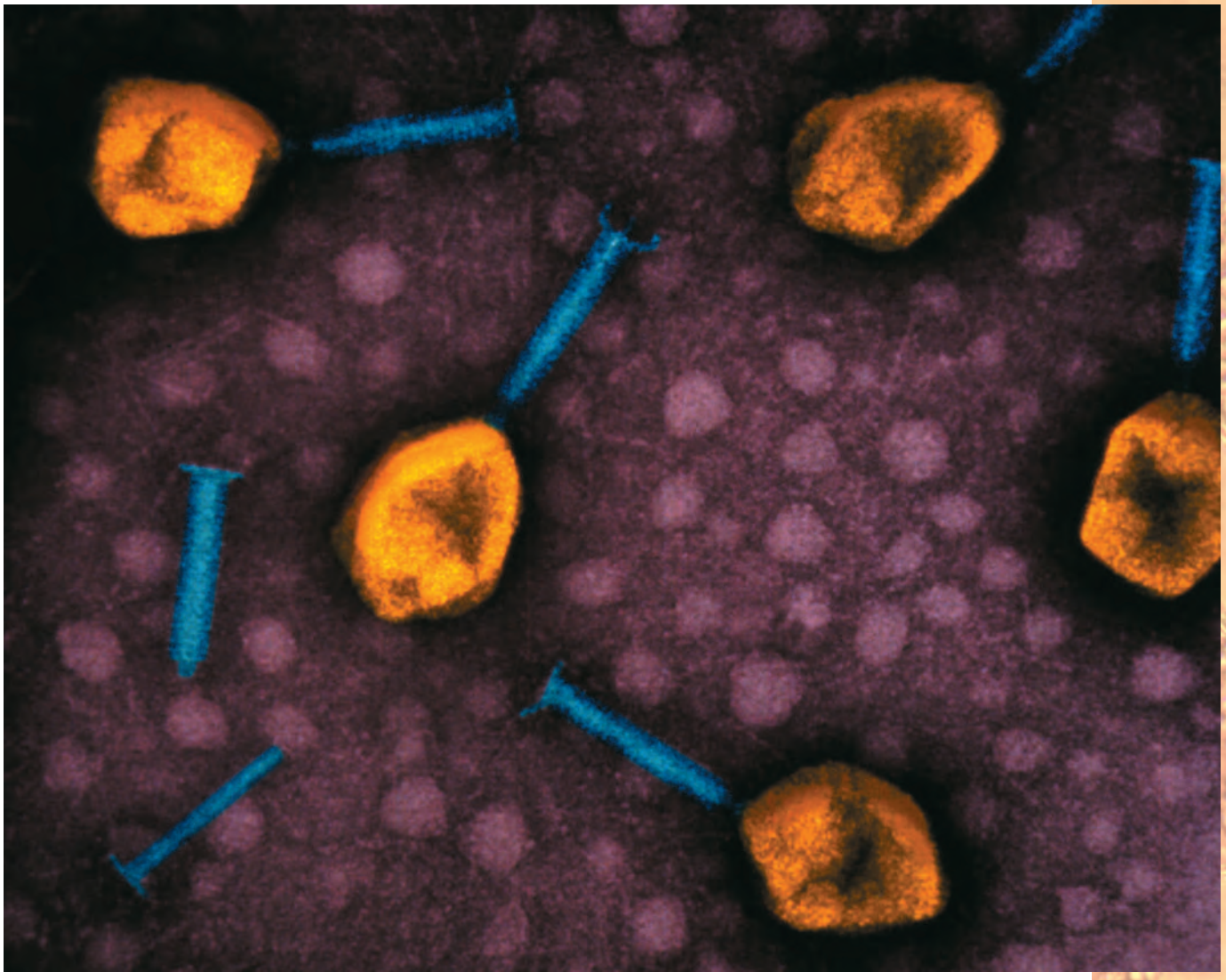
base pair two nucleotides (either DNA or RNA) linked by weak bonds

The λ genome is injected through the cell envelope into the cytoplasm, where it is converted from a linear to circular form. At this point a choice is made between two different programs: a lytic or lysogenic state. When λ phage undergo lytic growth, replication produces hundreds of copies of its genome and phage genes produce the proteins that make up the capsid, in which the phage genome is inserted to make the mature phage particles. These phage particles are released by **enzymes** that break open the bacterial cell. Lysogeny is a dormant state, where the λ genome becomes part of the bacterial genome and is inherited by the bacterial offspring as a prophage. Bacteriophage that produce lysogeny, like λ, are called temperate since they do not harm the bacteria, while those that can only replicate are called virulent, since they commonly kill the host cell.

enzyme protein that controls a reaction in a cell

There are many virulent phage in *E. coli*. The T even phage (such as T2, T4) and T odd phage (such as T1, T3) always replicate themselves and **lyse** the bacterial cell. In contrast, filamentous phage (for example, M13, fd) always replicate but produce new phage particles by extruding out of the bacterial membrane and never destroy the bacterial cell. When a prophage

lyse break apart



A scanning electron micrograph of T4 cells, a virulent phage in *E. coli.*

carries one or more genes that provide a selective advantage for the host bacterial cell, this is called lysogenic conversion. SEE ALSO BACTERIAL CELL; BACTERIAL GENETICS; DNA; DNA VIRUSES; REPLICATION; RETROVIRUS; VIRUS

Hank Seifert

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Beer-making, Biology of

Beer is made by fermentation of grains, principally barley (*Hordeum vulgare*). Other grains, including wheat and rice, may be added to develop particular flavors. The grain is first allowed to germinate by soaking it in water. As part of its germination process, the grain produces amylase **enzymes** that break down the starches of the **endosperm** (part of the seed) into sugars.

enzyme protein that controls a reaction in a cell

endosperm nutritive tissue within a seed

At a certain point, germination is halted by rapidly drying the grain, in a process called kilning, to produce "malt." More prolonged kilning produces a darker beer. The malt is then ground and mixed with more water to reactivate the amylases and complete the liberation of the sugars.

The resin-filled flowers of the hops plant (*Humulus lupulus*, Cannabinaceae family), are added for aroma and bitter flavor, and the mixture is boiled to bring out the flavor. Boiling also kills unwanted microorganisms that might spoil the fermentation that follows. Yeast is then added to ferment the sugars to ethyl alcohol. Ales are made at room temperature using the yeast *Saccharomyces cerevisiae*, whereas lagers use *Saccharomyces uvarum* at cooler temperatures. The final alcohol concentration of most beers is about 5 percent. Some beers are naturally carbonated by bottling before fermentation is complete, but most commercial beers require addition of carbon dioxide after fermentation.

Beer is probably the oldest of alcoholic beverages and has been made for thousands of years, at least as far back as classical Egyptian civilization of five thousand years ago. Modern beer styles originated in Germany, the Czech Republic, and the United Kingdom, which still claim production of some of the finest beers in the world. SEE ALSO AGRICULTURE; COFFEE, BOTANY OF; ENZYMES; GLYCOLYSIS AND FERMENTATION; WINE-MAKING, BOTANY OF

Richard Robinson

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Behavior, Genetic Basis of

A debate raged throughout the twentieth century, and probably will continue, about the relative influences of heredity and experience on human behavior. Behavioral scientists today largely regard this "nature versus nurture" debate as an outmoded dichotomy. Most scientists now believe that behavior results from a combination of these influences, never entirely from one or the other.

Genetic Influences in Animal Behavior

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

Clearly, **genes** significantly influence animal behavior. This is the only reasonable conclusion in cases where animals born and reared in isolation nevertheless develop age-appropriate, species-specific behaviors that they could not have possibly learned from other individuals. Such instincts that occur even in isolated animals include insect mating behavior; courtship, nesting, and brood-rearing behavior of pigeons; the songs of some (not all) birds; bird flight; and nut-cracking and nut-burying by squirrels. Animals are born "knowing" how to do certain things. Experiments that rule out social learning and trial-and-error learning leave heredity—that is, genes—as the only logical explanation for such behaviors.

People have long used artificial selection to produce animal breeds with desirable behavioral traits, such as dogs that herd sheep or hunt. Artificial

Experiments with honeybees have confirmed the relationship between genes and behaviors.

selection can also shape the reactions of fruit flies (*Drosophila*) to light and gravity and the ability of rats to learn mazes. Such results would not be possible if genes did not influence behavior. The fact that X rays and chemicals can induce mutations that alter behavior strengthens the link to genetics. Mutations have changed obstacle-avoidance behavior of *Paramecium* and biological clocks and several behaviors in *Drosophila*.

Experimental Evidence of Gene-Behavior Links

Breeding experiments confirm the relationship between genes and behaviors. For example, worker honeybees normally react to diseased or dead pupae by uncapping the honeycomb cell containing the pupa, dragging the pupa out, and removing it from the hive. This helps to prevent the spread of infections through the colony. Experiments in which normal honeybees were crossed with bees that do not bring out their dead traced the behavior to two genes: one that induces workers to uncap the diseased cell, and the other that induces the insects to remove the diseased pupa.

Hybrids between behaviorally different strains and species of animals exhibit behaviors intermediate between those of the parents, or combine the parental behaviors. This has been seen for aggression in honeybees, courtship in *Drosophila*, breeding behaviors of cichlid fishes, food preferences in garter snakes, bird migratory and nesting behaviors, and bird distress calls.

Genes and Human Behavior

The foregoing observations and experiments, and many others like these, no longer leave room for doubt that genes significantly influence animal behavior. The subject becomes very controversial, however, when we come to the behavior of the most complex of animals, *Homo sapiens*. Behavioral geneticists find evidence of a genetic influence on schizophrenia, alcoholism,

sleep disorders, depression, sexual orientation, intelligence quotient, and many personality traits.

Consider, for example, sexual orientation, an intensely heated issue in which one side argues that people are born with a hereditary predisposition to become homosexual or heterosexual, and the other side argues that homosexuals simply "choose to be that way" and could change if they wanted to, or that this behavior was caused by childhood influences and can be "corrected" by such means as psychotherapy. J. M. Bailey and R. C. Pillard studied families with two or more male siblings, at least one of whom was homosexual. In 52 percent of the cases where the brothers were monozygotic (genetically identical) twins, the other brother was also homosexual; in 22 percent of dizygotic (nonidentical) twin pairs, the second brother was homosexual; and in only 9 percent of nontwin brothers, the second brother was homosexual. The 52 percent figure shows that genes do not inevitably determine sexual orientation; if they did, this figure would be 100 percent. But the contrast between this datum and the other two does suggest that heredity significantly increases the likelihood of a given adult sexual orientation.

genome total genetic material in a cell or organism

nucleotide the building block of RNA or DNA

The sequencing of the human **genome** will provide a new tool to assess the genetic underpinnings of behaviors in the human species. A shortcut to sequencing the genomes of many people is to identify places in the genome where people tend to differ in the particular DNA base found. These sites are called single **nucleotide** polymorphisms, or SNPs, and already an international consortium of researchers has identified more than two million of them among the three billion bases of the human genome. Many research groups are now correlating specific SNP patterns to disease susceptibilities, and these include conditions that have behavioral components. One company, for example, is amassing SNP patterns among six hundred families in which two or more members have eating disorders. The researchers look at SNPs in genes known to be associated with eating behaviors and satiety, such as leptin and neuropeptide Y, and other, as yet unknown places in the genome where certain SNPs are statistically more common in people with these types of disorders. Even with this powerful new technology, it will be difficult to separate inherited tendencies from learned behaviors.

Political and Philosophical Issues

Much of the opposition to the idea of a genetic influence on human behavior stems from political and social philosophies that are reluctant to accept the idea that not all human behavior can be shaped by experience or changed at will. It would be discouraging to think that tendencies toward war, racism, or marital infidelity were genetic and unchangeable. Hereditary theories of human behavior were taken to despicable extremes in the twentieth century, including a eugenics movement in America that argued that some races and classes of people were genetically inferior to others and, most horrendously, the racial philosophy of Nazi Germany, which extolled the fictitious "white Aryan race" while trying to systematically exterminate another. In light of this horrific history, it is understandable that some people recoil from any latter-day suggestions that human behavior is hereditary.

PAVLOV, IVAN PETROVICH (1849–1936)

Russian biologist who won the 1904 Nobel Prize in physiology for his demonstration of the idea of a "conditioned reflex." Pavlov trained dogs to drool at the sound of a bell by feeding them immediately after sounding the bell.

Yet scientific evidence cannot be rejected simply because it does not conform to a political philosophy. In evaluating the influence of genes on human behavior, several points must be kept in mind. One is that behavioral geneticists are not arguing for genetic determinism: they are saying genes influence behavior, not that they rigidly determine it and destine people to behave in certain ways. Genes may influence human behavior, but they do not enslave people. All behaviors require at least some contribution from genes (to build sense organs, nervous systems, muscles, and the other equipment of behavior) and environment (to provide the raw materials to build this equipment and the experiences that sway **gene expression**). As evolutionary theorist Richard Dawkins puts it, behavior is like a chocolate cake, needing both a recipe and ingredients. Genes provide the behavioral recipe, and the environment the ingredients.

Finally, there is no such thing as a gene for any behavior. There is no aggression gene, no gay gene, no gene for bird song or nut-burying. Genes encode **proteins**, nothing more; but through proteins, they can influence behavior. Aggression and sexual behavior, for example, are influenced by testosterone, and testosterone is synthesized by **enzymes**, which are proteins encoded by deoxyribonucleic acid (DNA). Thus one can see how genes would influence these behaviors. All behavior, furthermore, depends on chemical signals (neurotransmitters) that are released by one **neuron** and bind to receptors on the next neuron. **Neurotransmitters**, too, are synthesized by enzymes encoded by DNA, and their receptors are proteins as well. Neurotransmitter levels control mood and probably aspects of personality. The list goes on and on. Indeed, it is impossible to see how genes could *not* play a role in behavior. SEE ALSO Biology of Race; Evolution; Sociobiology

Kenneth S. Saladin and Ricki Lewis

LORENZ, KONRAD (1903–1989)

Austrian biologist who founded the study of animal behavior, or ethology. Lorenz said that animal behavior evolves in the same way as physical structures, such as wings. Lorenz shared the Nobel Prize in physiology with fellow ethologists Karl von Frisch and Nikolaas Tinbergen.

gene expression use of a gene to create the corresponding protein

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

enzyme protein that controls a reaction in a cell

neuron nerve cell

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

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Behavior Patterns

There are millions of different species of animals, and each species behaves somewhat differently. Nevertheless, there are common patterns of behavior exhibited by many species, and a few behavior patterns that are exhibited by all species. Since all species need to reproduce, eat, and try not to be eaten by someone else, all species exhibit some type of reproductive behavior, foraging (eating) behavior, and defensive behavior. Over time, natural selection has also favored other behavior patterns that help species

Elk fighting for dominance in a Wyoming herd. Common patterns of behavior are exhibited by many species.

accomplish these basic goals, including communication behavior, territorial behavior, dispersal behavior, and social behavior.

Reproductive Behavior

Although some animals are able to reproduce asexually (such as some insects and a few species of lizards), most animals must find a mate in order to reproduce. In many cases, one of the individuals, usually the male, tries to attract a mate by performing a courtship display. This is often a visual display, as is the case with the peacock and many species of coral reef fish. Studies have shown that the females select males partly on the basis of their courtship displays. Scientists believe that vigorous and brightly colored displays might signal to the female that the male is strong and healthy. Thus, mating behavior plays an important role in determining which **genes** get passed on to the next generation.

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

Foraging Behavior

Animals exhibit several different types of foraging behavior. Some animals are quite selective in what they eat. These animals are called foraging specialists. For example, the diet of the lynx consists primarily of snowshoe hares. Some species of insects feed only on a single plant species; they are the ultimate feeding specialists. Other animals are generalists, eating a wide variety of food types. An example of a foraging generalist is the opossum, which eats everything from insects and berries to garbage. It is thought that natural selection has favored many animals to forage in an efficient manner. This means that the animals make feeding choices that maximize the amount of energy they can obtain in the shortest time possible. This type of foraging, sometimes referred to as "optimal foraging," leaves the animal with more time and energy for other important activities, such as finding a mate or caring for offspring.

Defensive Behavior

Virtually all animals are vulnerable to predation (being eaten by another animal) at least some time during their lives. Even wolves and lions can be

prey for other animals when they are very young. As a result, animals from worms to whales have evolved ways to reduce the likelihood they are eaten. This behavior, often referred to as defensive, or antipredator, behavior, can take many forms. Some animals, such as many moths and lizards, try to blend in with their surroundings so the predator cannot see them. This is called cryptic behavior. Other species have evolved effective escape behaviors, such as fast-running antelope and fast-swimming fish. Others fight back with stinging or biting behavior. In many cases, prey can deter predators with a threat display. Threat displays are special behaviors that tell the predator that the prey may fight back ferociously. A raccoon that bares its teeth and growls when cornered by a predator is giving such a threat display.

Communication Behavior

As illustrated above, effective communication behavior is vital for an animal. Besides communicating with sight and sound, some animals communicate using chemicals. For example, male moths find mates by detecting special chemicals called **pheromones** that the females release into the air. Ants also use pheromones to determine if another ant is an intruder or a member of the colony.

pheromone molecule released by one organism to influence another organism's behavior

Territorial Behavior

Setting up and maintaining a territory is another common pattern of behavior exhibited by many species of insects, fish, birds, reptiles, and mammals. Territories are used for a variety of purposes, including feeding, mating, and caring for offspring. The territory owner normally tries to keep other individuals of its species out of the territory.

Dispersal and Social Behavior

Other patterns of behavior include dispersal behavior, exhibited when individuals move away from the area in which they were born, and many types of social behavior. Social behavior is particularly common in animals that live in groups, such as ants, penguins, and primates. In all cases, scientists believe that these patterns of behavior have evolved over time because they have increased the ability of animals to survive and reproduce. SEE ALSO FEEDING STRATEGIES; HERBIVORY AND PLANT DEFENSES; MATING SYSTEMS; MIGRATION; MIMICRY, CAMOUFLAGE AND WARNING COLORATION; PREDATION AND DEFENSE; SEXUAL SELECTION; SOCIAL BEHAVIOR

Mark A. Davis

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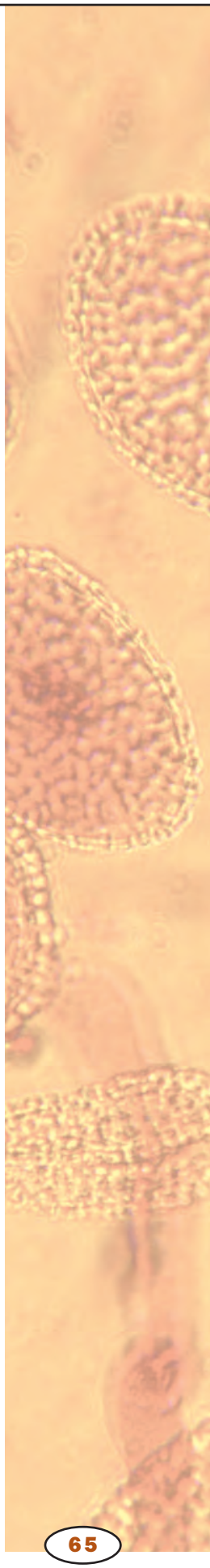
Biochemist

A biochemist is a scientist primarily concerned with the chemistry of biological processes. The four main branches of biochemistry are: a) nucleic acids, b) **proteins**, c) **carbohydrates**, and d) **lipids**. Most biochemists will generally specialize in one of these areas. The training and scientific focus of a biochemist is what distinguishes him or her from others in related

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



disciplines (molecular genetics, cell biology, analytic chemistry, and biophysics). Biochemists deal chiefly with scientific research of specific biochemical structures, interactions, or reactions. Two specific examples of research biochemists are enzymologists, who study catalytic proteins, and analytical biochemists, who may, for example, develop new DNA separation technologies.

Minimal training for a technician-level position in biochemistry generally requires a B.S. in biochemistry or chemistry, while those wishing more professional autonomy should attain a graduate degree. Ph.D.-level biochemists achieve the greatest autonomy. Before attaining their first independent position they will usually undergo additional training after completion of their in Ph.D., a postdoctoral position.

Biochemists work in the biopharmaceutical and agricultural biotechnology industries, academia, clinical laboratories, and a variety of regulatory and military posts in government. SEE ALSO BIOTECHNOLOGY; CARBOHYDRATES; DNA; LIPIDS; PHARMACOLOGIST

Michael L. Gleason

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Biodiversity

ecosystem an ecological community and its environment

Biodiversity is the sum total of life on Earth; the entire global complement of terrestrial, marine, and freshwater biomes and **ecosystems**, and the species—plants, animals, fungi, and microorganisms—that live in them, including their behaviors, interactions, and ecological processes. Biodiversity is linked directly to the nonliving components of the planet—atmosphere, oceans, freshwater systems, geological formations, and soils—forming one great, interdependent system, the biosphere.

Humankind's Relationship to Biodiversity

Humans depend entirely on this biodiversity and are an integral part of it. Directly or indirectly, be it from wild or domesticated components of biodiversity, humankind derives many goods critical to its sustenance, well-being, health, and enjoyment, such as food, medicine, building materials, and industrial products. Also, people enjoy many ecosystem services, including water regulation and supply, erosion control, soil formation, nutrient storage and cycling, pollination, pollution breakdown and absorption, climate stability, protection and recovery from natural disasters, and buffering against the spread of disease. These services, provided by nature free of charge, have an estimated value of $33 trillion per year.

Even though continued human welfare depends on it, our knowledge of biodiversity is seriously inadequate. As of 1998, scientists have described between 1.4 and 1.8 million species. However, later estimates indicate that the total number of species ranges between 5 and 30 million, and some scientists believe it may be higher than 100 million.

Clearly, much more work is needed to quantify and describe all biodiversity at three main levels: genetic diversity, or the variation of genes

within species; species diversity, or the variety of species within a biome or ecosystem, measured in species richness, species abundance, and taxonomic diversity; and ecosystem diversity, or the broad differences between ecosystem structures and biome types, and the diversity of habitats and ecological processes occurring within each of them. Taxonomists and other scientists in fields such as zoology, botany, ecology, and genetics study biodiversity.

Threats to Biodiversity

Species are becoming extinct faster than scientists can discover them. The loss of biodiversity is an irreversible process: once a species becomes extinct its loss is permanent and irrevocable. Late-twentieth-century estimates cite the extinction rate between one thousand and ten thousand times greater than it would be naturally. This means that Earth is losing species at the fastest rate in the planet's 4.5 billion-year history and, unlike prior extinction episodes (such as the mass extinction of dinosaurs 65 million years ago), this extinction spasm is mainly the result of human activity and not of a cosmic event. If extinctions continue at the current rate, in the next one hundred years humankind runs the risk of losing half of the planet's biodiversity.

Most threats to biodiversity have to do with pressures on natural resources due to human activities. These include habitat destruction and conversion of natural ecosystems to agriculture; flooding for hydroelectric projects; large-scale extraction of natural resources such as mining and logging; excessive hunting and overfishing; pollution from agricultural pesticides, human waste, and industrial processes; and poorly planned urban and suburban sprawl.

Conserving Biodiversity

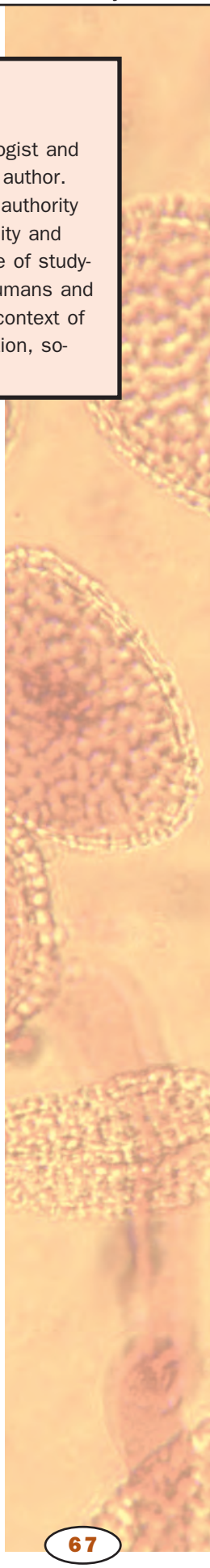
Conserving biodiversity is an urgent matter of common concern and should be an integral part of the development process, as was outlined in the Convention on Biological Diversity. This global, comprehensive agreement was drafted at the 1992 Rio de Janeiro Earth Summit and signed by 160 nations to address all aspects of biological diversity. Its objectives include "the conservation of biodiversity, its sustainable use and the fair sharing of the benefits derived from the utilization of genetic resources."

One conservation strategy aimed at reaching this goal recognizes that biodiversity is not evenly distributed over the planet: certain regions have higher species richness (the number of species in an area) and endemism (the number of species in that area that occur nowhere else) than others. Ironically, many of these sensitive areas are also preferred by humans to inhabit, placing tremendous pressure on local biodiversity. These areas are called the "biodiversity hotspots"; twenty-five of them have been described thus far, including Madagascar, the tropical Andes, the Philippines, and the Atlantic forest of Brazil. Conservationists believe that urgent conservation efforts should be targeted at these regions. Equally important are the so-called wilderness areas: Amazonia, the Congo Basin, and Papua New Guinea. These areas are also high in biodiversity but are not so immediately threatened. SEE ALSO Biome; Conservation; Ecosystem; Endangered Species; Extinction; Invasive Species

Cristina G. Mittermeier and Russell A. Mittermeier

WILSON, E. O. (1829–)

U.S. evolutionary biologist and Pulitzer Prize–winning author. Wilson is the world's authority on ants and biodiversity and was an early advocate of studying the behavior of humans and other animals in the context of evolution and adaptation, so-called "sociobiology."



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Biogeochemical Cycles

Biogeochemical cycles refer to the movement of chemical elements between living (biotic) and nonliving (abiotic) forms in the environment. Although many elements undergo this type of cycling to some extent, four elements—carbon, nitrogen, phosphorus, and sulfur—are most commonly discussed because of their importance (along with hydrogen and oxygen) for living organisms. The extent and rate of the cycling of these elements has important consequences, such as influencing the amount of phosphate available to forests and the ability of the oceans to slow down global warming by absorbing carbon dioxide.

Common Compounds

inorganic not bonded to carbon

ion an electrically charged particle

organic composed of carbon, or derived from living organisms

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

All the elements that undergo cycling are incorporated into compounds. Carbon may be found as **inorganic** CO_2 gas, carbonate **ions** (CO_3^{2-}) in rocks or the oceans, or in **organic** compounds, such as sugars and **proteins**, within living organisms. Nitrogen exists in the atmosphere as N_2 or ammonia (NH_3), in the soil as an ion such as nitrate (NO_3^-), and in living organisms in a variety of organic compounds, including proteins and nucleic acids. Wherever it occurs, phosphorus is largely bound to oxygen to make a phosphate ion (PO_4^{3-}). Sulfur exists as sulfur dioxide gas (SO_2), sulfate ions (SO_4^{2-}) in rocks, and in living organisms incorporated into proteins.

The atmosphere, oceans, fresh water, rocks, soil, and living organisms can each be thought of as a "pool" for storing these compounds. The time spent in any one pool is quantified as the mean residence time (MRT). For instance, the MRT for phosphate in rock may be thousands of years, whereas the MRT for the phosphate in a stand of corn is less than one year.

Transport Mechanisms

Elements move from one pool to another through meteorological, geologic, biological, or anthropogenic mechanisms. Meteorological mechanisms revolve around precipitation, such as rain carrying SO_2 into the soil. Geologic mechanisms include erosion, which can bring rock ions into solution, as well as sedimentation and volcanoes.

Biological mechanisms are those carried on by living organisms, such as photosynthetic conversion of CO_2 to sugar, or conversion of soil NH_3 to gaseous N_2 by soil bacteria. Marine birds can have a significant local impact on transport of phosphate and nitrogen from ocean to land. Many islands off

Soil erosion on a trail in the Adirondack mountains. Erosion is a geologic mechanism that helps to move chemical compounds between biotic and abiotic forms in the environment.

the western coast of South America, for instance, are covered with a layer of white guano, dropped by generations of birds feasting on anchovies. Harvest of this rich fertilizer forms part of the economies of Peru, Chile, and Ecuador.

Anthropogenic mechanisms are those carried on by humans and are therefore a subset of biological mechanisms. Humans have a profound effect on biogeochemical cycles through agriculture (for example, adding nitrogen to the global nitrogen cycle through fertilizer applications), forestry, and especially the use of carbon-based fossil fuels. The release of vast amounts of carbon from stored pools is likely to raise the world's temperature by at least several degrees over the coming decades, with the potential for significant consequences on many forms of life. An important, yet unanswered, question is whether the forests, soil, and especially the ocean can absorb this extra CO_2 and thereby reduce the extent of global warming. SEE ALSO CARBON CYCLE; ECOSYSTEM; GLOBAL CLIMATE CHANGE; NITROGEN CYCLE; PHOTOSYNTHESIS; PLANKTON

anthropogenic of, relating to the influence of human beings or nature

Richard Robinson

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Biogeography

An enormous variety of species live in the thin layer on Earth's surface that makes up the biosphere. None of these species is found everywhere on Earth's surface. Instead, the number and kinds of species change dramatically as one moves from one place to the next. The science that studies the past and present distribution patterns of organisms and seeks to understand the mechanisms that underlie these patterns is called biogeography.

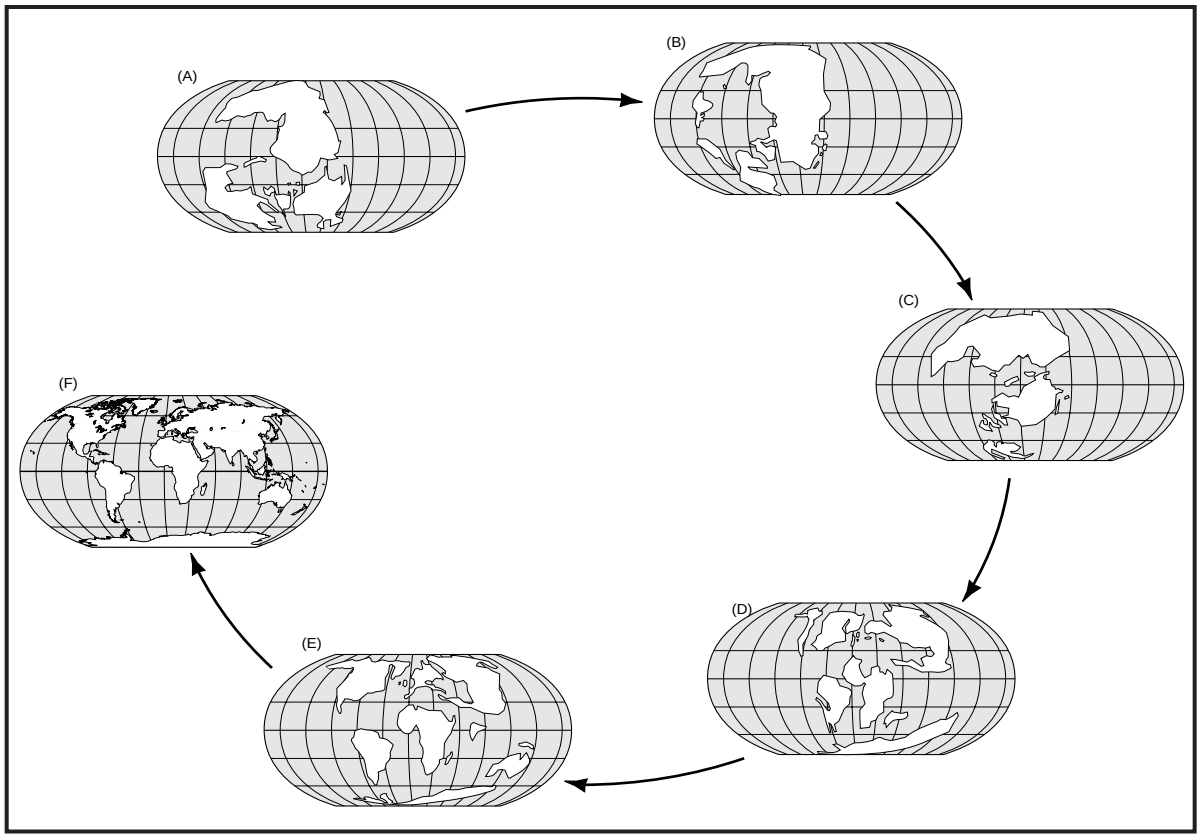
Biogeographers explain the distributions of species using four basic principles regarding the nature of Earth and the organisms that live on it:

1. Environmental variability: For a variety of reasons, the conditions that organisms experience change dramatically across Earth's surface. Climate and elevation are two major influences.
2. Ecological limitation: Every organism has a limited range of conditions that must be met in order to allow it to live and reproduce. Since a species is a population of reproductively compatible organisms that have similar biological properties, no species can be found everywhere.
3. Continental drift: The locations of landmasses across Earth's surface have not remained the same, but have changed slowly over the course of Earth's history. Therefore, the conditions experienced by organisms change over long periods of Earth's history.
4. Evolutionary change: Species do not stay the same over time, but are in a constant state of change as individuals best able to survive and reproduce within certain environments become more frequent, while others less capable die or fail to produce offspring. The ability of a species to evolve allows it to persist over long periods of time and track the changes occurring on Earth's surface.

The first two principles indicate that the current geographic distribution of a species is determined by how its ecological limitations are related to the environmental conditions it encounters. Species with similar requirements will be found together in the same locations. Regions on continents or in oceans where the species share similar ecological limitations are called biomes. For example, deserts are biomes where the species are all able to withstand relatively hot, dry climates.

The third and fourth principles indicate that as continents move about across the face of Earth, they carry with them the species that inhabit them. When continents that were once connected separate, populations are fragmented, and subsequent evolutionary changes in related species will occur independently. The timing of such independent evolutionary changes provides clues about the timing of Earth's history. Much of the history of continental drift, for example, can be reconstructed by examining the geographical distribution of fossils and of related groups of living species.

All four principles suggest that as the conditions on Earth change over long periods of time, each species will respond to these changes in one of three distinct ways. First, a species may change its geographic distribution to track changes in the location of its favored set of ecological conditions. For instance, during ice ages, many species moved southward. Second, a



The distribution of landmasses at points in Earth's history, illustrating the theory of continental drift and the changing conditions organisms experienced due to it: (A) 320 million years ago; (B) 250 million years ago; (C) 135 million years ago; (D) 100 million years ago; (E) 45 million years ago; (F) present.

species may undergo evolutionary change to adapt to changing conditions. Third, if a species cannot shift its geographic range or undergo evolutionary change, the species will go extinct. Over the history of Earth, no species has been able to persist unchanged as the biosphere has changed. SEE ALSO BIODIVERSITY; BIOME; EVOLUTION

Brian Maurer

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Bioinformatics

Bioinformatics is a new field that centers on the development and application of computational methods to organize, integrate, and analyze **gene**-related data. The Human Genome Project (HGP) was an international effort to determine the deoxyribonucleic acid (DNA) base sequence of the entire human genome, which includes about thirty thousand **protein**-encoding genes, their regulatory elements, and many highly repeated noncoding sections. In 1985, a group of visionary scientists led by Charles DeLisi, who was then the director of the office of health and environmental research at the U.S. Department of Energy (DOE), realized that having the entire human genome in hand would provide the foundation for a revolution in biology and medicine. As a result, the 1988 presidential budget submission to

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

A scientist at the Whitehead Institute in Cambridge, Massachusetts, studies a map of the human Y chromosome.

U.S. Congress requested funds to start the HGP. Momentum built quickly and by 1990, DOE and the U.S. National Institutes of Health had laid out plans for a fifteen-year project. An international public consortium and a private company announced completion of a rough draft of the human genome sequence on June 26, 2000, with papers describing the data published eight months later. This is the first generation bestowed with the "parts list" of life, as well as the daunting task of making sense out of it.

Data Management

The Human Genome Project and other genome projects have generated massive data on genome sequences, disease-causing gene variants, protein three-dimensional structures and functions, protein-protein interactions, and gene regulation. Bioinformatics is closely tied to two other new fields: genomics (identification and functional characterization of genes in a massively parallel and high-throughput fashion) and proteomics (analysis of the biological functions of proteins and their interactions), which have also resulted from the genome projects. The fruits of the HGP will have major impacts on understanding evolution and developmental biology, and on scientists' ability to diagnose and treat diseases. Areas outside of traditional biology, such as anthropology and **forensic** medicine, are also embracing genome information.

forensic related to legal proceedings

Knowing the sequence of the billions of bases in the human genome does not tell scientists where the genes are (about 1.5 percent of the human genome encodes protein). Nor does it tell scientists what the genes do, how genes are regulated, how gene products form a cell, how cells form organs, which mutations underlie genetic diseases, why humans age, and how to develop drugs. Bioinformatics, genomics, and proteomics try to answer these questions using technologies that take advantage of as much gene sequence information as possible. In particular, bioinformatics focuses on computational approaches.

Bioinformatics includes development of databases and computational algorithms to store, disseminate, and rapidly retrieve genomic data. Biologi-

cal data are complex and abundant. For example, the U.S. National Center for Biotechnology Information (NCBI), a division of the National Institutes of Health, houses central databases for gene sequences (GenBank), disease associations (OMIM), and protein structure (MMDB), and publishes biomedical articles (PubMed). The best way to get a feeling for the magnitude and variety of the data is to access the homepage of NCBI via the World Wide Web (http://ncbi.nlm.nih.gov). A bioinformatics team at NCBI works on the design of the databases and the development of efficient algorithms for retrieving data and comparing DNA sequences.

Applications

Bioinformatics also covers the design of genomics and proteomics experiments and subsequent analysis of the results. For instance, disease tissues (such as those from cancer patients) express different sets of proteins than their normal counterparts. Therefore protein abundance can be used to diagnose diseases. Moreover, proteins that are highly (or uniquely) expressed in disease tissues may be potential drug targets.

Genomics and proteomics generate protein abundance data using different approaches. Genomics determines gene abundance (which is a good indicator of protein abundance) using DNA microarrays, also known as DNA chips, which are high-density arrays of short DNA sequences, each recognizing a particular gene. By **hybridizing** a tissue sample to a DNA chip, one can determine the activities of many genes in a single experiment. The design of DNA chips—that is, which gene fragments to use in order to achieve maximum sensitivity and specificity, as well as how to interpret the results of DNA chip experiments—are difficult problems in bioinformatics.

hybridizing combining two different types

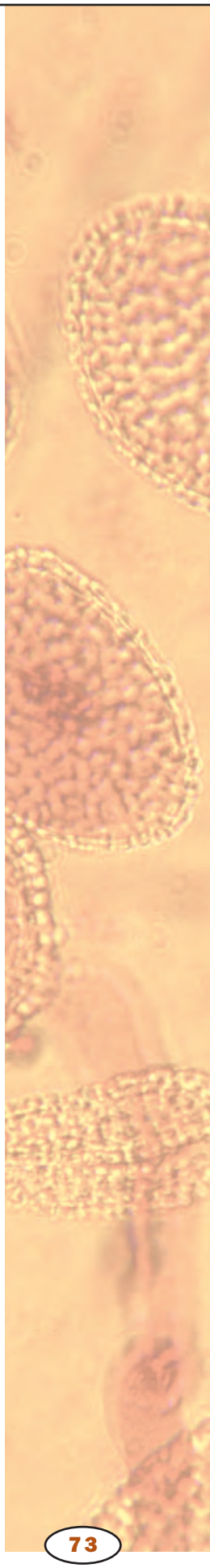
Proteomics measures protein abundance directly using mass **spectroscopy**, which is a way to measure the mass of a protein. Since mass is not unique enough for identifying a protein, one usually cuts the protein with **enzymes** (that cut at specific places according to the protein sequence) and measures the masses of the resulting fragments using mass spectroscopy. Such "mass distributions" for all proteins with known sequences can be generated using computers and stored. By comparing the mass distribution of an unknown protein sample to those of known proteins, one can identify the sample. Such comparisons require complex computational algorithms, especially when the sample is a mixture of proteins. Although not as efficient as DNA chips, mass spectroscopy can directly measure protein abundance. In fact, spectrometric identification of proteins has been the one of the most significant advances in proteomics.

spectroscopy process using light or other emitted radiation to determine properties of a sample

enzyme protein that controls a reaction in a cell

Bioinformatics can lead to discovery of new proteins. When the cystic fibrosis gene (CF) was first identified in 1989, for example, researchers compared its DNA sequence computationally to all sequences known at that time. The comparison revealed striking homology (sequence similarity) to a large family of proteins involved in active transport across cell membranes. Indeed, the CF gene encodes a membrane-spanning chloride **ion** channel, called the cystic fibrosis transmembrane regulator, or CFTR. The identification of gene function by searching for sequence homology is a widely used bioinformatics method. When no homology is found, one may still be able to tell if a gene codes for membrane-spanning channels using computational

ion an electrically charged particle



bilayer composed of two layers

lipid fat or waxlike molecule, insoluble in water

tools. Membranes are **bilayers** of **lipid** molecules, which are water insoluble. An ion channel typically has regions outside the membrane (water soluble) and regions inside the membrane (water insoluble) arranged in a certain pattern. Computer algorithms have been developed to capture such patterns in a gene sequence.

By thinking boldly and by setting ambitious goals, the Human Genome Project has brought about a new era in biological and biomedical research. Many revolutionarily new technologies are being developed, most of which have significant computational components. The avalanche of genomic data also enables model-based reasoning. The bright future of bioinformatics calls for individuals who can think quantitatively and in the meantime love biology—an unusual combination. SEE ALSO BIOTECHNOLOGY; GENOME; HUMAN GENOME PROJECT

Zhiping Weng

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Biological Weapons

rickettsia (pl. -sias or siae) any of a family of polymorphic microorganisms that cause various diseases

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

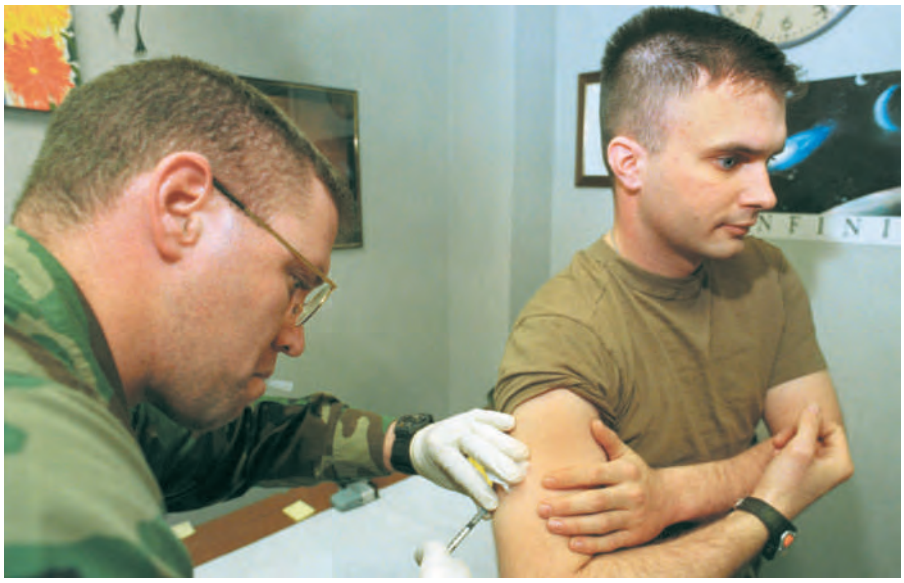
fungi major group of parasitic, lower plants that obtain their food from the products of organic decay (e.g. molds, smuts, etc.)

Biological weapons are organisms or their by-products used to deliberately spread disease. They include bacteria, viruses, **rickettsiae**, **protozoa**, **fungi**, and their toxins. The effects of biological warfare agents are diverse, but they generally incapacitate or kill their victims, or destroy crops or livestock.

Biological weapons have been used for centuries. The Tartar army catapulted plague-ridden corpses over city walls in the 1346 siege of Kaffa. All major participants in World War II developed biological weapons, however Japan, which dropped bubonic plague–infested debris on Chinese cities, was the only country known to have used them. In 1969 the United States abandoned research and production of biological weapons. Within three years, remaining U.S. stockpiles were destroyed. In 1975, 118 countries signed the Biological Weapons Convention that outlawed the development, possession, and stockpiling of biological weapons.

Biological weapons are often called "the poor man's weapon of mass destruction" because they are cheap and easy to produce. The production processes used to make biological weapons are similar to those used to develop medicines or make yogurt. Since facilities, equipment, and supplies resemble those for biotechnical and medical research, they can be hidden within legitimate facilities, making it difficult to track development of biological weapons. Compared to chemical or nuclear weapons, biological weapons are easily handled and effective in small amounts.

Exposure to most biological weapons occurs by inhaling an aerosolized agent. The most difficult part of producing the weapon is getting the agent into a small, stable form for dispersal. Agents can be dispersed as part of a



An American soldier receiving an anthrax vaccine before shipping out to Korea in February 2000. Inhalation of anthrax spores causes severe respiratory distress, shock, and death in about five days.

conventional warhead or sprayed from a plane or a small canister. Attacks are nearly impossible to detect in early stages and may not become known until symptoms of disease appear. Defense against biological weapons may include protective clothing and masks, vaccinations, and antibiotic or antiviral therapy. Quick identification of biological agents is essential to save lives and maintain military effectiveness.

There are more than sixty potential biological warfare agents. Two of the most common are anthrax and botulism. The anthrax bacteria, *Bacillus anthracis*, commonly cause disease in cattle, horses, and sheep. In humans, **cutaneous** anthrax, which causes skin ulcers, accounts for about 95 percent of U.S. cases, with little mortality. However, inhalation of anthrax spores destroys lung and intestinal membranes, causing severe respiratory distress, shock, and death in about five days. Although antibiotics can be used, the mortality rate for inhaled anthrax is nearly 100 percent after symptoms appear. Anthrax is easy to cultivate and forms highly resistant spores that can remain active and potentially lethal for at least forty years.

cutaneous related to the skin

Botulism is caused by *Clostridium botulinum* neurotoxin. Inhaling a very small amount of this bacterial toxin blocks electrical signal transmission in the nervous system and causes progressive muscular paralysis. Paralysis of respiratory muscles leads to asphyxiation and death. Tracheostomy and use of a ventilator reduce mortality, but recovery may take months of intensive nursing care.

Advances in biotechnology may produce biological weapons that are even more toxic, fast acting, and resilient. Genetic engineering may produce new organisms or toxins designed to target specific populations. Cloning techniques may allow for mass production. SEE ALSO NERVOUS SYSTEMS; NEURON; POISONS

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Biology

Biology is defined as the "study of life." The term life refers to all organisms (plants, animals, bacteria, fungi, and protists) inhabiting Earth and its atmosphere. Both scientists and laypeople are drawn to biology because it seeks to answer the question of how life began. All of the acquired evidence points to a single origin for all living things.

The study of evolution shows that there are significant similarities among organisms that are not obviously related. Virtually every organism uses the same **genetic code** to builds its **proteins**, from the tiniest bacterium to the blue whale and the giant sequoia. A fungus and a horse break down sugar to release energy using (more or less) the same **enzymes**. Indeed, evolution, the gradual change in a population over time, serves as a unifying concept in biology.

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

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

enzyme protein that controls a reaction in a cell

The more related two species of multicellular organisms are, the more similar their anatomies in almost all cases. Species that rely heavily on one another for life evolve in response to each other's habits and characteristics. Researchers use animals closely related to humans in order to predict the effects of new drugs or surgical techniques on human subjects, taking advantage of evolutionary relationships that yield similar anatomies and physiologies in different organisms.

Biology's Subdisciplines

Biology encompasses many diverse subdisciplines. Systematics is the study of the diversity and classification of organisms. Cell biology is concerned with the structure and function of cells but also includes the interactions that occur between cells (for example, the signaling that occurs among different cells of the human body). The field of ecology considers interactions among organisms that inhabit the same area. For example, ecologists might study the changes in population size of a group of birds in response to the presence of a predator, or the impact of pollution on frog populations. Someone interested in medicine would need a solid background in anatomy, the study of the structure of the bodies of animals and how different components of the body relate to one another.

Physiology, which is closely related to anatomy, describes the mechanisms by which these different components perform. One might also study the anatomy and physiology of plants to learn how different tissues within a plant perform and interact. Microbiology, a field driven largely by the study of disease, is concerned with the structure, function, and interactions of microorganisms. Genetics is concerned with the inheritance of characteristics from parents to offspring, and the expression of genes to create the living organism.

Much emphasis in biology is in biotechnology, the use of organisms to create products. This field opens unimaginable possibilities for the diagnosis and treatment of hereditary diseases, production of drugs, and advancement of agriculture. At the same time, these prospects will challenge scientists with serious ethical considerations in the years to come, as the use of biotechnology requires scientists to manipulate the course of evolution.

SEE ALSO BIODIVERSITY; BIOTECHNOLOGY; ECOLOGY; EVOLUTION

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Biology of Race

The biological definition of race is a geographically isolated breeding population that shares certain characteristics in higher frequencies than other populations of that species, but has not become reproductively isolated from other populations of the same species. (A population is a group of organisms that inhabit the same region and interbreed.) Human racial groups compose a number of breeding units that in the past remained geographically and perhaps temporally isolated, yet could interbreed and produce viable offspring within the species *Homo sapiens sapiens*. **Paleoanthropological** evidence suggests that these units have been interbreeding between populations for at least the last two hundred thousand years or longer in what may once have been considered racial groups.

paleoanthropological of, related to the branch of anthropology (the study of human beings) that is concerned with "fossil man"

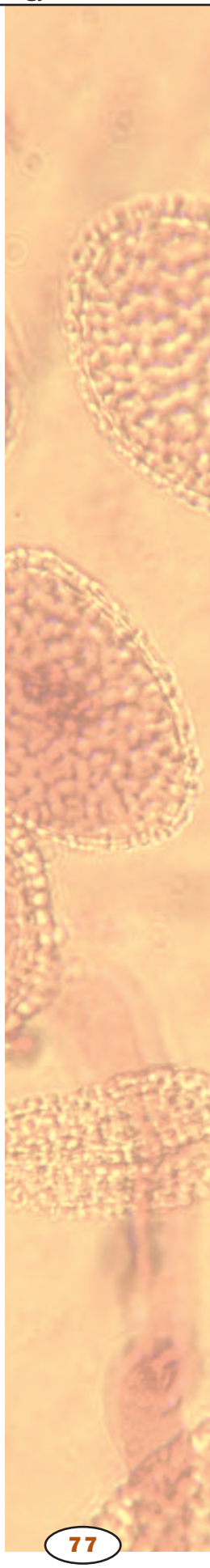
More recently, molecular techniques have developed to examine genetic differences between individuals and populations, including karyotypes providing chromosomal number and patterns, deoxyribonucleic acid (DNA) hybridization, **protein** sequences, and nuclear and **mitochondrial** base sequences from ancient and modern DNA. From all this evidence, it is clear that populational, but not racial, differences do exist within the human species. Race should not be equated with ethnicity, which has a sociological meaning. Ethnicity is a self-described category that has three components—ancestry, language, and culture—that all have affinities to certain ancestral groups.

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

mitochondrial of, relating to subcellular organelle that creates ATP used for energy-requiring processes in a cell

Early racial classification systems for humans used specific phenotypic characteristics that occurred in higher frequencies in certain populations. Initially, three classes were identified by anthropologists: Caucasoids, Mongoloids, and Negroids; later, Australoids and Capoids (Bushmen) were added. Following this, even more classifications were made, with no consensus among biological anthropologists. Difficulties with these early classification systems stem from the immense genotypic and phenotypic human variation found in modern living populations. While the genotypic variation was not studied in great detail in the early part of the twentieth century, phenotypic variation in skin color, body height, hair type, nasal width, and other characteristics was studied in great detail.

Some genetic differences do exists between groups, but these by and large do not correspond to historical racial categories. For instance, there are populational differences in the frequency of ABO blood types. Native North and South Americans have an incidence of nearly 100 percent type O (less than 1 percent have type AB), while Asians have a lower incidence of O (60 percent) and higher incidence of type B (22 percent). Some characteristics, such as skin color and body height, are considered to be polygenic traits. Skin color has a clinal distribution, with indigenous peoples with darker skin colors found in native peoples at the equator and lighter skin colors found in natives from higher latitudes.



The very large amount of variation within groups dwarfs the small differences between groups, therefore race in humans does not have a biological meaning.

Skin color is an adaptation to sunlight that provides protection from skin cancer, yet at the same time allows for vitamin D production for calcium absorption. Darker skin provides more protection, while lighter skin allows more penetration of the weaker sun in temperate regions. While body height is also considered a polygenic trait, it is very much affected by inheritance, as well as environmental stressors (such as malnutrition and infectious disease).

Some differences between populations may correlate with historical exposure to different infectious diseases. For example, certain genetic variants of **hemoglobin** (for example, those causing sickle-cell **anemia** in people of African descent and thalassemia in people of Mediterranean descent) were strongly selected because they provide defensive mechanisms against infection by the organism that causes malaria (*Plasmodium*). Such environmental selection pressures have caused more than three hundred variants of the hemoglobin molecule. Cystic fibrosis (CF), a disorder of a gene that produces a protein that forms a chloride pump in cell membranes, allows for the buildup of mucus in the respiratory tract, thereby leading to death from **pathogenic** invasion. Yet the **heterozygous** condition for CF protects against extreme dehydration due to cholera. Tay-Sachs disease, a disorder of an **enzyme** that breaks down a molecule in the myelin sheath of nerve fibers, is found more commonly in people of eastern European Jewish descent than in other populations. Whether the Tay-Sachs gene protects against an infectious disease is unknown, though some have made a connection to tuberculosis exposure.

hemoglobin oxygen-carrying protein complex in red blood cells

anemia lack of oxygen-carrying capacity in the blood

pathogenic causing, or capable of causing, disease

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

enzyme protein that controls a reaction in a cell

The molecular techniques outlined above now allow anthropologists to study the migration patterns of ancient peoples. Genetic diversity has resulted from the extensive hybridization that has occurred in the last two hundred thousand years, hiding any clear evidence for typological classification of race. Moreover, when selection pressures (temperature, altitude) are coupled with phenotypic variation, phenotypic expression defies taxonomic assignment of race. The genetic diversity *within* any histori-

cally defined race swamps the small amount of difference between such groups, making the boundaries of these categories entirely arbitrary. Therefore, race in humans does not have a biological meaning. SEE ALSO GENETIC DISEASES; HUMAN EVOLUTION; HYBRIDIZATION; SEXUAL SELECTION

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Biome

Earth's major terrestrial, marine, and freshwater **ecosystems** are known as biomes. They are classified according to similarities in species composition of plants and animals, and by environmental attributes. These attributes include temperature, precipitation, and soil type in terrestrial biomes and temperature, depth, and salinity in aquatic biomes. There are no hard boundaries between biomes and there is much intermixing of species between them.

ecosystem an ecological community and its environment

Biomes are divided into many kinds of ecosystems and habitats, according to local variations in species composition and physical environment (a cloud forest, mud flat, and meadow, to name a few). However, scientists generally recognize between twelve and fifteen major natural terrestrial biomes, including tropical rain forest, tropical deciduous forest, thorn woodland, tropical **savanna**, desert, **sclerophyllous** woodland, subtropical evergreen forest, temperate deciduous forest, temperate rain forest, temperate grassland, boreal forest, and tundra. Some scientists consider cultivated land to be a biome. There are seven major freshwater biomes: ice, spring, river, swamp, marsh, lake, and stream. There are six major marine biomes: coral reef; algal bed; estuary; upwelling zone; **continental shelf**; and open ocean.

savanna open grassland with sparse trees

sclerophyll small, tough evergreen leaves

continental shelf submerged offshore area demarcated by land on one side and deep sea on the other

Significant changes in the global environment and climate are causing major shifts in some biomes, such as glacier movement and polar cap melting, and are threatening the survival of others, such as the deforestation of tropical and temperate rain forests. SEE ALSO BIODIVERSITY; DESERT; ESTUARIES; FOREST, TEMPERATE; GRASSLAND; HABITAT; OCEAN ECOSYSTEMS; TUNDRA

Cristina G. Mittermeier and Russell A. Mittermeier

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Biotechnology

The term "biotechnology" was coined in 1919 by Hungarian scientist Karl Ereky to mean "any product produced from raw materials with the aid of living organisms." In its broadest sense, biotechnology dates from ancient times. Approximately 6000 B.C.E., the Sumarians and Babylonians discovered the use of yeast in making beer. About 4000 B.C.E., the Egyptians employed yeast to make bread and the Chinese bacteria to make yogurt.

The modern sense of biotechnology dates from the mid-1970s, when molecular biologists developed techniques to isolate, identify, and clone individual **genes**. These genes could then be manipulated in the test tube, and could be inserted into other organisms by "recombinant technology." The dawn of modern biotechnology dates from 1977 when the biotechnology company Genetech reported the production in bacteria of the first human **protein**, **somatostatin**, by recombinant technology. Shortly thereafter, human insulin and human growth **hormone** (hGH) were also produced by similar techniques.

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

somatostatin hormone produced by the hypothalamus that influences growth

hormone molecule released by one cell to influence another

Biotechnology promises dramatic discoveries in the twenty-first century, particularly in the areas of new drugs, antibiotics, and medicines. Plants and animals are being genetically manipulated ("plant and animal pharms") to produce useful reagents such as antibodies in milk and vaccines in potatoes. A new "green revolution" in biotechnology is taking place to improve food crops. Plants are being developed that produce their own nitrogen fertilizer and pesticides. Others are resistant to herbicides to eradicate weeds and improve crop yield. Rice, the primary foodstuff of one-third of the world's population, is deficient in vitamin A. By the insertion of a gene from a flower into rice, a new strain of "golden rice," rich in vitamin A, promises to alleviate vitamin A–deficient blindness in these populations. On the negative side, biotechnology, unfortunately, is being used to develop biological weapons by increasing the virulence of **pathogens** or creating new "superbugs." SEE ALSO Clone; DNA Sequencing; Gene Therapy; Genomics; Human Genome Project; Polymerase Chain Reaction; Recombinant DNA

pathogen disease-causing organism

Ralph Meyer

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Bird

Birds are warm-blooded vertebrates with feathers. They are thought to have evolved over 150 million years ago from a Mesozoic reptilian ancestor. Indeed, they share many characteristics with reptiles, including **nucleated** red blood cells, females as the heterogametic sex (having two different sex **chromosomes**), numerous skeletal features, and similar eggs. However, birds have evolved many unique characteristics.

nucleated having a nucleus

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

Characteristics of Birds

The most remarkable of the bird's characteristics is the feather. Feathers are the diagnostic trait of birds. No other living animal has feathers. The contours and strength of feathers make bird flight possible. At the same time they are lightweight and provide excellent insulation and physical protection to the bird's body. Feather coloration provides both concealment and a means of communicating with rivals and mates. Feathers are energetically inexpensive to produce, and a bird can grow at least a partial new feather coat each year.

Birds are highly skilled, powerful flyers. Flying, however, is an energetically costly activity, and there is hardly any aspect of **avian** anatomy that has not been influenced by the demands of flight. In the interest of weight reduction, some avian bones have been fused or reduced in size, and many of the bones in a bird's body are hollow and filled with air (pneumatized).

Birds have lightweight beaks instead of jaws filled with heavy teeth, and some internal organs are reduced in size or absent. Stability in flight is increased by the bird's overall body plan, which places its greatest mass in the centralized area between the wings, providing a compact center of gravity. To provide the power for flight, birds have exceptionally efficient circulatory and respiratory systems, the latter including a system of air sacs that assist with **thermoregulation** and buoyancy as well as offering some protection to internal organs. Control and rapid adjustments during flight are aided by the bird's sophisticated **central nervous system** and exceptional visual acuity.

A red-tailed hawk. Aside from birds, no other living animal has feathers.

avian concerning birds

thermoregulation temperature regulation

central nervous system brain and spinal cord

The Evolution of Birds

There are two primary theories about bird origins. One theory suggests that birds arose from early (nondinosaur) reptiles, possibly those called thecodonts. The other proposes that birds evolved from a common ancestor with theropod dinosaurs. If the latter idea is true, then modern birds are "living dinosaurs."

Proponents of the thecodont theory point out that there are skeletal similarities between birds and thecodonts, most notably the presence of **clavicles**, which dinosaurs were thought to lack. However, fossil finds and reexamination of previously collected dinosaur fossils show that many groups of dinosaurs did, indeed, have clavicles. Proponents of the dinosaur theory point out that *Archaeopteryx*, the earliest fossil to be conclusively identified as having a close affinity to birds, has many anatomical features in common with theropod dinosaurs.

clavicle collar bone

However, one argument against the dinosaur origin of birds has to do with the digits. In the avian wing, the bones of the "hand" include only three fingers. The "hand" of a theropod dinosaur also has only three fingers, but many paleontologists think that they are a different three than those that birds have retained.

Birds and the Environment

Birds range in size from the Cuban bee hummingbird, which is approximately 5.7 centimeters (2.25 inches) from bill tip to tail tip and weighs less than 31 grams (about 1 ounce), to the ostrich, which may stand 2.7 meters

(9 feet) tall and weigh over 136 kilograms (300 pounds). Birds are represented in the breeding fauna of all seven continents, and exploit habitats ranging from rainforests to deserts to oceans. The high mobility conferred by flight permits birds to colonize even the most remote areas. Some birds, however, particularly those residing on islands where there are few terrestrial predators, have secondarily evolved flightlessness.

Because birds are everywhere and highly visible, the health of bird populations can be valuable indicators of environmental health. Habitat destruction and/or fragmentation is probably the most important current threat to bird populations worldwide. Reducing a large area of **contiguous** habitat to several smaller parcels means that birds requiring large breeding territories will not be able to find them. Birds that can breed in the smaller parcels may also experience reduced breeding success because proximity of a nest to a habitat edge may increase the likelihood that it will be found by a predator or **parasite**.

contiguous adjacent to or touching

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

Pesticides have also been implicated in reductions of bird populations. In particular, poisons may accumulate in the tissues of predatory birds at the top of the food chain, such as eagles, which consume many smaller predators that have been exposed to pesticides. An example is DDT, which results in the thinning of eggshells and consequent egg breakage during incubation. Some bird species have also been threatened by the introduction of non-native competitors and predators. SEE ALSO AMNIOTE EGG; CARSON, RACHEL; CHORDATA; EVOLUTION; FLIGHT; REPTILE; RESPIRATION

Ann E. Kessen and Robert M. Zink

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Birth Control

Birth control refers to the practice of deliberately controlling the number of children born, especially by reducing or eliminating the possibility of conception. While there are many forms of birth control, they can be broadly classified as follows: behavioral methods; surgical methods; barrier methods; hormonal methods; and methods that prevent the continuation of pregnancy, namely abortion.

Behavioral methods include the practice of abstinence from intercourse, particularly during the fertile period of the woman's menstrual cycle, commonly known as the rhythm method. While the fertile days generally occur in the three to four days before and after ovulation, this particular method of birth control is frequently ineffective because of the difficulty in predicting ovulation with the necessary accuracy. Other behavioral methods include withdrawal of the penis from the vagina prior to male orgasm. This depends on complete and timely withdrawal, with no sperm deposited anywhere near the **vulva**. It is *not* an effective method of birth control.

vulva external female genitalia

Surgical methods of birth control can be used by both males and females. In males, this involves a vasectomy in which the **vas deferens** is severed. In females, a tubal ligation ties off the **fallopian tubes**, thus preventing sperm from reaching the egg. These methods offer a high degree of effectiveness but have the disadvantage of being difficult to reverse should the individuals ever want to regain fertility.

Barrier methods of birth control involve preventing the sperm from reaching and fertilizing the egg. For males, this entails the use of condoms to prevent the sperm from entering the vagina. In females, sponges, spermicides, or diaphragms are used to prevent the sperm from entering the uterus and ultimately the fallopian tubes. When used in combination and consistently, these methods can be highly effective, but they frequently fail due to inconsistent usage or failure of the barrier (for example, a broken condom or improperly inserted diaphragm).

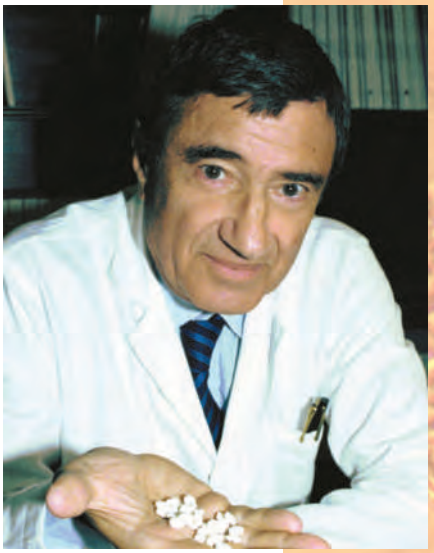
Hormonal methods are among the most common and effective means of birth control worldwide. These methods rely on the use of **hormones** (usually a combination of progesterone and estrogen) that disrupt the normal menstrual cycle in the female, resulting in a suppression of ovulation and hence conception. While the birth control pill is the most common of these methods, other common hormonal methods of birth control are implants (such as Norplant) that release hormone continuously or injections of hormones every few months that likewise suppress ovulation.

All of these hormonal methods are highly effective means of birth control with generally minor side effects. Major side effects, such as stroke, are rare and generally associated with increasing female age and smoking. The "morning after" pill is also hormonal in nature. It is often referred to as an "emergency form" of birth control, and is taken following intercourse. It prevents the embryo from successfully implanting in the uterine wall.

Another effective means of birth control is the intrauterine device (IUD), plastic and metal (often copper) devise that is inserted into the uterus. While earlier versions were linked to side effects including pelvic inflammatory disease, the currently available forms have few serious side effects and have the advantage of being easily removed when a restoration of fertility is desired. It remains unclear how exactly the IUD exerts its contraceptive effects, but it is thought that it alters the uterine environment to prevent sperm passage or to prevent implantation of the fertilized egg.

The final category of birth control is abortion, which involves the cessation of a pregnancy. It is not a contraceptive technique, given that it does not prevent conception from occurring, but rather, one that terminates an existing pregnancy. This could be performed surgically by removing the fetus from the womb. More recently, drugs that induce a medical abortion such as Ru486 have become available in certain countries, including the United States. This drug, taken during the first trimester of pregnancy, inhibits the effects of progesterone, a hormone that is essential to the continuation of the pregnancy. Thus the fetus is ultimately expelled from the uterus.

While a wide variety of alternatives exist for or birth control, the selection of an appropriate method depends on a wide array of individual circumstances and should be made in conjunction with a knowledgeable health



Emile-Etienne Beaulieu, inventor of Ru486.

vas deferens tube through which sperm travel from testes to urethra

fallopian tubes tubes through which eggs pass to the uterus

hormone molecule released by one cell to influence another

care provider. SEE ALSO FEMALE REPRODUCTIVE SYSTEM; MALE REPRODUCTIVE SYSTEM; SEXUAL REPRODUCTION; SEXUALLY TRANSMITTED DISEASES

Margaret Somosi Saha

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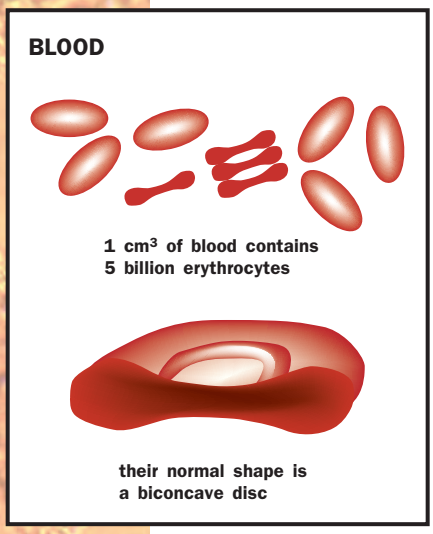
Blood



Erythrocytes (red blood cells) are very small cells, usually with no nucleus or internal membranes, and are stuffed full of the oxygen-binding protein hemoglobin.

Blood is the bodily fluid responsible for transport of materials and waste products throughout the body. It carries oxygen from and carbon dioxide to the lungs, nutrients from the digestive system or storage sites to tissues that require them, and waste products from the tissues to the liver for detoxification and to the kidneys for disposal. Blood delivers hormones to their sites of action and circulates numerous critical parts of the immune system throughout the body. Blood regulates its own **pH**, as well as that of the intercellular fluid in the body, and aids in **thermoregulation** by redistributing heat. Blood also carries the **proteins** and other factors it needs to clot, thereby preventing its own loss in the event of injury to the vessels in which it travels.

A human adult has 4 to 6 liters (1 to 1.5 gallons) of blood, approximately 92 percent of which is water. Nearly half its volume is red blood cells (RBCs, or erythrocytes). Proteins, sugars, salts, white blood cells, and platelets make up the remainder. The noncellular portion is termed plasma, while the cellular parts are collectively referred to as the formed elements. Blood forms in the bone marrow, a spongy tissue contained in the bones.

Red Blood Cells and Hemoglobin

Only a small amount of the oxygen needed for life can dissolve directly in plasma. Oxygen transport instead relies on red blood cells. At any one time, there are more than 25 trillion RBCs in circulation in an adult, more than the combined total of all other cell types in the body. As RBCs develop, they extrude their cell **nucleus**, so that at maturity they have almost nothing inside their membranes except the oxygen-carrying protein, **hemoglobin**. The absence of a nucleus contributes to the RBC's short life, as does the constant physical stress it experiences squeezing through capillaries that are narrower than it is. The average RBC circulates for approximately 120 days before being destroyed in the liver, bone marrow, or spleen. The iron from hemoglobin is recycled, while the cyclic nitrogen compound that holds it, called heme, is converted to bilirubin. Bilirubin is transported to the liver for elimination from the body as bile. Liver disease can cause jaundice, a yellowing of the skin due to bilirubin in the blood.

The iron in hemoglobin is critical for oxygen transport. Lack of dietary iron is one cause of anemia, a condition in which the blood cannot carry enough oxygen. The heme group binds oxygen tightly when the concen-

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

thermoregulation temperature regulation

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

nucleus membrane-bound portion of cell containing the chromosomes

hemoglobin oxygen-carrying protein complex in red blood cells

tration of O_2 is high (as it is in the lungs), but quickly releases it when the concentration is low, as it is in the tissues. The iron can also bind carbon monoxide (CO), which is produced by car engines and other combustion sources. CO binds much more tightly than oxygen does and prevents oxygen binding, making CO a deadly poison.

A genetic variant of the hemoglobin gene causes a single **amino acid** change in the hemoglobin molecule. This change causes the red blood cell to become sickle-shaped at low oxygen concentrations, so that it tends to become lodged in small capillaries, depriving tissues of oxygen. A person with one such variant hemoglobin gene does not suffer ill effects, but with two variants will develop sickle-cell anemia. Despite this, the sickling variant is common in populations historically exposed to malaria, because having one variant helps protect against malaria infection.

amino acid a building block of protein

CO_2 Transport and Blood Buffering

Carbon dioxide (CO_2) does not bind to iron, but rather to the protein portion of hemoglobin. CO_2 is a product of cell respiration, and is picked up in the tissues and transported to the lungs. Most of the CO_2 transported is actually in the form of bicarbonate **ion**, HCO_3^-. Bicarbonate is formed by the **enzyme** carbonic anhydrase, which is present in the red blood cells. This enzyme **catalyzes** the conversion of CO_2 and H_2O to carbonic acid (H_2CO_3), which immediately splits to form H^+ and HCO_3^-. Besides serving as a transport form of CO_2, HCO_3^- also participates in blood buffering. It can react with excess H^+ (acid ion) formed in other reactions. In this way, it prevents excess acidity in the blood. Similarly, HCO_3^- can react with excess OH^- (base ion) to form water and CO_3^{2-}, absorbing excess base. Along with phosphate, bicarbonate keeps the blood buffered at a pH of 7.4.

ion an electrically charged particle

enzyme protein that controls a reaction in a cell

catalyze aid in the reaction of

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

excrete deposit outside of

metabolism chemical reactions within a cell

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

Nutrient Transport, Regulation, and Clotting

Blood also transports nutrients, hormones, and immune system components. Nutrients from the gut are dissolved directly in the plasma for transport, but are quickly shuttled to the liver for processing and storage of excess. Insulin and glucagon, hormones produced by the pancreas, control the level of blood sugar by promoting storage or release of **glucose**. The kidney performs the vital function of excreting excess salts and water, as well as metabolic wastes, helping to maintain blood levels of these substances within narrow limits. One waste product the kidneys cannot **excrete** is heat, produced by cell **metabolism** through out the body. Blood performs the vital function of carrying heat from the body core to the periphery, where it can be cooled before returning.

Hormones are released by **endocrine** organs directly into the bloodstream for wide and rapid circulation. White blood cells also use the circulatory system as a highway through the body, traveling in the blood until they exit in response to chemical signals from wounded or infected tissues. Platelets and clotting proteins in the blood work together to prevent blood loss when a vessel is broken. Clotting relies on chemical signals from damaged tissue and from platelets, and the activation of a complex cascade of more than a dozen different plasma proteins. SEE ALSO BLOOD CLOTTING; HEART AND CIRCULATION; HORMONES; RESPIRATION

Richard Robinson

DREW, CHARLES (1904–1950)

African-American surgeon who invented a way to preserve blood plasma so that it could be stored. Drew's plasma saved the lives of thousands of Londoners during the Nazi bombings in World War II. But when the U.S. military refused to accept blood donated by black Americans, Drew resigned from his post as head of the Red Cross's "Plasma for Britain" program.

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Blood Clotting

Blood clotting (coagulation) is the process by which blood vessels repair ruptures after injury. Injury repair actually begins even before clotting does, through vascular spasm, or muscular contraction of the vessel walls, which reduces blood loss. Clotting itself is a complex cascade of reactions involving platelets, **enzymes**, and structural **proteins**.

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

Platelets are not whole cells, but rather small packets of membrane-bounded **cytoplasm**. There are approximately one million platelets in a drop of blood. Damage to the lining of a blood vessel (the endothelial lining) exposes materials that cause platelets to stick to the endothelial cells; additional platelets then stick to these. These aggregating platelets release factors that promote accumulation of fibrin, a circulating protein. A blood clot is a meshwork of platelets and blood cells woven together by fibrin.

cytoplasm material in a cell, excluding the nucleus

Accumulation of fibrin must be tightly regulated, of course, to prevent clot formation where there is no wound. Thrombosis is an abnormal localized activation of the clotting system. Disseminated intravascular coagulation is a **pathological** condition in which the clotting system is activated throughout the circulatory system in response to bacterial toxins, trauma, or other stimuli. A clot may break off, forming an embolus, which can lodge in a small blood vessel, cutting off circulation. If this occurs in the heart, it may cause ischemia (lack of blood flow) or myocardial infarction (heart attack). In the lungs, it causes pulmonary embolism, with loss of capacity for oxygen exchange. In the brain, it can cause stroke.

pathological related to disease

Because of this need for tight regulation, and the need for rapid response, the clotting mechanism involves a multistep cascade of enzymes, most of whose jobs are to activate the next enzyme in the cascade. In this way, the effect of the initial stimulus (the damaged blood vessel) can be quickly magnified, as a single enzyme at the first stage activates many copies of another enzyme at the next stage, each of which activates many more at the next, and so on. At the same time, the many levels of interaction provide many points of control over the process. This coagulation cascade begins from thirty seconds to several minutes after the injury.

Coagulation can begin with either of two pathways, called the extrinsic and intrinsic pathway, both of which feed into a common pathway that completes the process. The extrinsic pathway begins with a substance called tissue factor (tissue thromboplastin) released by damaged blood vessels and surrounding tissues. In the presence of other plasma proteins (clotting factors) and calcium **ions**, this leads to the activation of a protein called factor X. The intrinsic pathway begins with a substance called factor XII, released by blood platelets. Through a series of additional clotting factors, and again in the presence of calcium ions, this pathway also leads to the activation of

ion an electrically charged particle

factor X. One of the necessary factors of the intrinsic pathway is called factor VIII. A mutation in the **gene** for this factor is the most common cause of hemophilia.

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

The common pathway begins with the activation of factor X. In the presence of calcium ions and other clotting factors, factor X activates an enzyme called prothrombin activator. This enzyme them converts the plasma protein prothrombin into thrombin. Thrombin is an enzyme that, in turn, converts fibrinogen to fibrin. Here the cascade ends, because fibrin is not an enzyme, but a fibrous protein. It forms strands that stick to the platelets and endothelial cells at the wound, forming a meshwork that, in turn, traps other cells.

Once the clot forms, contraction of the platelets pulls the edges of the wound closer together, and fresh endothelial cells then grow across it, repairing the damaged blood vessel. Over time, fibrin is degraded by plasmin. This enzyme is formed from circulating plasminogen by tissue plasminogen activator (t-PA). Synthetic t-PA is used to dissolve blood clots in stroke, myocardial infarction, pulmonary embolism, and other conditions. SEE ALSO BLOOD; BLOOD VESSELS; CONTROL MECHANISMS

Richard Robinson

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Blood Sugar Regulation

Most cells in the human body use the sugar called **glucose** as their major source of energy. Glucose molecules are broken down within cells in order to produce adenosine triphosphate (ATP) molecules, energy-rich molecules that power numerous cellular processes. Glucose molecules are delivered to cells by the circulating blood and therefore, to ensure a constant supply of glucose to cells, it is essential that blood glucose levels be maintained at relatively constant levels. Level constancy is accomplished primarily through negative **feedback** systems, which ensure that blood glucose concentration is maintained within the normal range of 70 to 110 milligrams (0.0024 to 0.0038 ounces) of glucose per **deciliter** (approximately one-fifth of a pint) of blood.

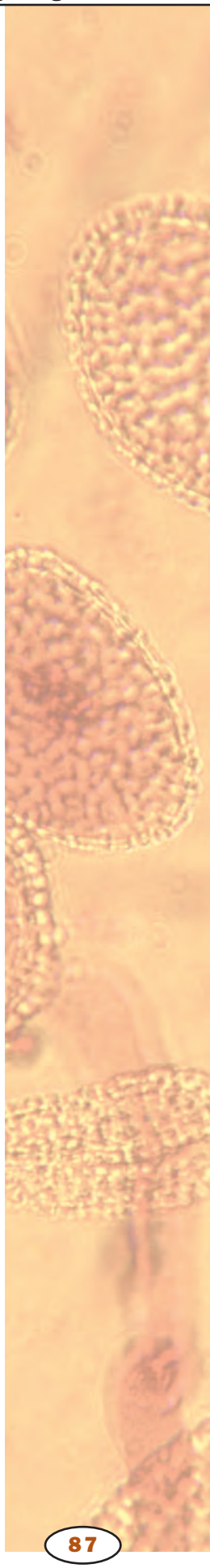
glucose simple sugar that provides energy to animal cells and is the building block of cellulose in plants

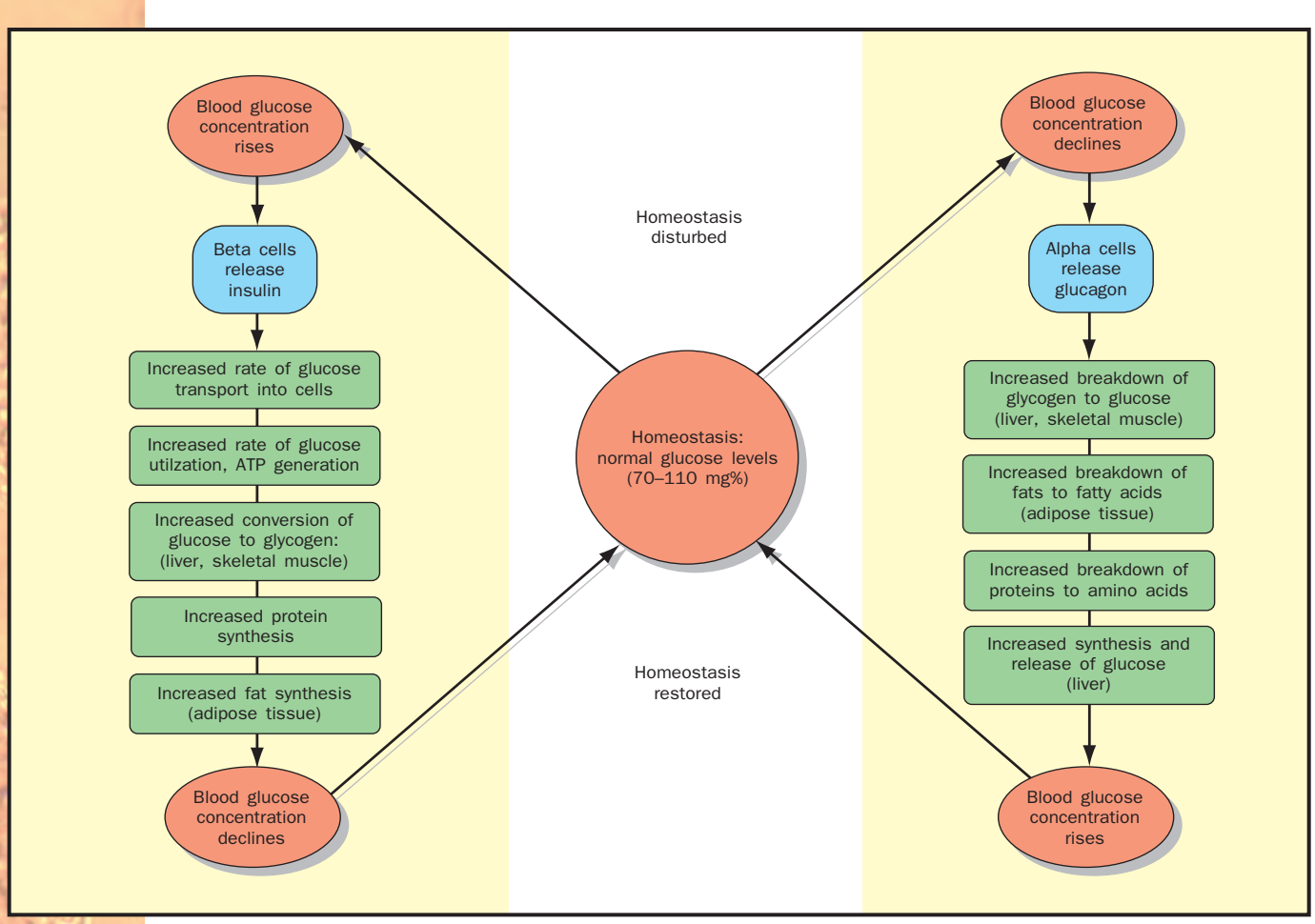
feedback process in which the output or result influences the rate of the process

deciliter one-tenth of a liter; a unit of volume

Negative feedback systems are processes that sense changes in the body and activate mechanisms that reverse the changes in order to restore conditions to their normal levels. Negative feedback systems are critically important in homeostasis, the maintenance of relatively constant internal conditions. Disruptions in homeostasis lead to potentially life-threatening situations. The maintenance of relatively constant blood glucose levels is essential for the health of cells and thus the health of the entire body.

Major factors that can increase blood glucose levels include glucose absorption by the small intestine (after ingesting a meal) and the production of new glucose molecules by liver cells. Major factors that can decrease blood





The homeostatic regulation of glucose concentrations.

glucose levels include the transport of glucose into cells (for use as a source of energy or to be stored for future use) and the loss of glucose in urine (an abnormal event that occurs in diabetes mellitus).

Insulin and Glucagon

hormone molecule released by one cell to influence another

In a healthy person, blood glucose levels are restored to normal levels primarily through the actions of two pancreatic **hormones**, namely insulin and glucagon. If blood glucose levels rise (for example, during the fed or absorptive state, when a meal is digested and the nutrient molecules are being absorbed and used), the beta cells of the pancreas respond by secreting insulin. Insulin has several notable effects: (1) it stimulates most body cells to increase their rate of glucose uptake (transport) from the blood; (2) it increases the cellular rate of glucose utilization as an energy source; (3) it accelerates the formation of **glycogen** from glucose in liver and skeletal muscle cells; and (4) it stimulates fat synthesis (from glucose) in liver cells and adipose (fat) tissue. These effects collectively cause a decrease in blood glucose levels back to normal levels.

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

secretion material released from the cell

If blood glucose levels fall below normal levels (for instance, during the post-absorptive or fasting state, when nutrients from a recently digested meal are no longer circulating in the blood, or during starvation), insulin **secretion** is inhibited and, at the same time, the alpha cells of the pancreas respond by secreting glucagon, a hormone that has several important effects:

(1) it accelerates the breakdown of glycogen to glucose in liver and skeletal muscle cells; (2) it increases the breakdown of fats to fatty acids and glycerol in adipose tissue and, consequently, the release of these substances into the blood (which cells can thus use for energy); and (3) it stimulates liver cells to increase glucose synthesis (from glycerol absorbed from the blood) and glucose release into the blood. These effects collectively cause an increase in blood glucose levels back to normal levels.

In addition to insulin and glucagon, there are several other hormones that can influence blood glucose levels. The most important ones are epinephrine, cortisol, and growth hormone, all of which can increase blood glucose levels.

Diseases and Blood Sugar Regulation

Glucose levels above or below the normal range are indicative of the presence of disease states. For example, elevated glucose levels are present in diabetes mellitus, Cushing's syndrome, liver disease, and hyperthyroidism, while decreased glucose levels are present in Addison's disease, hyperinsulinism, and hypothyroidism.

The most prevalent of these diseases is diabetes mellitus. There are two types of this disease: Type I (insulin-dependent or juvenile-onset) diabetes mellitus, and Type II (noninsulin-dependent or maturity-onset) diabetes mellitus. In Type I diabetes, pancreatic beta cells are destroyed by an erroneous attack by the body's own immune system, and thus insulin secretion is reduced to negligible levels. In Type II diabetes, insulin secretion is not reduced; however, there is a reduced sensitivity of target cells to insulin, a phenomenon known as insulin resistance. SEE ALSO AUTOIMMUNE DISEASE; DIGESTION; DIGESTIVE SYSTEM; HOMEOSTASIS; HORMONE; LIVER; PANCREAS; THYROID GLAND

Izak Paul

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HODGKIN, DOROTHY CROWFOOT (1910–1994)

English chemist who won the 1964 Nobel Prize in chemistry for describing the structure of vitamin B_{12}. In 1969, she completed a thirty-four-year effort to decipher the three-dimensional structure of insulin, the protein that helps people regulate blood sugar levels.

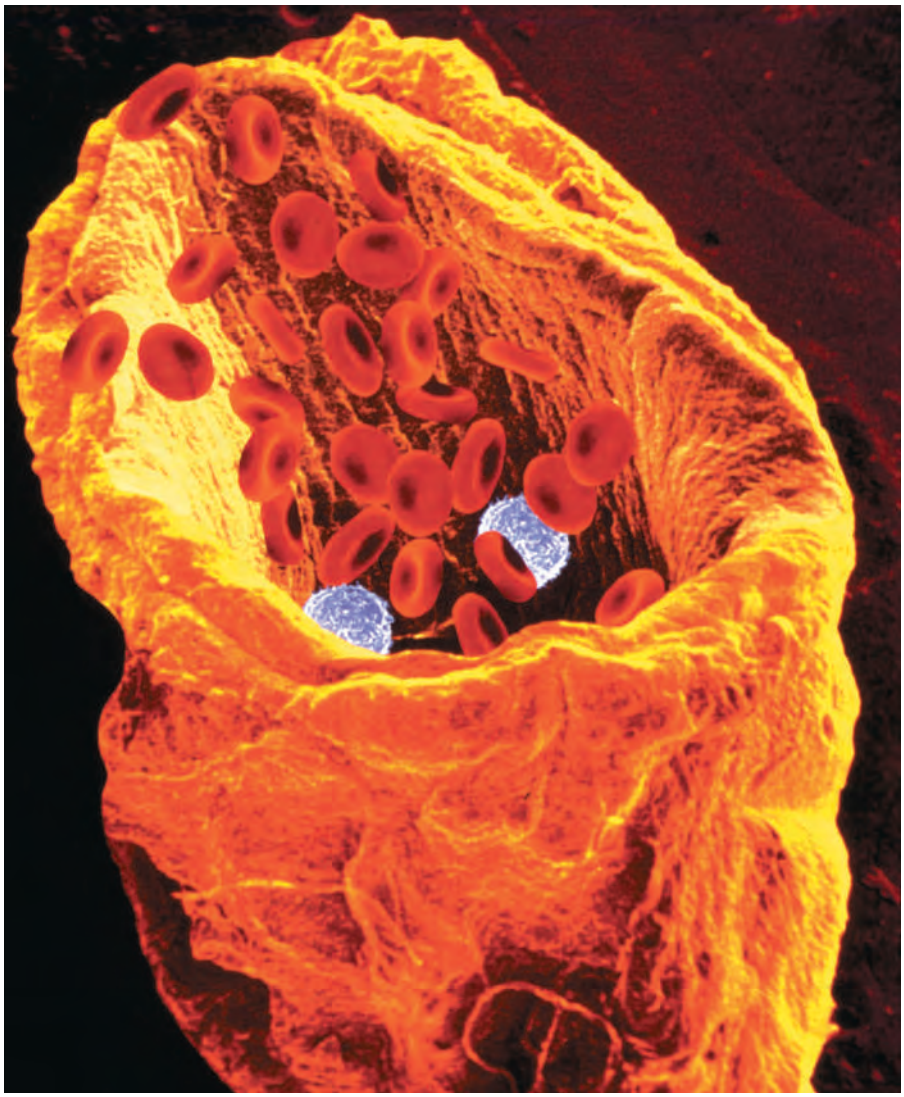
Blood Vessels

The cardiovascular system includes the heart (cardio) and blood vessels (vascular). The heart pumps blood throughout the body. Sixty thousand miles of blood vessels transport the blood, enough to encircle Earth more than twice. Arteries carry blood away from the heart; capillaries reach all of the body's seventy trillion cells; and veins carry blood back to the heart. Because blood vessels form a circular route, this system is also called the circulatory system.

The cardiovascular system has two main parts. In the pulmonary circuit, blood is pumped from the right **ventricle** of the heart through the pulmonary arteries, which lead to the lungs. Here the blood gives up carbon dioxide and picks up oxygen. The oxygen-rich blood returns to the left atrium of the heart through pulmonary veins. From the left atrium, blood passes to the left ventricle of the heart, which pushes the blood through the **systemic** circuit beginning with the aorta, which branches to all body parts.

ventricle fluid-filled chamber

systemic throughout the body



A scanning electron micrograph of red and white blood cells flowing through a vein.

After delivering oxygen and picking up carbon dioxide, blood returns to the right atrium of the heart and then to the right ventricle. The journey begins anew.

Arteries

Thick walls enable arteries to withstand the pressure created by the pumping of the heart (blood pressure). The pulmonary arteries and the aorta are the largest arteries (the aorta is as wide as a thumb!). Some arteries are named for the organ that they supply, such as the hepatic artery (liver) and the coronary arteries (heart). Others have special names, such as the carotid arteries that supply the head and brain. Arteries branch many times into smaller arteries and eventually into minute branches called arterioles.

Arteries consist of an inner lining, one cell thick, called endothelium, a middle layer of smooth muscle and elastic tissue, and an outer layer that is mostly loose **connective tissue**, which holds the multilayered tube together. The muscle layer in arteries and arterioles is thick and the overall structure quite elastic, enabling these vessels to withstand greater blood pressure than can veins.

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

Veins

Veins and arteries are so similar that portions of veins are used to replace damaged arteries in **coronary artery** bypass surgery. Veins have the same three layers as arteries and are elastic, but they have a less-muscular middle layer, making their walls thinner. Also, unlike arteries, some veins have valves (tissue flaps) that permit blood to flow in only one direction, back to the heart. Valves help maintain blood flow in places such as the legs where the blood pressure has to push blood uphill, against the force of gravity. Despite the valves, accumulation of blood in leg veins can stretch the thin walls, resulting in varicose veins.

coronary artery artery supplying blood to the heart

Veins are named in much the same way as arteries. Pulmonary veins return blood from the lungs to the heart, and a hepatic vein returns blood from the liver. Some veins have special names. The jugular veins return blood from the head, and the great saphenous veins return blood from the legs; these are used as grafts in coronary artery bypass surgery. The median cubital vein, which extends from side to side in the bend of the elbow, is a common site for drawing blood. The smallest veins arise from minute venules, and then merge to form larger and larger veins.

Capillaries

Capillaries are the shortest, narrowest, and thinnest blood vessels. They connect **arterioles** to **venules** to complete the circuit. Capillaries consist only of endothelium with some connective tissue binding the cells. Red blood cells squeeze through capillaries single file. Unlike arteries and veins, capillaries do not have specific names, but are named collectively for the region that they supply. Capillaries in the lungs, for example, are called pulmonary capillaries, and those in the stomach are the gastric capillaries.

arterioles any of the small, terminal twigs of an artery that ends in capillaries

venule any of the minute veins connecting the capillaries with the larger systemic veins

The body will always have one heart, but the number of blood vessels may change. Because blood vessels bring oxygen-rich blood to cells, areas that have increased oxygen demands actually develop more blood vessels, primarily capillaries. New blood vessel growth is called angiogenesis. For example, new capillaries permeate the muscles of a conditioned athlete. Cancerous tumors also grow new capillary networks. One approach to fight cancer is to starve it with drugs that block angiogenesis. SEE ALSO BLOOD; BLOOD CLOTTING; CARDIOVASCULAR DISEASES; CIRCULATORY SYSTEMS; HEART AND CIRCULATION

David Shier

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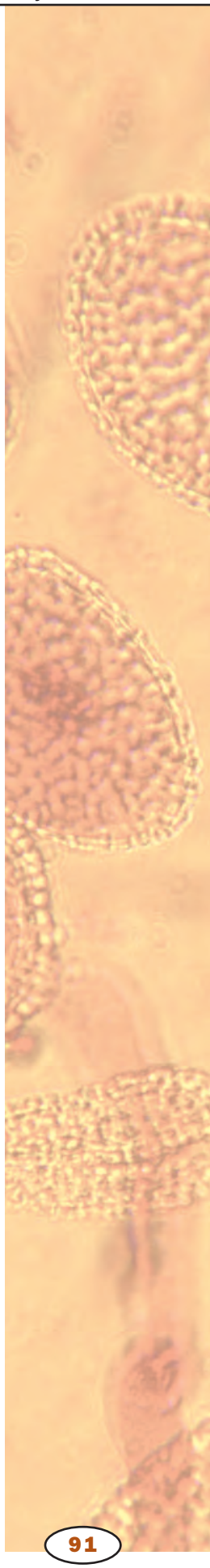
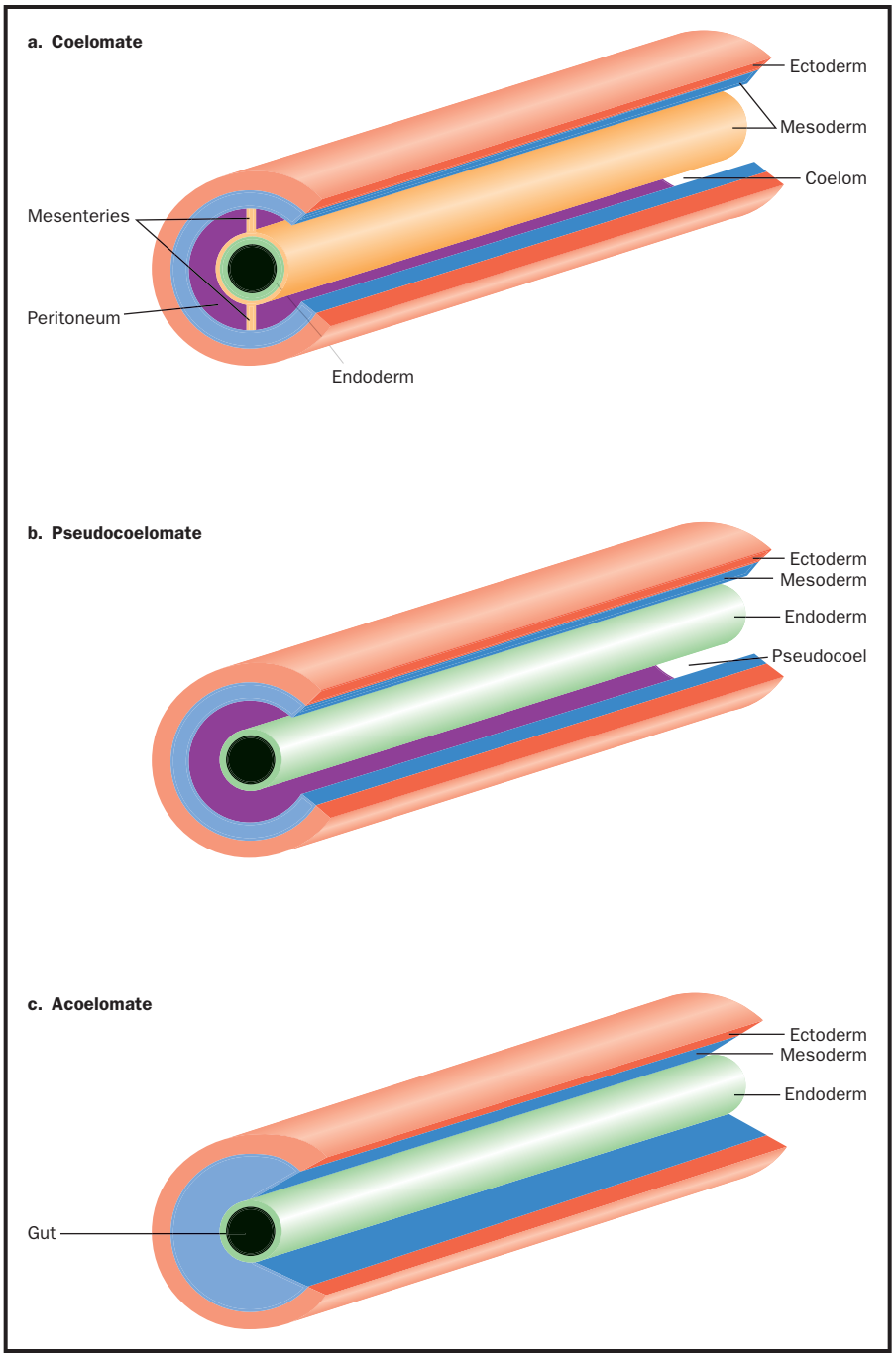
Body Cavities

A body cavity can be defined as the space that remains after the organs inside it are removed, but this definition does not do justice to the variety and



Schematic diagrams of the bodies of animals with coeloms, with pseudocoeloms, or without body cavities.



functions of body cavities. Humans have four body cavities: (1) the dorsal body cavity that encloses the brain and spinal cord; (2) the thoracic cavity that encloses the heart and lungs; (3) the abdominal cavity that encloses most of the digestive organs and kidneys; and (4) the pelvic cavity that encloses the bladder and reproductive organs. The **cranial** cavity cushions and protects the brain within a rigid skull. The other body cavities also cushion internal organs, but instead of being rigid, they have to be flexible for the heart, lungs, digestive organs, and reproductive organs to expand.

cranial related to the cranium, or brain cavity

In humans all but the cranial cavity develop from the coelom (pronounced SEE-lum). A coelom is a cavity that is entirely enclosed within cells

derived from the middle layer of embryonic tissue. A few groups of animals, such as roundworms (Nematoda), have a body cavity that is only partly enclosed by tissue from the middle layer. Such a body cavity is called a pseudocoelom (pronounced SOO-doe-SEE-lum). In a few other groups, such as flatworms (Platyhelminthes), there is no body cavity. SEE ALSO DEVELOPMENT; PLATYHELMINTHES

C. Leon Harris

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Bone

Bone serves many important functions. Bones support the body, protect underlying organs, and provide a movable skeleton against which the muscles can work. In addition, bone forms all the cells of the blood, plus takes part in calcium and acid-base balance, and storage of trace elements (such as zinc) needed by cells elsewhere.

Bone Structure

Bone is created from **osseous connective tissue**. Like other types of connective tissue, osseous tissue is composed of relatively sparse cells surrounded by an extracellular network, or **matrix**. Bone matrix is a tough, resilient mixture of **protein** and **minerals**. Osteoblasts, a type of bone cell, secrete proteins into the matrix, which provide tensile strength (resistance to stretching and twisting). The principal protein of the bone matrix is collagen, which accounts for almost one-third of the dry weight of bone. Most of the rest of the bone's weight is due to the minerals of the matrix. These are mainly calcium phosphate and calcium carbonate. Embedded in the protein network, the minerals provide hardness and compressive strength.

osseous related to bone

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

matrix a network, usually of threadlike fibers

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

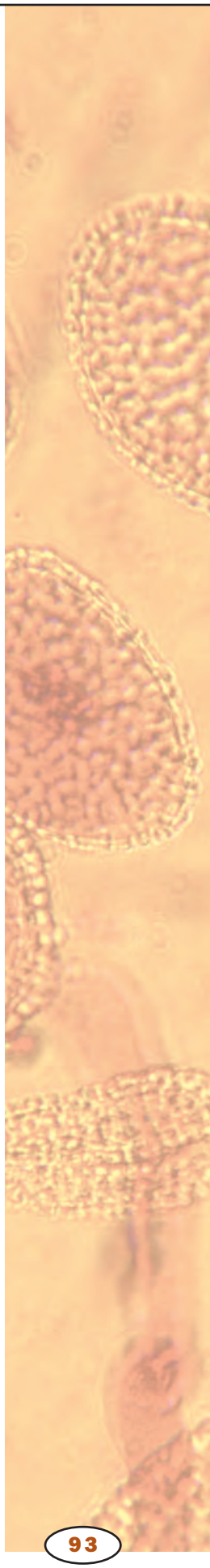
minerals iron, calcium, sodium, and other elements needed by living organisms

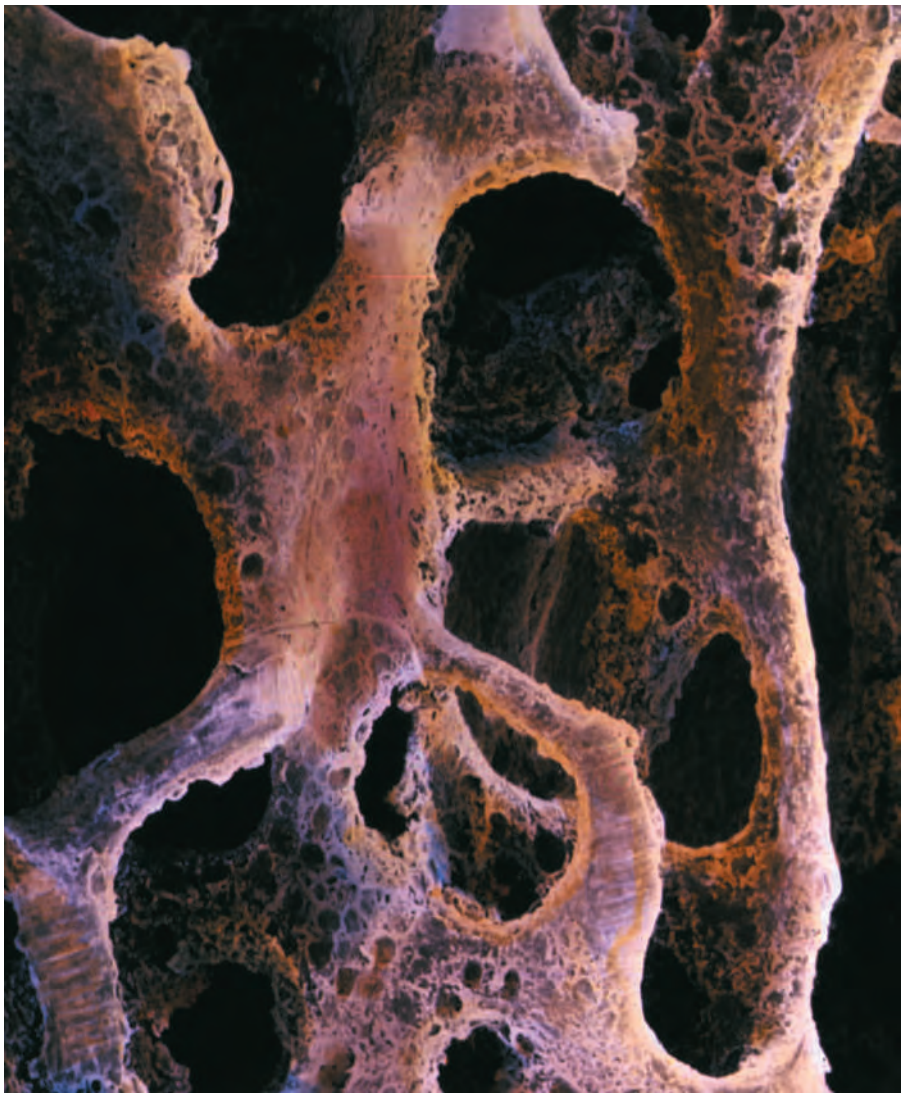
Bone cells remain alive and, like other cells in the body, must be nourished by blood. In order to deliver nutrients to and remove waste from the bone interior, the hard, compact surface is pierced by "canals" through which blood vessels can travel. Once inside, these canals branch, allowing blood vessels to reach cells throughout the bone. This canal system gives bone its characteristic appearance under the microscope, with bone cells embedded in concentric rings (lamellae) of calcified matrix, all surrounding a hollow canal. These units of structure, called osteons, all run parallel in compact bone, but form a looser and less-ordered network in spongy bone. Compact bone forms in the perimeter of long bone shafts, such as those of the legs and arms, where stress forces tend to be all in the same direction. In contrast, spongy bone is found in the ends of bones, where forces come from many different directions. Spongy bone also occurs where bone is not subject to significant stress.

Formation and Growth

Ossification (bone formation) occurs in one of two ways. Intramembranous ossification occurs within parts of the skull and part of the **clavicles**. In this process, osteoblasts deposit matrix on a membranous network within the

clavicle collar bone





A false-color scanning electron micrograph of cancellous bone tissue affected by osteoporosis.

future bone. Once their own extracellular matrix traps the osteoblasts, they become fully mature osteocytes.

By contrast, most of the body's bones form by endochondral (within cartilage) ossification. In this process, a temporary model in the shape of the future bone is made from cartilage laid down by chondrocytes (cartilage-forming cells), which later die within the shaft of the future bone. The space created by the death of these cells is invaded by osteogenic (bone-forming) cells. These cells differentiate into osteoblasts and secrete the matrix. As osteoblasts build bone, another type of cell, the osteoclast, dissolves older matrix, enlarging the cavity within. Osteoclasts dissolve matrix by secreting hydrochloric acid, which attacks the mineral portion, and **enzymes** that digest the collagen and other proteins. Within the shafts of the long bones, the spaces created are filled with blood-forming tissue, the bone marrow.

enzyme protein that controls a reaction in a cell

Hormonal Control

Growth in bone length is stimulated by sex **hormones** and growth hormone during puberty, accounting for the pubertal growth spurt. Growth is later

hormone molecule released by one cell to influence another

halted, and bones cannot grow in length during adulthood. However, bone is constantly remodeled by the combined action of osteoblasts and osteoclasts, and can grow in width in response to mechanical stresses such as weight lifting. When a bone is fractured, chondrocytes, osteoblasts, and osteoclasts go to work repairing it and cleaning up the damage.

Some forms of osteoporosis (brittle bones) are caused by overactive osteoclasts.

The interactions of three hormones—parathyroid hormone, calcitonin, and calcitriol—control bone growth and remodeling, as well as the calcium concentration in the blood serum. Calcium is necessary for a variety of critical functions outside of bone, including muscle contraction, **neuron** function, glandular **secretion**, and blood clotting. Because of this, serum calcium is kept within very narrow limits, 9.2 to 10.4 milligrams per **deciliter** of blood. Calcium excesses and deficiencies are prevented by using bone as a storage pool.

neuron nerve cell

secretion material released from the cell

deciliter one-tenth of a liter; a unit of volume

Calcitriol promotes calcium absorption from the gut and prevents its loss through the kidneys. Calcitriol is made from vitamin D, either supplied from the diet or manufactured by skin cells exposed to sunlight. A lack of vitamin D can lead to rickets in childhood, osteomalacia in adulthood, or osteoporosis later in life. Once calcium is absorbed by the gut, it enters the blood, and, if in high concentration, is deposited in bone by osteoblasts, stimulated by calcitonin. When serum calcium levels drop, parathyroid hormone indirectly causes osteoclasts to break down bone and release calcium into the blood. Bone, therefore, is constantly cycling between deposition and resorption, and about one-fifth of the skeleton is built and demolished each year. SEE ALSO BLOOD; CONNECTIVE TISSUE; MUSCULOSKELETAL SYSTEM; VITAMINS AND COENZYMES

Angie Kay Huxley

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Bony Fish

The class Osteichthyes (literally "bony fish") gets its name from the bony skeleton and scales of its members. The group comprises nearly all living fish, with notable exceptions being sharks and other cartilaginous fish, and the primitive lampreys and their kin. Bony skeletons and scales are the primary features that differentiate these fish from other cartilaginous fish, whose skeleton is composed of cartilage and whose skin is leathery. Other important differences include the swim bladder, a lunglike, gas-filled organ that helps bony fish to regulate their buoyancy.

Osteichthyes is the most numerous and diverse group of vertebrates, occupying virtually all large bodies of water, from polar seas to hot undersea vents to land-locked lakes. Because of their numbers (more than 20,000 species), diversity, and range, the bony fish play a major role in virtually all

ecosystem an ecological community and its environment

marine and freshwater **ecosystems**. They range from the tiny seahorses to giant sunfish (weighing thousands of pounds) to the salmon on one's dinner plate.

Most of the bony fish—thirty-nine of the forty-two orders—are ray-finned fish; subclass Actinopterygii. The other three orders are fleshy-finned fish, members of the subclass Sacropterygii. Although much less numerous and diverse than the ray-fins, the fleshy finned fish are still interesting and important. In two orders, the fleshy finned fish have lungs instead of swim bladders, and can survive their ponds drying up by burrowing into the mud. The final order contains only one species: the coelacanth (pronounced SEE-low-kanth), an ancient species of fish once thought to be long extinct. Living coelacanths, virtually identical to its fossil relatives that lived 20 million years ago, were first found in 1938. This discovery was doubly important because the coelacanth is a close relative of the fish from which amphibians evolved, making it closely related to the ancestors of all terrestrial vertebrates. SEE ALSO CARTILAGINOUS FISH; LIMNOLOGIST; OCEAN ECOSYSTEM

Robbie Hart

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Botanist

A botanist is a scientist who studies plants. The study of plants encompasses their evolution, classification, anatomy, physiology, development, genetics, diversity, ecology, and economic uses. Professional botanists typically specialize in one of these areas, or more likely in a smaller subspecialty, such as the evolution of the angiosperms (flowering plants), the biochemistry of photosynthesis, or the cultivation of roses for the wholesale market. Botanists may be employed by universities as professors or researchers; by the government to (for instance) conduct field studies of plant diversity in a national park or to compare crop planting systems; by agricultural industries to perform research on crops or to breed new types of plant varieties; or by pharmaceutical companies to discover new sources of plant-based drugs in the tropical rain forest, or to develop them in the lab from plant sources.

Botanists may work in laboratories or greenhouses performing experiments, or they may work outside in fields, forests, or other plant habitats. For many botanists, the opportunity to work with plants in their natural settings is a principal attraction of the discipline, along with an intellectual curiosity about how plants work, or a desire to improve their usefulness to humans. A career in botany requires at least a bachelor's degree from a four-year college. This would enable someone to begin work as a research assistant, for instance. Most professional botanists entering the field today earn a Ph.D., which gives them the qualifications and credentials to conduct research or manage a plant breeding program, for example. To pursue botany as a major in college, high school students should take courses in biology, chemistry, physics, and math, and would benefit from getting hands-on experience with plants, either by gardening, farming, working in a nursery or

greenhouse, or simply exploring the natural world around them. SEE ALSO ANGIOSPERMS; AGRONOMIST; ANATOMY OF PLANTS; CONIFERS; EVOLUTION OF PLANTS; PHOTOSYNTHESIS; PLANT

Richard Robinson

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Brain

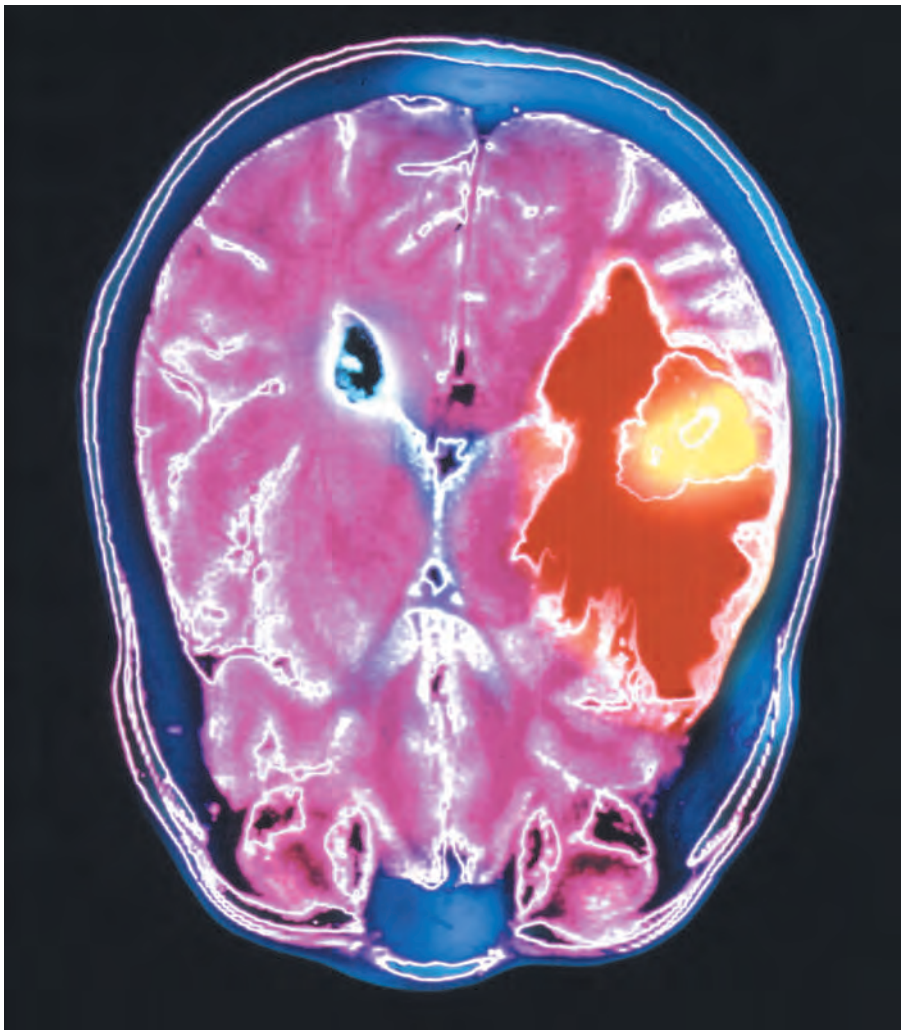
The vertebrate brain is the large **anterior** portion of the **central nervous system**. The "cranial vault" of the skull encases the brain in most vertebrates. In invertebrates, the enlarged and specialized anterior ganglion of the central nervous system is often referred to as a brain, although not all scientists regard it as a true brain.

anterior toward the front

central nervous system brain and spinal cord

The brain receives and processes sensory information, initiates and controls movement, and executes **cognitive** (thought) processes. The human brain has an extraordinary capacity, correlated with the great enlargement

cognitive related to thought or awareness



A colored magnetic resonance imaging (MRI) scan of the axial section of the human brain showing a metastatic tumor (yellow).

of the cerebrum, for information storage and retrieval, thought, emotions, and initiation of behavior.

Gross Anatomy

The mammalian brain has three primary subdivisions: the cerebrum (including the outer, wrinkled cortex), cerebellum, and brainstem. The brainstem is further divided into the diencephalon, midbrain, pons, and medulla. The human brain is about 85 percent cerebrum, 11 percent cerebellum, and 4 percent brainstem.

neuron nerve cell

cerebral cortex outermost wrinkled portion of the brain

The human brain has more than 100 billion **neurons**, with 14 to 16 billion in the **cerebral cortex** and nearly 100 billion in the cerebellum alone. In addition, there are perhaps nine times as many glial cells, whose exact roles are unclear, but which help to support and maintain neurons. Most neurons are present shortly after birth, and as the brain continues to grow, the number and complexity of neuronal connections increases. These neurons are arranged into gray matter and white matter. Gray matter composes areas rich in neurons, their dendrites, and synapses. White matter is tissue rich in **axons** (nerve fibers), but with a few cell bodies or dendrites. It gets its color from an insulating wrap called myelin around the nerve fibers. The high **lipid** content of white matter makes it light and easily distinguished from gray matter in fresh, unstained tissue.

axon long extension of a nerve cell down which information flows

lipid fat or waxlike molecule, insoluble in water

Multiple sclerosis is an autoimmune disease in which myelin degenerates.

The cerebrum and cerebellum each have a multilayered sheet of cells on the surface called the cortex, composed of gray matter. The white matter lies deep to this and consists of axons that send information to and from the cortex or connect different regions of the cortex to each other. Deeper masses of gray matter are also found embedded in the white matter.

ventricle fluid-filled chamber

The central nervous system (brain and spinal cord) develops as a hollow tube whose internal space eventually forms a system of fluid-filled cavities called **ventricles**. The first two ventricles are a pair of C-shaped lateral ventricles, one in each cerebral hemisphere. Each of these communicates through a small pore with a slitlike third ventricle between the two hemispheres, surrounded by the diencephalon. From here, a slender canal, the cerebral aqueduct, passes down the middle of the midbrain and leads to a triangular fourth ventricle, between the cerebellum and the brainstem. Pores from the fourth ventricle open into a subarachnoid space that surrounds the brain. These ventricles are filled with a liquid, the cerebrospinal fluid (CSF), which also bathes the outside of the brain and cushions the organ in the cranial cavity. The CSF is secreted in part by a complex of blood vessels, the choroid plexus, in each ventricle.

Inflammation of the meninges occurs in meningitis, which may be caused by a viral or bacterial infection.

Around the brain and spinal cord, between the nervous tissue and bone, are found three membranes called meninges: the dura mater just under the bone; a middle arachnoid; and a delicate pia mater on the surface of the tissue.

The brain receives most of its input from, and sends most of it output to, the spinal cord, which merges with the brainstem at the base of the brain. The twelve cranial nerves provide input and output pathways to and from the structures in the head.

The Cerebrum

The cerebrum, the largest subdivision of the human brain, consists of a pair of cerebral hemispheres. Each hemisphere consists of an outer mantle of gray matter (the cerebral cortex), an extensive underlying of white matter, and deep aggregations of gray matter, the basal nuclei, or **ganglia**. Each hemisphere develops from a lateral outgrowth of the embryonic forebrain. Near its attachment to the forebrain, immature neurons **aggregate** to form the basal nuclei. As the basal nuclei grow, the remainder of the hemisphere continues to balloon outward and posteriorly, forming the cerebral cortex. This outgrowth is hollow, and its cavity becomes the lateral ventricle.

ganglia cluster of nerve cell bodies

aggregate clump together

In adults, the right and left hemispheres are separated from each other by a deep midline cleft, the longitudinal fissure, and are separated from the cerebellum by a deep horizontal groove, the **transverse** fissure. The hemispheres are connected to each other by a massive bundle of nerve fibers, the corpus callosum, on the floor of the longitudinal fissure. Many of these fibers connect regions of one hemisphere to corresponding points in the opposite hemisphere.

transverse situated or lying across

As the cortex continues to grow, it is thrown into folds called gyri (singular, gyrus), separated by shallow grooves called sulci (singular, sulcus). A few especially prominent sulci appear early in development and are consistent from brain to brain. They serve as landmarks to divide the cortex into areas called lobes. (Gyri are not as numerous or pronounced in most other mammals.)

Imbalance between production and drainage of cerebrospinal fluid can lead to hydrocephalus, a potentially fatal disorder.

The frontal, parietal, temporal, and occipital lobes are visible on the surface of the brain. The frontal lobe extends from the region of the forehead to a groove called the central sulcus at the top of the head. The parietal lobe begins there and progresses posteriorly as far as the parieto-occipital sulcus, which is visible only on the medial surface of the brain. The occipital lobe extends from there to the rear of the head. A conspicuous lateral fissure separates the temporal lobe, in the region of the ear, from the frontal and parietal lobes above it. The insula is a fifth lobe of the cerebrum not visible from the surface. It lies deep to the lateral fissure between portions of the frontal, parietal, and temporal lobes.

The limbic system is a ring of tissue on the medial surface of each hemisphere, surrounding the corpus callosum and diencephalon and incorporating parts of the frontal, parietal, and temporal lobes. A major component of this system is the hippocampal formation, deep in the temporal lobe.

Functional Areas of the Cerebral Cortex

Considerable knowledge of **cortical** function has come from patients with damage to specific cortical areas, and from electrical stimulation and recording from the cortex, often as a necessary prelude to neurosurgery. Imaging procedures developed in the 1980s and 1990s, such as positron emission tomography (PET), enable neuroscientists to follow changes in cortical activity over time. PET scans can show sequential changes in brain activity during such tasks as planning and executing movement and learning and storing information.

cortical related to the cortex, or outer portion

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

Motor Areas. Four motor areas collectively occupy almost half of the frontal lobe. One of these, the primary motor cortex, is the precentral gyrus just anterior to the central sulcus. The motor areas are extensively connected to the basal ganglia and cerebellum. Working together in complex **feedback** loops, these areas are essential for motor coordination, postural stability and balance, learned movements, and the planning and execution of voluntary movement.

Sensory Areas. Primary sensory areas receive incoming sensory information. One of these, the primary somatosensory cortex, receives input for pain, temperature, touch, and pressure. It is located in the postcentral gyrus, the first gyrus of the parietal lobe posterior to the central sulcus. The primary auditory cortex, for hearing, is on the super (upper) margin of the temporal lobe, deep in the lateral fissure. The primary visual cortex, for sight, is in the occipital lobe, especially the medial surface.

Primary sensory areas are organized into precise sensory maps of the body. The primary somatosensory cortex, for example, has a point-for-point correspondence with the opposite (contralateral) side of the body, so that, for instance, the first and second fingers of the left hand send sensory information to adjacent areas of the right primary somatosensory cortex. Similarly, the primary visual cortex has a point-for-point map of the contralateral visual field. The primary auditory cortex has a tonotopic map of the cochlea of the inner ear, with different points in the cortex representing different sound frequencies.

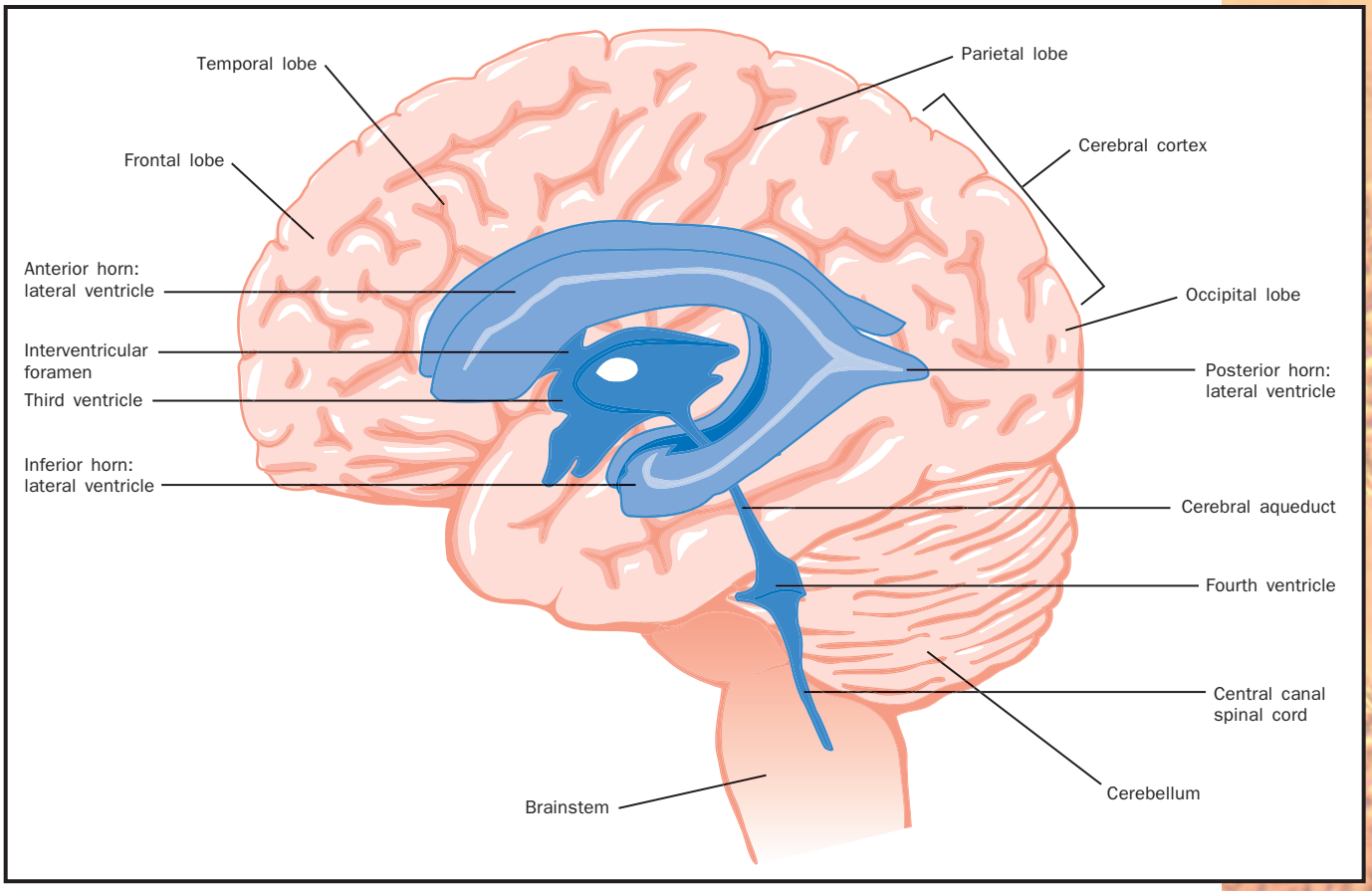
Association Areas. Once received by a primary sensory area, information is sorted and relayed to adjacent sensory association areas for processing. Association areas identify specific qualities of a stimulus and integrate stimulus information with memory and other input. To hear a piece of music, for example, involves the primary auditory cortex, but to recognize that music as Mozart or Elvis Presley involves the auditory association area just below the primary auditory cortex.

The human brain differs from that of other primates in its large amount of association cortex. Association areas not only integrate immediate sensory data with other information, but are also responsible for human ingenuity, personality, judgment, and decision making.

Cortical Lesions

The posterior region of the parietal lobe integrates motor and sensory information. Damage to this region often results in neglect or unawareness of the contralateral side of the body and the space around that side of the body. This can be reflected in such oversights as forgetting to shave one side of the face or dress one side of the body. The degree of behavioral dysfunction depends on the specific areas of the brain that are damaged and the extent of the damage. Temporal lobe lesions often cause difficulty performing tasks that require keen visual discrimination. Damage of the inferior (lower) area of the temporal lobe may produce short-term memory loss, while damage of the inferior and anteromedian (front-middle) regions may cause long-term memory loss. Lesions in the prefrontal cortex (far anterior portions of the frontal lobe) may produce problem-solving deficits, inability to make informed decisions, unpredictable emotional states, and bizarre, socially unacceptable behaviors.

Epilepsy is associated with unregulated electrical activity in the cerebrum.



Anatomy of the brain.

"Left Brain" and "Right Brain"

The two cerebral hemispheres are neither anatomically nor functionally identical. Cortical functions are said to be lateralized when one hemisphere is dominant over the other for a particular function. The side containing the speech centers is called the dominant hemisphere, and is usually the left hemisphere. Most people are highly lateralized for language skills, and lesions in the dominant cortex can cause complete loss of specific language functions. The posterior, superior part of the dominant temporal lobe is important for understanding spoken and written language. Lesions in the language centers produce various forms of aphasia, difficulty understanding or using written or spoken language. The language-dominant hemisphere is also a site of mathematical skills, and intellectual decision making and problem solving using rational, symbolic thought processes.

The nondominant hemisphere is more adept at recognition of complex, three-dimensional structures and patterns of both visual and tactile kinds. It is also the site for recognition of faces and other images, and for nonverbal, intuitive thought processes. Creative and artistic abilities reside in the nondominant hemisphere. Thus, the dominant hemisphere tends to be the more analytical one, and the nondominant hemisphere more intuitive.

The Basal Nuclei

The basal nuclei, or basal ganglia, are four masses of gray matter deep in the cerebrum: the **caudate nucleus**, putamen, globus pallidus, and amyg-

caudate toward the tail

nucleus group of cell bodies in the central nervous system

Parkinson's disease, due to degeneration of the substantia nigra, causes slowed movements and tremor.

dala. Functionally related nuclei of the midbrain, such as the substantia nigra, are sometimes considered to belong to the basal nuclei as well. The basal nuclei receive nerve fibers from all areas of the cerebral cortex and are important in motor skills and processing a broad range of cortical information. Skilled motor tasks such as tying one's shoes—things learned and now done with little thought—are controlled by the basal nuclei.

The Brainstem

The brainstem occupies the base of the brain and includes the diencephalon, midbrain, pons, and medulla.

Diencephalon. The diencephalon is a paired structure with right and left halves. The largest component is the egg-shaped thalamus, which relays incoming information from lower levels of the brain to the cerebral cortex. Little information reaches the cerebral cortex without passing through synapses (neural junctions) in the thalamus. Some information processing occurs here, but the thalamus functions more as a dynamic filter for incoming information.

Immediately **ventral to** the thalamus is the smaller hypothalamus, the control center for the **endocrine** system and involuntary **visceral** motor system. The hypothalamus regulates diverse functions ranging from body temperature to gastrointestinal motility. All functions of the **autonomic** nervous system are regulated by the hypothalamus, although the hypothalamus can be overridden by input from the cerebrum; for example, in rage, fright, or sexual arousal. The hypothalamus also synthesizes the **hormones** released by the posterior lobe of the pituitary gland and produces other hormones that control the anterior lobe of the pituitary. The small epithalamus, containing the pineal gland, is posterior to the thalamus. One cranial nerve, the optic nerve (cranial nerve II), is associated with the diencephalon.

ventral to toward the belly side

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

visceral related to the viscera, or internal organs

autonomic independent; regulating involuntary actions

hormone molecule released by one cell to influence another

reticular netlike

Midbrain. The midbrain is the smallest division of the brainstem. Four small humps, the two inferior and two superior colliculi, form the roof of the midbrain. They are involved in auditory and visual reflexes, respectively. Ventral to the cerebral aqueduct is a region of midbrain called the tegmentum. The floor of the midbrain is formed by two massive cerebral peduncles, stalks that attach the cerebrum and lower brainstem. The midbrain gives rise to two cranial nerves associated with eye movements: the oculomotor nerve (III) and trochlear nerve (IV).

Pons. The most striking feature of the pons is a large, rounded, ventral mass, the basal pons, which relays information from the cerebrum to the cerebellum. The tegmentum of the pons lies between the basal pons and the fourth ventricle. It contains nuclei for several cranial nerves, although only cranial nerve (V), the trigeminal nerve, exits and enters the pons itself.

Medulla. The medulla oblongata forms a transition from brain to spinal cord. Many columns of nerve fibers pass vertically through the medulla, going between the spinal cord and higher levels of the brain. The ventral surface of the medulla has a pair of ridges, the medullary pyramids, that contain motor nerve fibers carrying signals down to the spinal cord. Lateral to each pyramid is a mound, the inferior olive, containing neurons that relay information to the cerebellum. A central core of neurons, the **reticular** formation, contains control centers for the heartbeat and respiration. Three cranial

LEVI-MONTALCINI, RITA (1909–)

Biologist with dual U.S. and Italian citizenship who received, with Stanley Cohen, the 1986 Nobel Prize in physiology for her discovery of a substance ("nerve growth factor") that stimulates and guides the growth of nerve cells. During World War II, the Jewish Levi-Montalcini continued her research on the nervous system of chick embryos while hiding from the Germans.

nerves enter or leave the brainstem at the junction between the pons and medulla: the abducens nerve (VI), involved in eye movements; the facial nerve (VII), which controls the muscles of facial expression; and the vestibulocochlear nerve (VIII), which carries signals for hearing and balance. Motor rootlets of the hypoglossal nerve (XII) leave the ventrolateral surface of the medulla and supply muscles of the tongue. **Dorsal to** the olive are rootlets of the glossopharyngeal nerve (IX) and vagus nerve (X). The glossopharyngeal nerve is involved in taste, salivation, swallowing, and other functions. The vagus nerve supplies many organs of the thoracic and abdominal cavities. Inferior to the rootlets of the vagus nerve are those of the spinal accessory nerve (XI), which **innervates** several neck and shoulder muscles.

dorsal to to the back of

innervates supplies with nerves

The Cerebellum

The cerebellum, located beneath the occipital lobe and posterior to the medulla and pons, is an important regulator of motor function. It connects to the brainstem by three paired bundles of nerve fibers called the superior, middle, and inferior cerebellar peduncles. Integrity of the cerebellum is necessary to perform smooth, accurate, coordinated movements; to maintain posture; and to learn and regulate complicated motor patterns. Damage to the cerebellum does not produce muscle paralysis or paresis (weakness), but rather a loss of muscle coordination called ataxia.

Comparative Anatomy of the Brain

During the course of vertebrate evolution, the control of body functions other than simple reflexes has become concentrated in the brain. Neurons with related functions have become clustered in specific regions, and axons with similar functions have become bundled into discrete tracts. However, the primitive reticular formation of the brainstem is retained in even the most complex brains. More recently evolved centers and tracts have been added to this primitive core.

Lateral views of four brains illustrate this evolutionary trend in vertebrates. The frog has a relatively simple brain. Its cerebrum and cerebellum are small, but its olfactory and visual centers are well developed. These centers trigger reflexive activity needed for survival. The alligator brain shows a growth of both the cerebrum and cerebellum without significant reduction of the visual or olfactory centers. The cerebrum and cerebellum are more developed in the goose, and the visual and olfactory centers remain well developed. These differences reflect higher levels of cortical function and more complex, coordinated motor functions.

There is extensive enlargement of the cerebrum in the horse. Extensive cortical enlargement throws the cortex into gyri and sulci, accommodating a greater cortical area within the cranial vault. The cerebellum also is larger and more convoluted. Human brains have the most extensive cerebral and cerebellar development. The vertebrate brains have the same twelve pairs of cranial nerves, with the same functions. SEE ALSO CENTRAL NERVOUS SYSTEM; HEARING; HYPOTHALAMUS; NERVOUS SYSTEMS; NEUROLOGIC DISEASES; NEURON; PAIN; PERIPHERAL NERVOUS SYSTEM; PITUITARY GLAND; SYNAPTIC TRANSMISSION; TOUCH

Alvin M. Burt

RAMON Y CAJAL, SANTIAGO (1852–1934)

Spanish biologist who received, with Camillo Golgi, the 1906 Nobel Prize in physiology for showing that the nerve cell is the basic unit of the nervous system, a discovery that suggested how nerves could send signals to one another. Ramon y Cajal improved Golgi's silver stain, which revealed how the long threads (dendrites) of nerve cells connect to form a network.

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Bryophytes

Bryophytes are seedless plants without specialized water-conducting tissues. Bryophytes include mosses (phylum Bryophyta), liverworts (phylum Marchantiophyta Hepatophyta), and hornworts (phylum Anthocerophyta). They are plants that virtually everyone has seen, but many have ignored. The most commonly encountered group is the green mosses that cover rotting logs, anchor to the bark of trees, and grow in the spray of waterfalls, along streams and in bogs. Even though mosses often thrive in wet habitats, many mosses and some liverworts can survive in relatively dry environments such as sandy soils and exposed rock outcrops.

superficial on the surface; not deep

The liverworts can take leafy forms, which are very similar **superficially** to mosses, but differ in the details of leaf size and arrangement. Other liverwort genera are characterized by a thallus made up of relatively small, flattened, ribbonlike segments of photosynthetic tissue, which have the general appearance of short, branched pieces of rich dark green egg noodles or linguini.

The leafy liverworts and the mosses differ in the appearance of their spore-forming structures. The mosses have thin stalks called seta extending from the ends of leafy branches. Seta bear capsules, which produce spores. The leafy and thalloid liverworts have very small, balloon-shaped spore-producing stages that remain virtually hidden within, and totally dependent upon, the photosynthetic plant tissues. The third major group of bryophytes is the hornworts. They received this common name because their spore producing structures, called sporangia, are generally long, slender, hornlike, and without capsules. More than eighteen thousand different bryophyte species have been identified throughout the world, and there are perhaps ten thousand species of moss, approximately eight thousand liverwort species, and only a little more than one hundred species of hornworts.

Characteristics of Bryophytes

xylem water-transporting system in plants

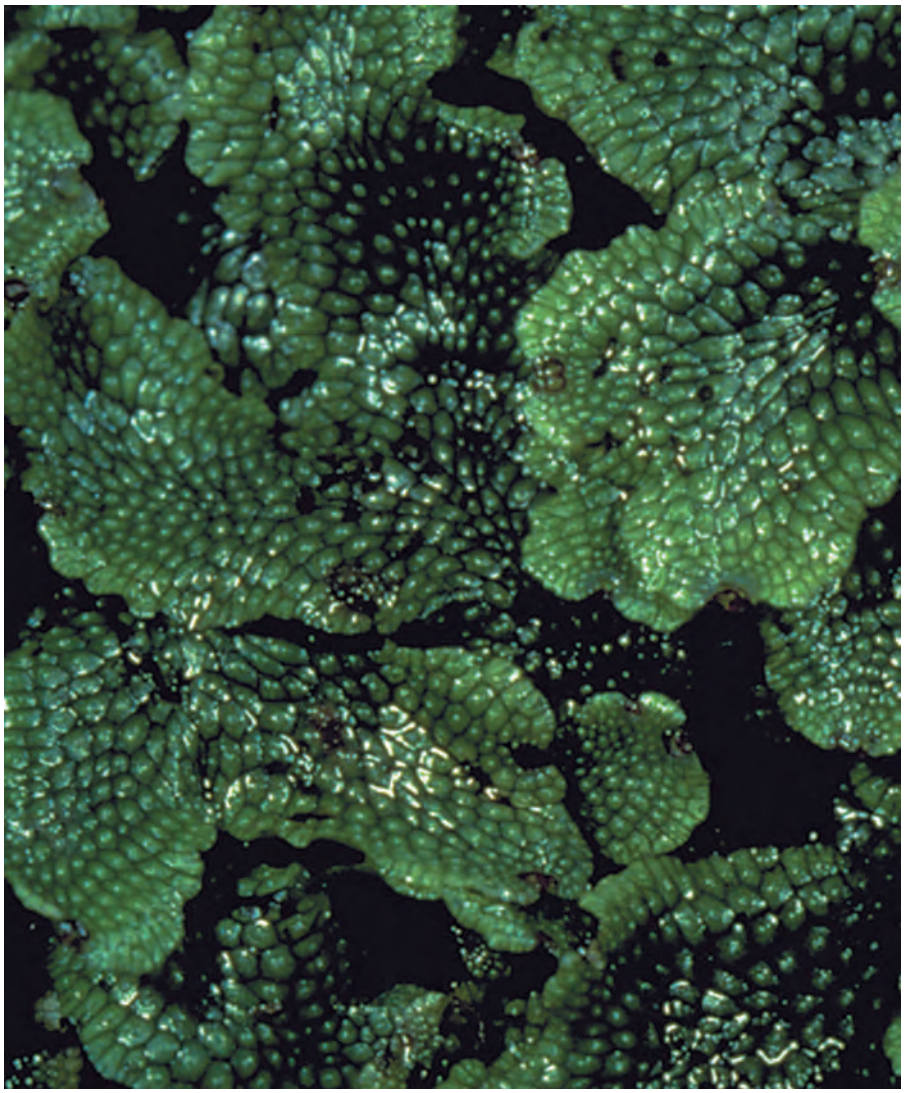
phloem plant tissue that conducts sugars from leaves to roots and other tissues

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

substrate the molecule acted on by an enzyme

There are several characteristic features of bryophytes. First, the green tissue that makes up most of the plant body is not vascularized; it does not have **xylem** and **phloem** cells. This absence of specialized tissues for transporting water and dissolved food throughout the organism limits terrestrial forms to being very short plants, since the only way to move substances through the plant body is by **osmosis** and diffusion from surface moisture.

Second, bryophytes do not have roots, but have rhizoids, which are relatively simple, sometimes multicellular filaments of thin-walled cells that extend from the photosynthetic tissue into the soil or other **substrate**. They anchor the plant somewhat and in some cases facilitate water and nutrient uptake.



Liverworts can either resemble mosses or have the general appearance of short, branched pieces of rich, dark green egg noodles.

Sexual Reproduction

The third characteristic of bryophytes is something that one could not guess by just looking at the conspicuous green tissue. Unlike other plants (and indeed most other multicellular organisms), the conspicuous portion of bryophytes is composed of **haploid** cells, containing only one set of **chromosomes**.

Sexual reproduction in animals involves the union of an egg and a sperm to form a fertilized egg (zygote). This **diploid** (2n) cell divides mitotically to produce an embryo, and ultimately a mature adult organism. These adults have specialized cells, which divide meiotically to produce haploid (n) sperm or eggs depending on the sex of the individual. In the plant kingdom, this cycle of **fertilization** and **meiosis** involves an alternation of generations between the haploid **gamete**-producing stage (gametophyte) and the diploid organism (sporophyte).

Vascular plants, including flowering plants, conifers, and many, such as ferns, that do not produce seeds, have life cycles with the diploid sporophyte being the predominant generation. In the bryophytes, it is the haploid

haploid having single, non-paired chromosomes in the nucleus

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

diploid having pairs of chromosomes in the nucleus

fertilization union of sperm and egg

meiosis cell division that forms eggs or sperm

gamete reproductive cell, such as sperm or egg

gametophyte a haploid plant that makes gametes by mitosis

gametophyte that produces the leaves and thali and therefore predominates. This change from predominant gametophyte to sporophyte was a major evolutionary advancement, which along with the development of vascular tissue facilitated the ultimate success of plants in a diversity of terrestrial habitats.

In order to accomplish sexual reproduction, bryophyte gametophytes produce eggs (n) in the archegonium, a vase-shaped structure that is the female reproductive organ. The sperm (n) are produced in antheridia, which may occur on the same gametophyte, but are often located on separate male plants. Water is generally required for them to swim to the eggs for fertilization. The resulting **zygote** (2n) develops into the sporophyte (2n). The sporophytes remain attached to and dependent on the female gametophyte. These parasitic sporophytes produce spores (n) by meiosis that then divide mitotically to produce the obvious multicellular gametophyte. SEE ALSO ALTERNATION OF GENERATIONS; ANGIOSPERMS; PLANT; PTERIDOPHYTES; SEEDLESS VASCULAR PLANTS; TRANSLOCATION; WATER MOVEMENT IN PLANTS

zygote fertilized egg

Dean Cocking

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Buffon, Count (Georges-Louis Leclerc)

French naturalist and philosopher
1707–1788

Enlightenment eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

Georges-Louis Leclerc, Comte de Buffon (Count Buffon), was one of the greatest French naturalists and a key philosopher of the **Enlightenment**. Born to a wealthy family, Buffon became interested in Newton's physics before turning to biology.

Buffon's life's work was a monumental encyclopedia of all that was known about the natural world, from astronomy to zoology. The first three volumes of his *Histoire Naturelle* were published in 1749. The work eventually grew to 44 volumes, the last of which was published after his death. Buffon's clear writing gave the encyclopedia a broad audience, and his ideas were widely discussed in the salons of Paris. Buffon's influence spread to America as well, and he corresponded with the statesmen Benjamin Franklin and Thomas Jefferson.

Buffon was one of the first philosophers to grapple with the questions of evolution, both of Earth and of living creatures. At the time, church doctrine insisted that Earth was only six thousand years old and that each type of creature had been made independently by the Creator. Volume 1 of the *Histoire* proposed instead that Earth was much older and that the seven days of biblical creation could be understood as seven epochs, each many thou-

sands of years long. Buffon was chastised by French authorities and published a recantation in volume 4.

Elsewhere in the encyclopedia, Buffon recognized the existence of change in species. He proposed that embryos were guided in their development by an "internal mold," fueled by "organic molecules," which recombine into the form of the developing organism. He thought that a change in the environment might lead to a change in the fuel molecules, and therefore cause a change in the form of the species. These ideas were advanced for their time, although they were later shown to be incorrect in their particulars. Buffon also proposed, in sharp contrast to his contemporary Carolus Linnaeus, that species are defined not by simple similarity of appearance but by reproductive fertility over time. SEE ALSO DARWIN, CHARLES; LAMARCK, JEAN-BAPTISTE; LINNAEUS, CAROLUS

Richard Robinson

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C4 and CAM Plants

C4 and CAM plants are plants that use certain special compounds to gather carbon dioxide (CO_2) during photosynthesis. Using these compounds allows these plants to extract more CO_2 from a given amount of air, helping them prevent water loss in dry climates.

All photosynthetic plants need carbon to build sugars, and all get their carbon from CO_2 in the air. CO_2 must first be bound, or "fixed," to another molecule inside the plant cell in order to begin its transformation into sugar. In most plants, carbon fixation occurs when CO_2 reacts with a five-carbon compound called RuBP (ribulose 1,5-bisphosphate). The product splits immediately to form a pair of three-carbon compounds, and therefore this pathway is called the C3 pathway. Further reaction leads to the creation of a sugar (glyceraldehyde-3-phosphate) and the regeneration of RuBP. This series of reactions is known as the Calvin-Benson cycle after the two scientists who elucidated it.

The **enzyme** that **catalyzes** the joining of RuBP and CO_2 is known as RuBP carboxylase, also called Rubisco. Rubisco is believed to be the most abundant **protein** in the world. However, Rubisco is not very efficient at grabbing CO_2, and it has an even worse problem. When the concentration of CO_2 in the air inside the leaf falls too low, Rubisco starts grabbing oxygen instead. The ultimate result of this process, called photorespiration, is that sugar is burned up instead of being created. Photorespiration becomes a significant problem for plants during hot, dry days, when they must keep their stomates (leaf pores) closed to prevent water loss.

Diverse groups of plants have evolved different systems for coping with the problem of photorespiration. These plants, called C4 plants and CAM plants, initially bind carbon dioxide using a much more efficient enzyme. This allows a more efficient harvest of CO_2, allowing the plant to trap suf-

enzyme protein that controls a reaction in a cell

catalyze aid in the reaction of

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

ficient CO_2 without opening its stomates too often. Each then uses the CO_2 in the Calvin-Benson cycle.

C4 ("four-carbon") plants initially attach CO_2 to PEP (phosphoenolpyruvate) to form the four-carbon compound OAA (oxaloacetate) using the enzyme PEP carboxylase. This takes place in the loosely packed cells called mesophyll cells. OAA is then pumped to another set of cells, the bundle sheath cells, which surround the leaf vein. There, it releases the CO_2 for use by Rubisco. By concentrating CO_2 in the bundle sheath cells, C4 plants promote the efficient operation of the Calvin-Benson cycle and minimize photorespiration. C4 plants include corn, sugar cane, and many other tropical grasses.

CAM ("crassulacean acid metabolism") plants also initially attach CO_2 to PEP and form OAA. However, instead of fixing carbon during the day and pumping the OAA to other cells, CAM plants fix carbon at night and store the OAA in large vacuoles within the cell. This allows them to have their stomates open in the cool of the evening, avoiding water loss, and to use the CO_2 for the Calvin-Benson cycle during the day, when it can be driven by the sun's energy. CAM plants are more common than C4 plants and include cacti and a wide variety of other succulent plants. SEE ALSO LEAVES; PHOTOSYNTHESIS; WATER MOVEMENT IN PLANTS

Richard Robinson

Cambrian Explosion

Scientists agree that the Cambrian explosion is one of the most significant events in the history of life. It is marked by a series of biological changes that took place over a relatively short period of geologic time during the early Cambrian, 543 to 520 million years ago. (The entire Cambrian period ranged from 543 to approximately 490 million years ago.) First and foremost, the Cambrian explosion is marked by the global appearance of organisms with skeletal hard parts in the fossil record in contrast to the strictly soft-bodied creatures prior to this. Initially, these skeletal structures were simple in design, such as minute cylindrical tubes, tiny cones, and rudimentary jawlike **appendages**. However, they evolved rapidly into larger and more elaborate structures comparable to the **exoskeletons** of many living invertebrate groups. These early skeletons were constructed from a diverse array of materials that form the building blocks of skeletons to this day, including calcium carbonate, calcium phosphate, and silica.

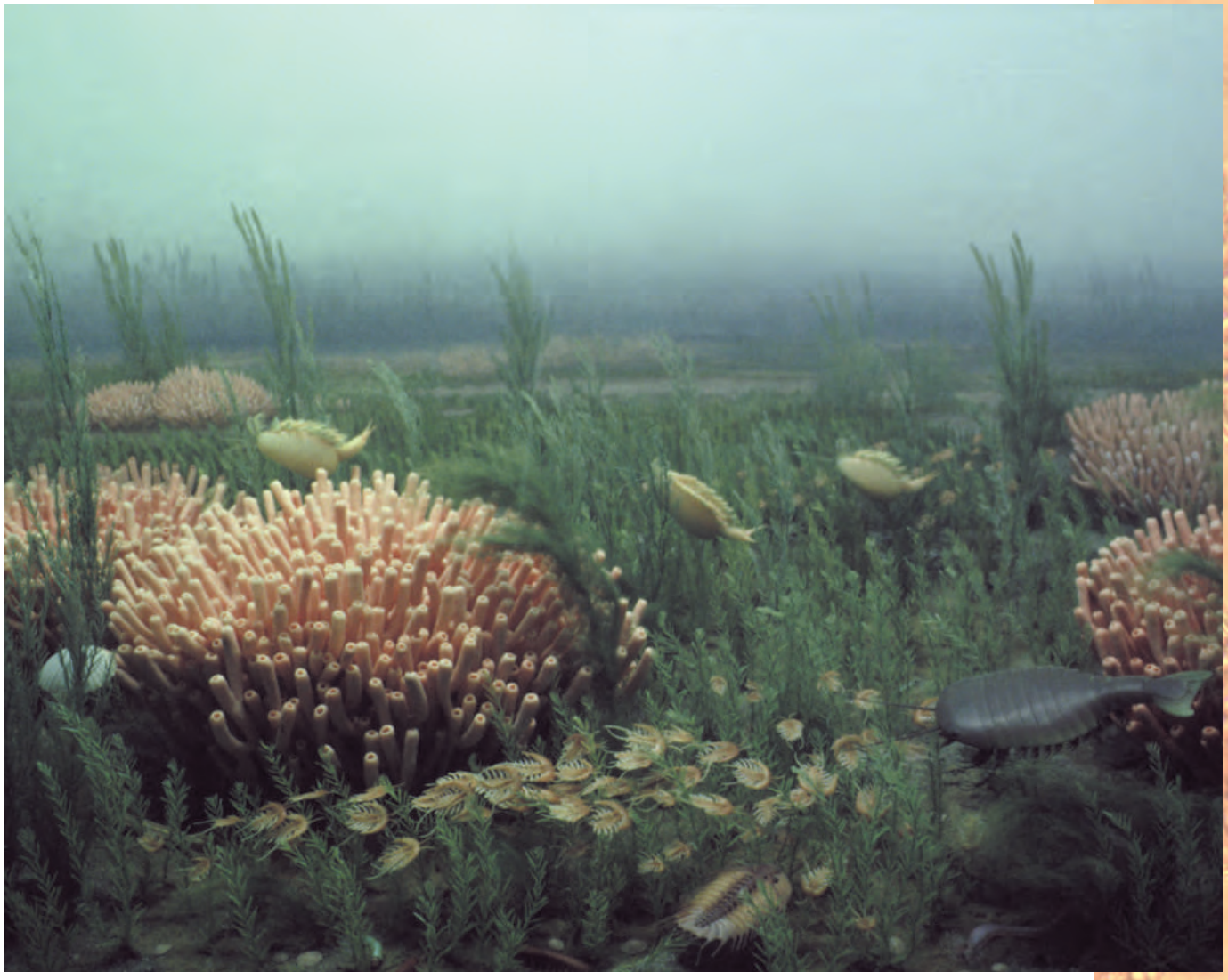
appendage attached organ or structure

exoskeleton external skeleton

Coincident with the appearance of skeletons was the phenomenal diversification of metazoan life. Paleontologists Stephen Jay Gould in *Wonderful Life* (1989) and Simon Conway Morris in *Crucible of Creation* (1998) provide detailed, popular accounts of the amazing evolution of Cambrian animals, though they reach somewhat different conclusions with regard to the implications for the subsequent history of life.

However, all paleontologists agree that virtually all of the modern invertebrate groups made their first definitive appearance in the early Cambrian, including **phylum** Annelida (worms), phylum Mollusca (clams, snails, cephalopods), phylum Echinodermata (starfish, urchins, sea lilies), phylum

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



Marine life from the Cambrian period. Virtually all of the modern invertebrate groups made their first definitive appearance in the early Cambrian period.

Arthropoda (trilobites, crabs, lobsters, insects), and phylum Brachiopoda (lamp shells). Along with these familiar groups came more obscure animals such as the Archaeocyatha, which are an interesting assemblage of sponge-like fossils that presumably led a quiet existence on the Cambrian seafloor filtering food particles from the water column. The Archaeocyatha became extinct by the middle Cambrian. A significant geological phenomenon associated with this great diversification of metazoan life is the enhanced record of bioturbation (the mixing of sediments by organisms seeking food and/or shelter) in rocks of Cambrian age. Prior to the Cambrian, most marine sediments were relatively undisturbed by animal activity.

Many scientists correlate the abrupt appearance of skeletons and the burst of **biotic** evolution in the early Cambrian with chemical changes in the world ocean, specifically an increase in the concentration of oxygen. Many scientists also point to the evolutionary first appearance of predatory lifestyles, with organisms adapting to this new ecological pressure with the construction of protective skeletons and the selection of burrowing habits. (An animal residing beneath the sediment surface is far less likely to be preyed upon.) Still others suggest that the relatively wide-open

biotic living

Cambrian oceans were an ideal setting for large-scale evolutionary experimentation and the origin of Phyla. Regardless of the driving mechanisms, the Cambrian explosion will forever remain one of the defining episodes in the history of life on Earth. SEE ALSO EVOLUTION

Raymond R. Rogers

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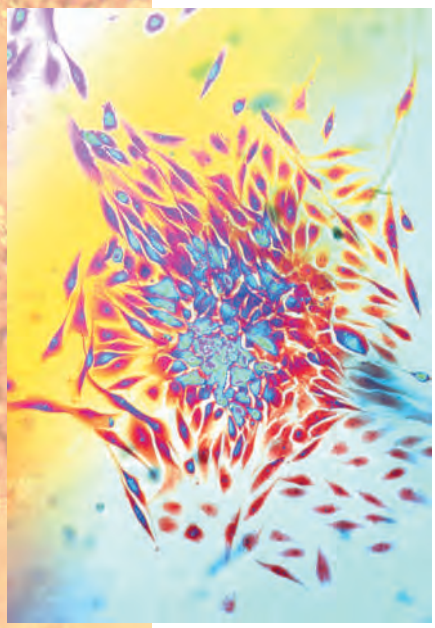
Cancer

Normal tissue development depends on a balance between cell multiplication and cell death. When cells multiply faster than they die, the result is an abnormal tissue growth called a tumor (neoplasm). The study and treatment of tumors is a branch of medicine called oncology.

Not all tumors are cancerous. Benign tumors are surrounded by a fibrous capsule, grow slowly, and do not spread to other organs; although they are nevertheless sometimes fatal. A wart is a benign tumor. Malignant tumors have no capsule, grow rapidly, and shed cells that can "seed" new tumors in other organs, a phenomenon called **metastasis**. The word *cancer* refers only to malignant tumors. The word literally means "crab." It was coined by the ancient Greek physician Hippocrates when the tangle of blood vessels in a breast tumor reminded him of the legs of a crab.

Cancers are classified according to the type of tissues or cells in which they originate (see Table on page 112). A primary tumor is a tumor in the site of origin, and a secondary (metastatic) tumor is a tumor in a new site resulting from the spread of cells from the original tumor, for example, a brain tumor resulting from cells that originated in colon cancer.



Human breast cancer cells metastasizing and spreading outward in a culture (blue).

metastasis breaking away of cancer cells from a solid tumor to travel elsewhere in the body

ionizing radiation high-energy radiation that destroys chemical bonds

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

oncogene gene that causes cancer

secretion material released from the cell

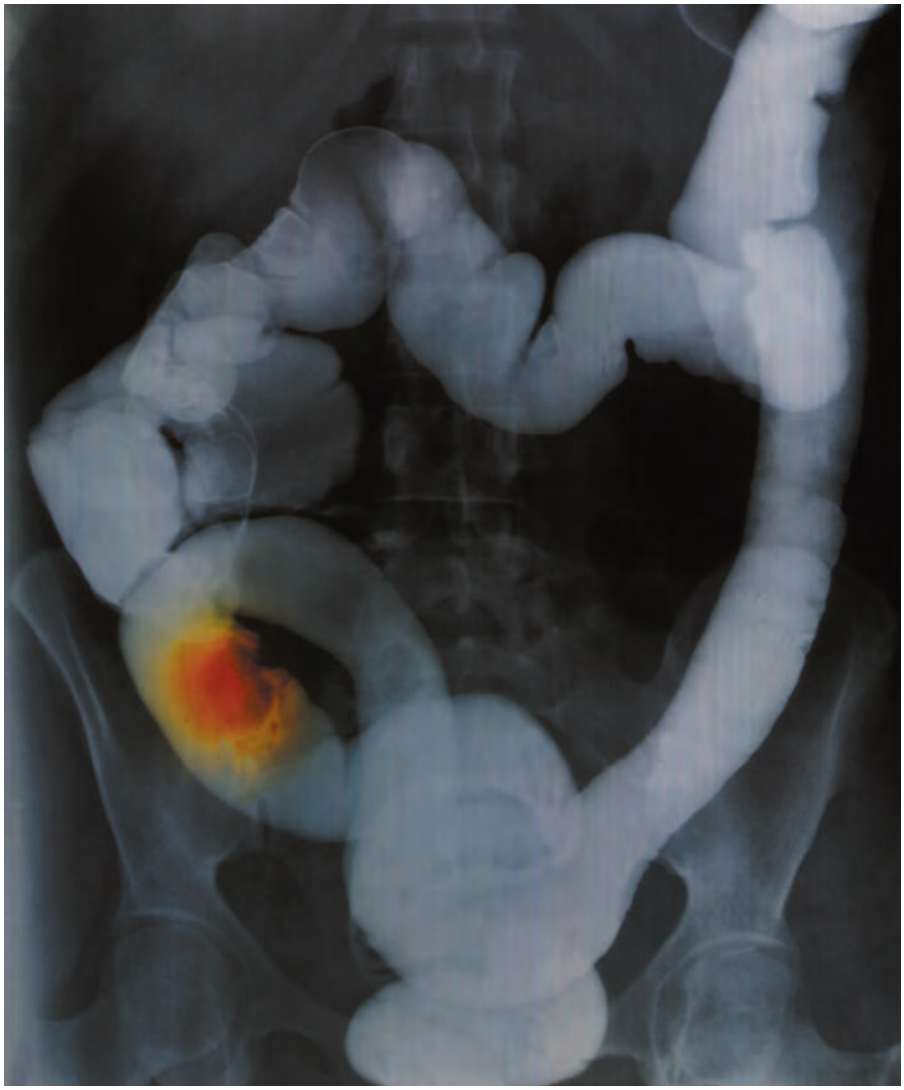
Causes of Cancer

Most cancer is caused by environmental agents called carcinogens. Carcinogens include chemicals such as cigarette tar, nitrites (used as food preservatives), and many industrial chemicals; viruses such as the hepatitis B and herpes simplex 2 viruses; and **ionizing radiation** such as X rays and gamma rays. All of these agents are mutagens; that is, they cause mutations, or changes in deoxyribonucleic acid (DNA) and chromosome structure, which in turn result in uncontrolled cell division.

Cancer Genes

The risk of cancer is often hereditary, and many forms of cancer have been traced to two types of **genes**: **oncogenes** and tumor-suppressor genes.

Oncogenes. Oncogenes are mutated, "misbehaving" genes that normally code for growth factors or their receptors. Growth factors are chemical signals that trigger cell division. Some oncogenes cause excessive **secretion** of growth factors, and thus excessive cell division. Other oncogenes code for



Colored barium enema X ray of a human abdomen showing cancer of the ascending colon. The tumor appears over the right pelvic bone (left on image).

dysfunctional receptors that act like switches stuck in the "on" position, sending signals for cell division even when there is no growth factor bound to them. Many cases of breast and ovarian cancer are due to an oncogene called erbB2.

Tumor-Suppressor Genes. Tumor-suppressor (TS) genes normally inhibit cancer by opposing the action of oncogenes, promoting the repair of mutated DNA, or controlling tissue development. When TS genes are mutated, these protections are lost. A TS gene called p53 has been implicated in leukemia and colon, lung, breast, liver, brain, and esophageal cancer.

Thus, oncogenes promote cancer and TS genes suppress it. They can be loosely compared to the accelerator and brake on a car, respectively. A defect in either one causes the "car," cell division, to run out of control. Cancers typically require more than one mutation before they develop; thus, colon cancer involves damage to at least three TS genes on chromosomes 5, 17, and 18, plus activation of an oncogene on chromosome 12. It may take many years for so many mutations to accumulate in a single cell, which is one reason cancer is more common among the elderly than among young people.

The top ten causes of cancer mortality in the United States, ranked from highest to lowest, are cancers of the lung, colon, breast, prostate, pancreatic, leukemic, ovarian, stomach, nervous system, and bladder.

Type of cancer	Site of origin
Carcinoma	Epithelial cells
Melanoma	Pigment-producing skin cells (melanocytes)
Sarcoma	Bone, other connective tissues, or muscle
Leukemia	Blood-producing tissues (bone marrow and lymphatic tissue)
Lymphoma	Lymph nodes

Effects of Cancer

Cancer is almost always fatal if it is not treated. Four ways in which cancer can kill are:

1. By displacing normal tissue, so the function of an organ deteriorates; an example of this is when a lung tumor replaces so much lung tissue that the blood can no longer get enough oxygen, or a brain tumor compresses and kills brain tissue
2. By invading blood vessels, causing fatal hemorrhages
3. By compressing vital passages, for example shutting off air flow into the lung or obstructing blood flow through a major vein or artery
4. By competing with healthy tissues for nutrients, often causing the body to break down its own proteins (muscle, for example) to feed the "hungry" tumor, or failing to make enough red blood cells and platelets because stem cells are diverted into producing the abnormal white blood cells of leukemia.

Cancer is normally treated by surgery, chemotherapy, or both, depending on its location, type, and extent. Other approaches are radiotherapy (using radiation to destroy tumors) and immunotherapy (providing antibodies or immune cells to attack cancer cells). Some forms of cancer are highly treatable, such as skin cancer, whereas others offer much less hope of recovery, such as pancreatic cancer. SEE ALSO CELL CYCLE; GENETIC DISEASES; MUTATION; ONCOGENES AND CANCER CELLS

Kenneth S. Saladin

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Carbohydrates

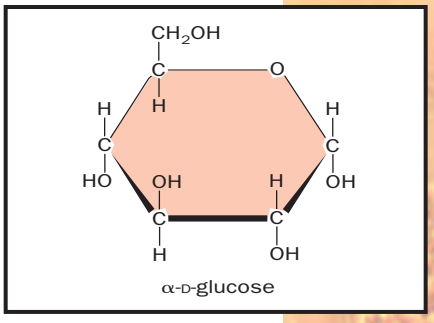
lipid fat or waxlike molecule, insoluble in water

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

Carbohydrates are one of four major classes of biological molecules, along with nucleic acids, **lipids**, and **proteins**. They are the most abundant biological molecules, and are an important nutritional component of many foods. Carbohydrates are usually composed solely of carbon,

hydrogen, and oxygen, although some also contain nitrogen, sulfur, or phosphorus.

Carbohydrates are classified according to size. The smallest carbohydrates are called monosaccharides (*mono* means "one"; *saccharide* means "sugar"). As the name implies, these are single sugar molecules. The most common monosaccharides, such as fructose and **glucose**, have six carbon atoms, but monosaccharides can have as few as three or as many as seven. Monosaccharides with five or more carbons usually have a ring-shaped structure when they are in a solution.



Glucose, a common monosaccharide

Oligosaccharides (*oligo* means "few") are more **complex carbohydrates** composed of chains of two or a few (up to about twenty) simple sugars joined with a type of covalent bond called a glycosidic bond. The longer **oligosaccharides** may be linear or branched. The most common oligosaccharides, composed of only two sugars, are called disaccharides (*di* means "two"). The most common disaccharide, sucrose, or cane sugar, consists of a glucose molecule bonded to a fructose molecule. Other important disaccharides are maltose (two glucoses joined together) and lactose, or milk sugar (glucose joined to galactose). Longer oligosaccharides are usually bound to other molecules, such as lipids or proteins, to form glycolipids and glycoproteins, respectively (*glyco* means "sweet"), rather than being free in solution. These kinds of molecules are important in cell recognition, signaling, and **adhesion**, and are commonly found on the outer surface of cell membranes.

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

complex carbohydrate molecules formed by linking simpler carbohydrates such as sugars

oligosaccharide chain of several sugar molecules

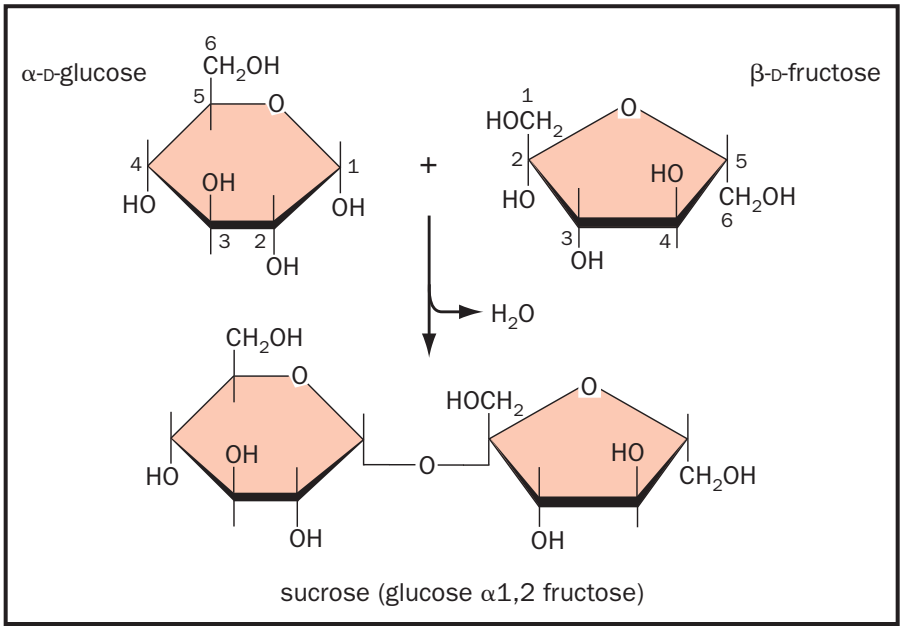
adhesion attachment; sticking to the surface of

Polysaccharides (*poly*, means "many") are important energy-storage and structural molecules. They are formed of long chains of sugars, most commonly glucose. Like oligosaccharides, they may be linear or branched. Important **polysaccharides** are starch, glycogen (animal starch), **cellulose**, and **chitin**. Starch and glycogen are similar energy-storage molecules found in plants and animals, respectively. Both are made of glucose molecules that are bonded in the same manner; however, glycogen has a higher degree of branching compared to starch.

polysaccharide carbohydrate composed of many individual units of sugar

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

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



sucrose (glucose α1,2 fructose)

Sucrose, a common disaccharide.

Cellulose is also made of glucose, but the individual glucose units are linked differently, resulting in a long, fibrous structure that is not soluble in water. Cellulose is the main structural component of most plant and some protozoan and bacterial cell walls. Wood is largely cellulose, and paper is an almost-pure sheet of cellulose prepared from wood. Cotton is also nearly pure cellulose.

Chitin is similar to cellulose, but its sugar subunits are a modified form of glucose called *N*-acetyl glucosamine. Chitin is the main structural component of fungal cell walls and of animal **exoskeletons**, such as the shells of insects and crustaceans. Other important structural polysaccharides form the **matrix** of cartilage and other **connective tissues** of animals. Carbohydrates are at the center of cellular metabolic pathways. The most fundamental process, **glycolysis**, uses glucose to produce energy for cellular needs. SEE ALSO CELL WALL; EXTRACELLULAR MATRIX; GLYCOLYSIS AND FERMENTATION

David W. Tapley

exoskeleton external skeleton

matrix a network, usually of threadlike fibers

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

glycolysis initial stages of sugar breakdown in a cell

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Carbon Cycle

The carbon cycle involves the circulation of carbon dioxide (CO_2) from the atmosphere into plants and other living organisms; the transfer of carbon from these organisms into other temporary storage pools, living or nonliving, containing **organic** and **inorganic** carbon compounds; and the return of CO_2 to the atmosphere through respiration or combustion processes. The carbon cycle provides a unifying framework for examining exchanges or storage of carbon associated with photosynthesis and energy assimilation by organisms, respiration and **metabolism**, productivity and biomass accumulation, and the decay and recycling of organic matter at the level of a single organism, an **ecosystem**, or the global biosphere.

organic composed of carbon, or derived from living organisms

inorganic not bonded to carbon

metabolism chemical reactions within a cell

ecosystem an ecological community and its environment

Analysis of the carbon cycle in a forest ecosystem, for example, requires the estimation of pools of carbon in live biomass, dead wood, decaying litter (branches and leaves), and soil organic matter. This information is combined with estimates of major transfers within the cycle such as carbon fixation via photosynthesis, CO_2 release by respiration, carbon flow to the soil as litterfall and root turnover, and carbon flow through grazing and decomposer food chains.

On a global scale, the primary carbon storage pools are the oceans and marine sediments, fossil fuels and shale deposits, terrestrial plants and soils, and the atmosphere. The global carbon cycle is characterized by large exchanges of carbon between Earth and its atmosphere. Photosynthesis and ocean uptake processes remove CO_2 from the atmospheric carbon pool, whereas CO_2 is returned to the atmosphere by biological respiration, deforestation and land clearing, forest fires, and fossil fuel combustion associated with human activities. As of 2001, the atmosphere is experiencing a net gain of 3 billion tons of carbon per year from CO_2 emissions derived from human combustion of coal, oil, and gas, as well as from deforestation and land clearing activities. This imbalance in the global carbon cycle is

reflected in the rising concentration of atmospheric CO_2, which has increased 15 percent from 320 ppm (parts per million) to 368 ppm since the mid-1960s. SEE ALSO BIOGEOCHEMICAL CYCLES; ECOSYSTEM; GLOBAL CLIMATE CHANGE; PLANKTON

Christopher S. Cronan

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Cardiovascular Diseases

Cardiovascular diseases affect the heart or the blood vessels. Because the cardiovascular system provides oxygen and nutrients to cells and removes wastes from them, these diseases have profound impacts on health.

Arrythmias

Heart dysfunction can range from mild abnormalities to complete failure. The heart beats almost forty million times a year. Variants of the heartbeat can affect health and are called arrhythmias. A persistent resting heart rate above one hundred beats per minute is called tachycardia, and below sixty, bradycardia. If the cause is in the **ventricles,** the condition is termed ventricular tachycardia or bradycardia. If the cause is in the **atria**, it is termed supraventricular.

ventricles fluid-filled, lower chambers of the heart

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

A number of factors can cause arrhythmias, including abnormal circulating levels of **electrolytes**, particularly potassium and calcium, and damage to the heart from insufficient blood flow (ischemia). An electrocardiogram (ECG) may be helpful in determining the cause. An ECG measures the electrical activity of the heart from the skin, even though the heart is deep within the thoracic (chest) cavity.

electrolytes ions in body fluids

Heart Failure

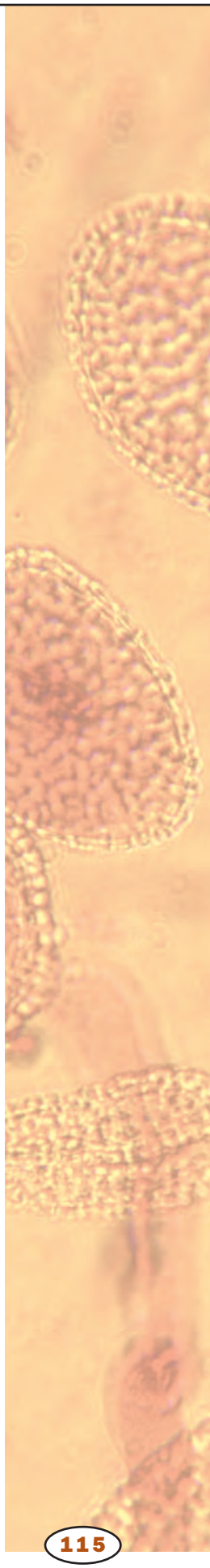
In heart failure, the heart is unable to contract with sufficient force to pump blood to all body parts. Eventually, the lack of adequate blood flow causes death. Heart failure has several causes. Disease of the heart muscle, called cardiomyopathy, is one cause that can be inherited, or have no known origin. More commonly heart failure is associated with insufficient blood flow, which may reflect a blockage in the circulatory pathway.

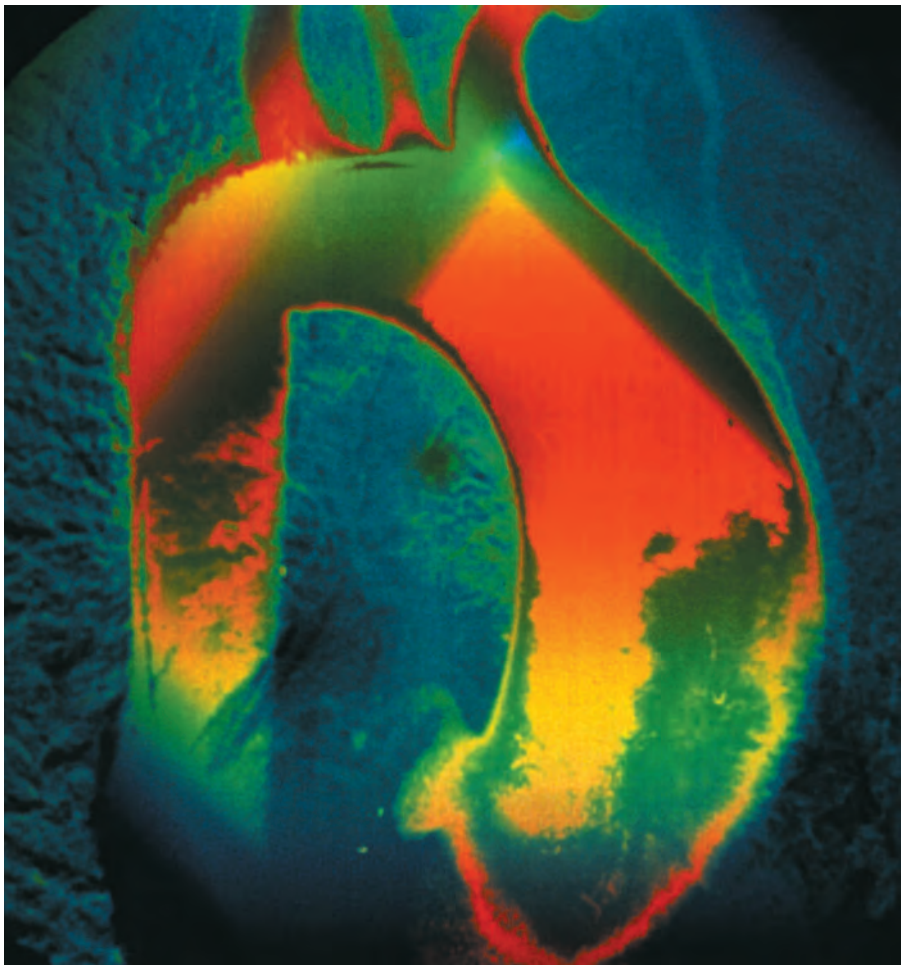
Heart failure is commonly associated with hypertension (high blood pressure), in which the muscular walls of blood vessels contract, impeding blood flow. The heart must work harder to pump the blood and may hypertrophy, or overgrow, to meet the challenge. Eventually, the increased mass requires more oxygen than blood flow to the heart can provide, and the heart muscle begins to fail.

Hypertension

Hypertension may stretch and weaken areas of blood vessel walls, leading to an **aneurysm**, in which the weakened area balloons out and may burst. In a major blood vessel, this can be rapidly fatal. If such a ruptured vessel

aneurysm bulging of the wall of a blood vessel





An image of a human heart undergoing angiography to repair a massive aneurysm of the aortal arch.

occurs in the brain, brain cells are killed and a stroke results. Stroke may also occur when a blood clot blocks blood flow to part of the brain, a condition called an embolism. Embolisms can occur in any blood vessel, but those in the brain can be especially devastating.

Heart Attack

Decreased blood flow to heart muscle cells can result in a heart attack, or myocardial infarction. This is more likely to occur when heart oxygen demands increase, as during exercise, or if blood vessels to the heart are partially blocked, as in atherosclerosis, in which fatty deposits form on the inner linings of coronary arteries. Initially, decreased blood flow causes angina pectoris, which is a sensation of heavy pressure or squeezing in the chest that may be accompanied by sweating, difficulty breathing, nausea, and vomiting. Complete blockage causes a heart attack, in which heart muscle cells die. It can be fatal.

Valve Disorders

Valves in the heart ensure that pumped blood always leaves through the arteries, and does not reverse direction through the veins. Valve defects can seriously impair the heart's ability to pump blood. Mitral valve prolapse is a common abnormality in which the valve separating the atrium and ven-

tricle bulges back into the atrium when the ventricle contracts. It produces a distinctive type of heart murmur that can be heard through a stethoscope. Symptoms include chest pain, fatigue, and anxiety. Infection by certain species of *Streptococcus* bacteria can lead to mitral valve damage. The bacteria and the mitral valve have similar surface chemistry. When the immune system attacks the bacteria, it may also attack the valve. SEE ALSO AUTOIMMUNE DISEASE; BLOOD CLOTTING; BLOOD VESSELS; CIRCULATORY SYSTEMS; HEART AND CIRCULATION; SMOKING AND HEALTH

David Shier

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Carson, Rachel

American science writer and naturalist
1907–1964

Rachel Louise Carson was a career government biologist and author who forever changed public attitudes about the environment. Her eloquent writing about environmental pollution and the natural history of the oceans earned Carson the title "founder of the modern environmental movement."

Carson was the youngest of three children and grew up near the western Pennsylvania town of Springdale. Her mother inspired in Rachel a lifelong love of nature and biology. In 1929, Carson graduated with honors from the Pennsylvania College for Women, and in 1932 earned a master's degree in zoology from Johns Hopkins University.

Soon after, the U.S. Bureau of Fisheries hired Carson to write radio scripts, and the *Baltimore Sun* newspaper published her feature articles about natural history. In 1936, when she was twenty-nine, Carson began working as a biologist for the U.S. Fish and Wildlife Service, eventually becoming editor in chief for all its publications. Carson also wrote lyric prose about nature for national magazines and published a half dozen books. Among these were *The Sea Around Us* (1951), which won a National Book Award, and *Silent Spring* (1962), which created a worldwide awareness of the dangers of pesticides.

Carson was attacked by the chemical industry as an hysterical alarmist who didn't know what she was talking about. But history has proved that she was right. At the time, her calm demeanor, impeccable credentials, and articulate arguments persuaded the world that human-made chemicals could indeed drive birds and other animals to extinction. President John F. Kennedy read Carson's book, and was inspired to call for safety testing of pesticides. These tests eventually lead to the banning of DDT, a pesticide that persists in the environment and harms humans as well as most other animals. SEE ALSO ENDANGERED SPECIES; POLLUTION AND BIOREMEDIATION

Jennie Dusheck

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Cartilaginous Fish

The cartilaginous fish, or Chondricthyes, include the sharks, rays, skates, and chimaeras. There are over eight hundred living species of sharks and rays, and about thirty species of chimaeras. Cartilaginous fish are true fish. They have fins and breathe with gills. Unlike the more familiar bony fish, the Osteichythes, the skeletons of the cartilaginous fish are made of cartilage. Other features that distinguish the cartilaginous fish from the bony fish are multiple gill slits, tiny toothlike scales, nostrils on the side of the head, teeth that are not fused to the jaw, and internal **fertilization**. Internal fertilization also occurs in some bony fish such as sea horses, guppies, and mollies. The ancestors of cartilaginous fish and bony fish diverged in the late Silurian, more than 400 million years ago.

fertilization union of sperm and egg

Sharks are large, long-lived, slow-growing ocean predators. The whale shark (*Rhincodon typhus*) is the world's largest fish; adults can be as long as 18 meters (59 feet). The spiny dogfish shark (*Squalus acanthias*) is the most studied shark, and while it rarely grows longer than 1.2 meters (almost 4 feet), it matures at 35 years and lives to be 70 or 80 years old. Sharks have internal fertilization and many shark species bear live young after a **gestation** of six or more months. The number of sharks in a clutch is often low, but can range from one or two to hundreds, depending on the species. The combination of slow maturity, long gestation, and small clutches means that shark populations cannot increase very rapidly. As a result, shark populations are very vulnerable to overfishing.

gestation period of fetal development within the mother

Sharks are tremendous predators, with their mouths full of ever-sharp teeth and jaw strength capable of exerting over 2,500 kg/cm2 (30,000 psi) of pressure at the tooth tips. (A single shark may produce over ten thousand teeth in its lifetime, and as a result, the most common fossils of the cartilaginous fish are their teeth.) Sharks also have excellent senses of smell, waterborne vibrations, and the ability to sense the faint magnetic fields generated by the muscles of their prey. The large white shark (*Carcharodon carcharias*) preys on seals, sea lions, and large fish, and has been known to attack swimmers and boats.

Rays are bottom-dwelling fishes that are able to "fly" through the water with their enlarged and flattened pectoral fins. Stingrays can cause excruciating pain using a venomous stinger at the base of their tail. Electric rays can generate a shock of 200 volts. The manta ray has a wing span of up to 7 meters (almost 23 feet) and is sometimes seen following ships in the open ocean.

Chimearas, also known as ratfishes, are a small group of rarely seen bottom-dwelling cartilaginous fish with large platelike teeth, no scales, and long skinny tails. SEE ALSO Bony Fish; Ocean Ecosystems

Virginia Card

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Cell

A cell is the smallest unit of living matter. Cells were first identified in Europe in the seventeenth century by Antoni van Leeuwenhoek and others. They were named by Robert Hooke, an Englishman, who said they reminded him of the rooms or "cells" in a monastery. The cell theory describes some fundamental characteristics of all cells and is one of the unifying concepts in biology. It states that: (1) all organisms are made of cells, a cell is the structural and functional unit of organs, and therefore cells are organisms; and (2) cells are capable of self-reproduction and come only from preexisting cells.

Prokaryotic Cells

Cells come in many shapes and sizes and have different structural features. Bacteria are single-celled organisms approximately 1 to 10 micrometers (.00004 to .0004 inch) in size and can be spherical, rod-shaped, or spiral-shaped. They are known as **prokaryotes** (from the Greek *pro*, meaning "before" and *karyon*, meaning "kernel" or "nucleus") because they contain a nucleoid region rather than a true **nucleus** where their **genetic** material is found. All bacteria have cell walls that may be surrounded by a capsule and/or a gelatinous slime layer.

Beneath the cell wall is the plasma membrane responsible for regulating the flow of materials into and out of the cell's **cytoplasm** within the interior of the cell. The cytoplasm is composed of fluid known as **cytosol** and solid materials. Within the cytosol are **ribosomes**, granular bodies that di-

prokaryote single-celled organism without a nucleus

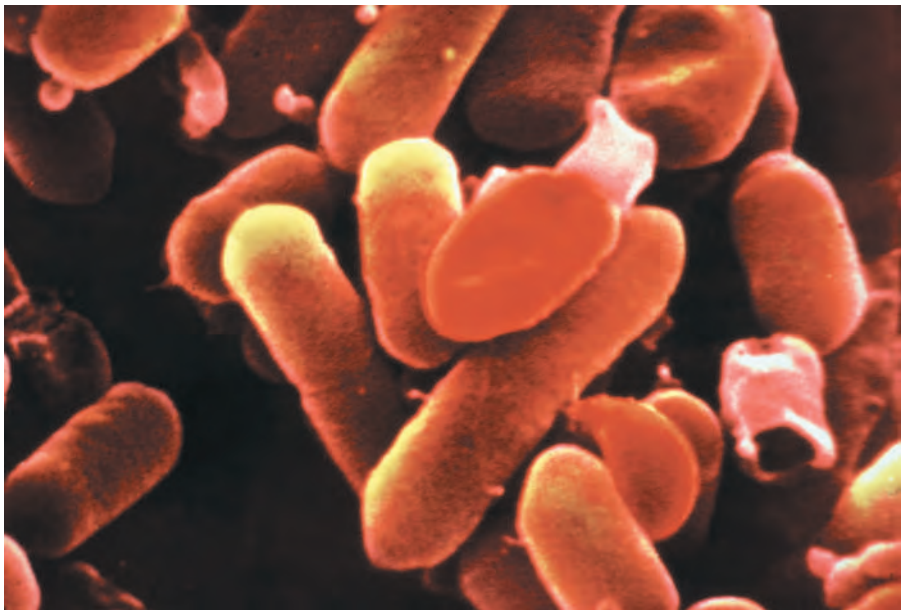
nucleus membrane-bound portion of cell containing the chromosomes

genetic of, relating to the portion of DNA that codes for a protein or RNA molecule

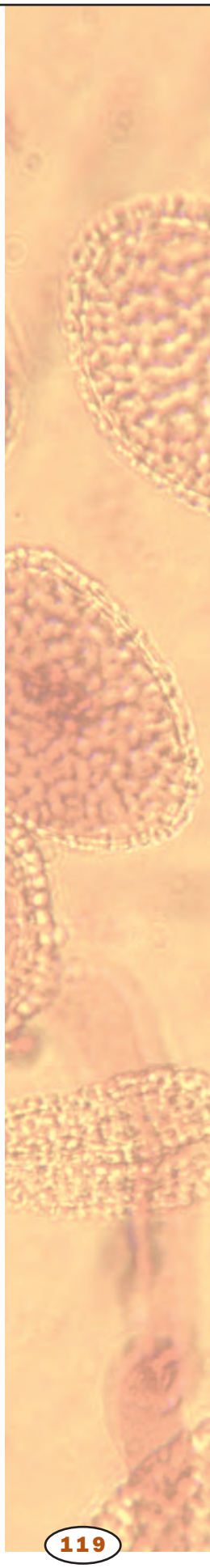
cytoplasm material in a cell, excluding the nucleus

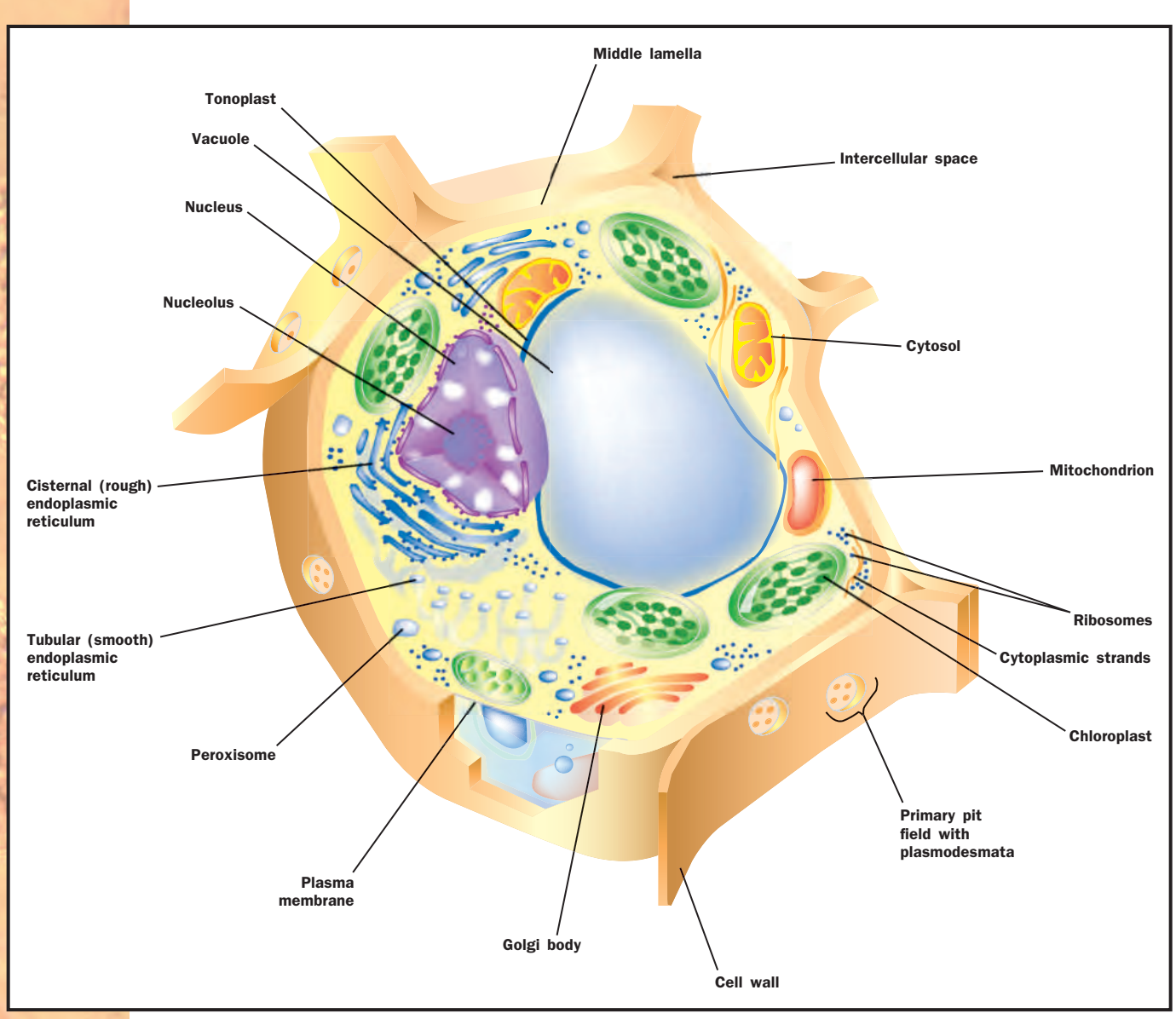
cytosol fluid portion of a cell, not including the organelles

ribosome protein-RNA complex in cells that synthesizes protein



A scanning electron micrograph of Listeria monocytogene cells.





Components of a plant cell.

rect the synthesis of all bacterial **proteins**. Some bacteria have whiplike **appendages** called flagella that enable them to move. The genetic material of bacteria is deoxyribonucleic acid (DNA), which is contained within a single circular **chromosome** in the nucleoid region and sometimes also in a smaller ring called a **plasmid**.

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

appendage attached organ or structure

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

Eukaryotic Cells

Eukaryotic cells (from the Greek *eu*, meaning "true" and *karyon*, meaning "kernel" or "nucleus") are more complex than prokaryotic cells and are found in both unicellular organisms like the **amoeba** and multicellular organisms like sunflowers, mushrooms, and humans. They are generally larger than prokaryotic cells, ranging from about 10 to 100 micrometers (.0004 to .004 inch) in size. In multicellular organisms, there are many different types of cells that perform specialized functions. In animals, for instance, pancreatic cells make and secrete **hormones**, whereas red blood cells are specialized

for transporting oxygen throughout the body. Cells with specialized functions such as these are called "differentiated."

All eukaryotic cells share specific structural characteristics. These include a true nucleus that is bounded by a double-layered membrane known as the nuclear membrane. Within the nucleus is housed the cell's genetic material in the form of linear chromosomes of DNA contained in thread-like structures called **chromatin**. All eukaryotic cells have a plasma membrane that encloses the cytoplasm. Cells of plants, fungi, and many protists have an additional outer boundary called a cell wall that differs significantly in structure and composition from that of a prokaryotic cell.

Eukaryotic cells have many different kinds of small membrane-bound structures called **organelles** that, with the exception of ribosomes, are absent from prokaryotic cells. Eukaryotic ribosomes (which are not enclosed by a membrane) float freely in the cytosol or are attached to another organelle known as the **endoplasmic reticulum** (ER). The ER is a series of membrane-bound, fluid-filled spaces in contact with the nuclear membrane. Its function is to synthesize and/or modify proteins, phospholipids, and cholesterol and to transport substances from the nucleus to the rest of the cell.

When the ER is studded with ribosomes it is called the rough ER. When ribosomes are absent it is called the smooth ER. The Golgi apparatus is a system of membrane-enclosed sacs responsible for transporting newly synthesized proteins and **lipids** from the ER to other organelles and the plasma membrane. It is also the site of **polysaccharide** synthesis and modification of proteins and lipids by addition of sugars.

Both animal and plant cells have **mitochondria**, power houses that convert energy stored in the chemical bonds of nutrients like **carbohydrates**, proteins, and fats into adenosine triphosphate (ATP), a high-energy chemical compound that is required for many cellular processes. Many plant cells also have chloroplasts, organelles that contain the pigment chlorophyll. Chloroplasts conduct photosynthesis, in which plants use sunlight, water, and carbon dioxide to synthesize the sugar **glucose**.

Organelles in Eukaryotic Cells

Structure	Function
Nucleus	Contains genetic material
Ribosomes	Protein synthesis
Endoplasmic reticulum	Synthesis/modification and transport of proteins and lipids
Golgi apparatus	Processing, distribution of proteins, lipids
Lysosomes	Digestion of substances in cell
Peroxisomes	Digestion and detoxification
Chloroplasts	Photosynthesis
Flagella/Cilia	Cell movement
Vacuole and vesicle	Storage of cellular substances
Centriole	Cytoskeletal organization

plasmid small ring of DNA found in many bacteria

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

hormone molecule released by one cell to influence another

chromatin complex of DNA, histones, and other proteins making up chromosomes

organelle membrane-bound cell compartment

endoplasmic reticulum network of membranes within the cell

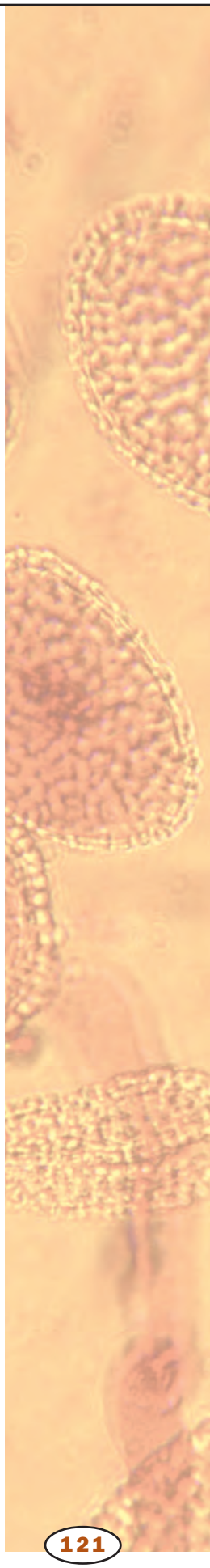
lipid fat or waxlike molecule, insoluble in water

polysaccharide carbohydrate composed of many individual units of sugar

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

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

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



enzyme protein that controls a reaction in a cell

Lysosomes are membrane-enclosed bodies in plant and animal cells that contain **enzymes** responsible for digesting substances within the cell. In animal cells, peroxisomes contain enzymes that metabolize lipids and alcohol. In plants, peroxisomes also convert fatty acids into molecules that are precursors of sugars. Both plant and animal cells have vacuoles, membranous sacs that store substances such as water, sugars, and salts. Protozoans, a type of unicellular protist, have specialized contractile vacuoles for removing excess water from the cell.

intracellular within a cell

cytoskeleton internal scaffolding in a cell, composed of protein

Most organelles do not flow freely in the cytoplasm but are anchored to a complex **intracellular** framework known as the **cytoskeleton**, which is made of three different types of protein fibers: microfilaments, intermediate filaments, and microtubules. The cytoskeleton is involved in maintaining cell shape and participates in cell movement and cell division. The centrosome contains a pair of organelles called centrioles close to the nucleus of animal cells. It is responsible for organizing some of the cytoskeletal components.

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

Some plant and animal cells have projections from the plasma membrane known as flagella or **cilia** that are capable of movement. For example, a single flagellum is responsible for the movement of sperm cells. SEE ALSO CELL WALL; CHLOROPLAST; CYTOSKELETON; DNA; GOLGI; HISTORY OF BIOLOGY: CELL THEORY AND CELL STRUCTURE; MITOCHONDRION; NUCLEUS; RIBOSOME; VACUOLE

Michele D. Blum

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Cell Culture

enzyme protein that controls a reaction in a cell

dissociate break apart

medium nutrient source

Cell culture describes the laboratory growth of cells derived from plants or animals. To put cells into culture, the tissue of interest is exposed to **enzymes** that **dissociate** the tissue to release the component cells. In some cases, for example with blood-forming tissues, suspensions can be produced more simply by mechanical means, such as forcing them through a syringe. Dispersed cells are then transferred to a suitable growth **medium** and allowed to attach to the surface of culture flasks. When cells have grown (by dividing) to cover the flasks' surface, the process of enzymic dissociation can be repeated and the cells replanted to additional flasks. This process is referred to as subcultivation or "splitting."

hormone molecule released by one cell to influence another

Cell culture requires careful attention to the growth medium to ensure cells are given all the components they require to grow. Often the culture medium requires growth factors or **hormones** to stimulate growth.

biopharmaceuticals drugs produced by and harvested from living organisms

The general process of cell culture has been used extensively since the early 1900s for research on tissue growth and development, virus biology, properties of cancer cells, studies relating to aging, genetics, and gene therapy. More recently, large-scale cell culture systems have been developed to produce **biopharmaceuticals** in quantities, another facet of the broad field of biotechnology.

A central advantage of the cell culture technique is its simplicity compared to the difficulties of studies using whole plant or animal organs, which are usually composed of many different cell types. With cell culture, it is possible to observe, in a well-defined environment, small numbers of cells of a single type derived by expanding an original population. In contrast, with an intact organ, one could be working with forty or more differing cell types, a nondefined fluid, and literally billions of cells.

The limitations of cell culture include the finite doubling potential of most normal cells, the possibilities for unexpected infection with viruses or microorganisms, or even cross-contamination with other cell types. Media used to propagate cells are rich in nutrients and, therefore, support growth of a multitude of organisms. Accordingly, most culture methods require sterile conditions. Often antibiotics are used to inhibit growth of unwanted microbial contaminants. Another difficulty with some cultured cells is their tendency to change their **morphology**, functions, or the range of genes they express.

Cell culture has had a tremendous impact on human health. The ability to culture cells allowed the laboratory growth of polio virus to produce vaccines that nearly eliminated polio as a disease. Two of the many areas of scientific study where uses of cell culture techniques have had major impact are human aging and cancer research. In the 1960s, biologists found that normal human fibroblasts, cells derived from **connective tissue**, had a predictable limit in their ability to proliferate in culture. Subsequently, the observation was extended to other normal cell types and species. Furthermore, the number of subcultivations that could be achieved was age related. Cells from young donors were able to divide more times than those isolated from older donors. After extensive research on this phenomenon, in the 1990s it was determined that the telomeres, small segments at the end of human **chromosomes**, become shorter with age both in cultured cells and in cells taken directly from individuals. An enzyme, telomerase, which acts to maintain telomeres, decreased in activity with age. Interestingly, cells engineered to express more telomerase retained telomeres and the ability for extended proliferation. Cancer cell lines, which can grow indefinitely in culture, also retain long telomeres.

Scientists have also learned much about cancer initiation and progression through the use of cells in culture. Normal fibroblasts from mouse embryos generally declined in proliferation rate with subcultivation. After an extended, so-called "crisis" phase, they seemed to recover and eventually returned to active division. However, the chromosome number of the resultant cell population was abnormal. Furthermore, if the cells were subcultivated extensively, they acquired malignant properties characteristic of cancer cells. This change results when normal genes are expressed under inappropriate circumstances. Their products overcome the normal controls of the cell division cycle to allow abnormal proliferation. SEE ALSO CELL CYCLE; CHROMOSOME, EUKARYOTIC

Robert Hay

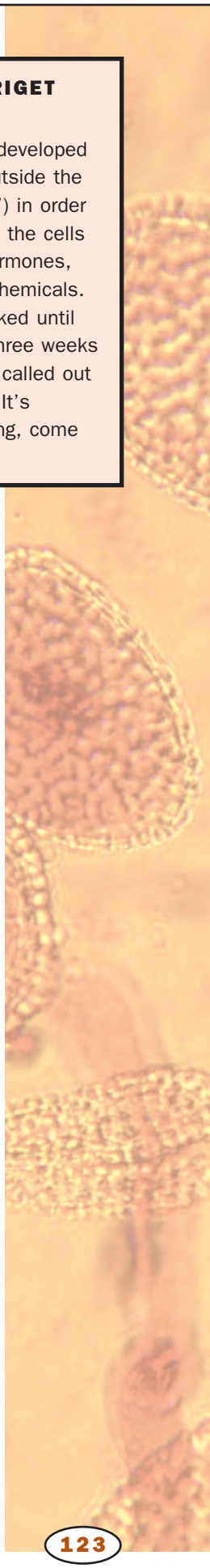
FELL, HONOR BRIGET (1900–1986)

British biologist who developed ways to grow cells outside the body ("tissue culture") in order to more closely study the cells and the effects of hormones, vitamins, and other chemicals. The vigorous Fell worked until the end of her life. Three weeks before she died, she called out from her lab bench, "It's worked, isn't it exciting, come see the results!"

morphology related to shape and form

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

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



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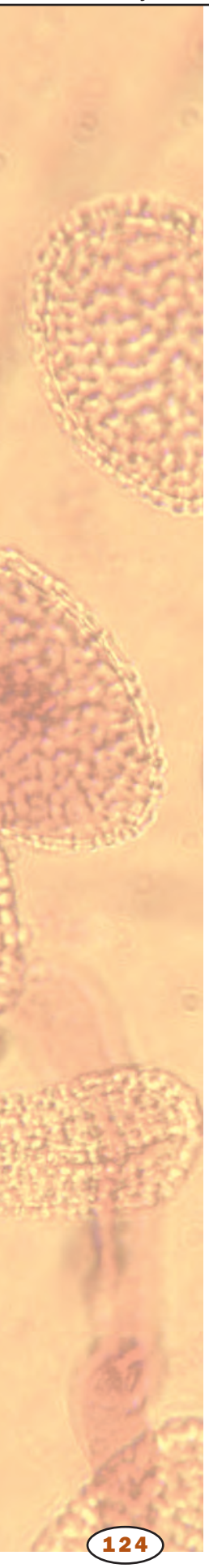


Cell Cycle

The cell cycle is the ordered series of events required for the faithful duplication of one **eukaryotic cells** into two genetically identical daughter cells. In a cell cycle, precise replication of deoxyribonucleic acid (DNA) duplicates each **chromosome**. Subsequently, the duplicated chromosomes separate away from each other by **mitosis**, followed by division of the **cytoplasm**, called cytokinesis.

eukaryotic cell a cell with a nucleus

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

mitosis separation of replicated chromosomes

cytoplasm material in a cell, excluding the nucleus

organelle membrane-bound cell compartment

cytosol fluid portion of a cell, not including the organelles

genome total genetic material in a cell or organism

These monumental transformations in the chromosomes are accompanied by general cell growth, which provides enough material of all sorts (membranes, **organelles**, **cytosol**, nucleoplasm) required for the resultant doubling of cell number. This cycle continues indefinitely in specialized cells called stem cells, found in skin or bone marrow, causing constant replenishment of cells discarded by natural physiological processes.

Repetition of the cell cycle may produce a clone of identical cells, such as a colony of baker's yeast on a petri dish, or it may be accompanied by intricate changes that led to differentiation into distinctive cell types, or ultimately to the development of a complex organism. In all cases, the DNA sequence of each cell's **genome** remains unchanged, but the resultant cellular forms and functions may be quite varied.

Stages of the Cell Cycle

From the viewpoint of chromosomes, four distinct, ordered stages constitute a cell cycle. DNA synthesis (S) and mitosis (M) alternate with one another, separated by two "gap" phases (G_2 and G_1) of preparation and growth. Though a generic cell cycle possesses no definitive starting stage, the term "start" of the cell cycle has nonetheless been given to the initiation of chromosomal DNA replication or synthesis. During S phase, every chromosome replicates to yield two identical sister chromosomes (called **chromatids**) that remain attached at their kinetochores. G_2, a period of apparent chromosomal inactivity, follows S phase. In G_2, cells prepare for the dynamic chromosomal movements of mitosis. In mitosis, the duplicated chromosomes separate into two equal groups through a series of highly coordinated events. First, condensed sister chromatids attach to the mitotic spindle at the center of the cell. The mitotic spindle, a fanlike array of microtubules, mediates the separation of all sister chromatid pairs as the chromatids, now called chromosomes, **synchronously** move to opposite poles of the cell.

chromatid a replicated chromosome before separation from its copy

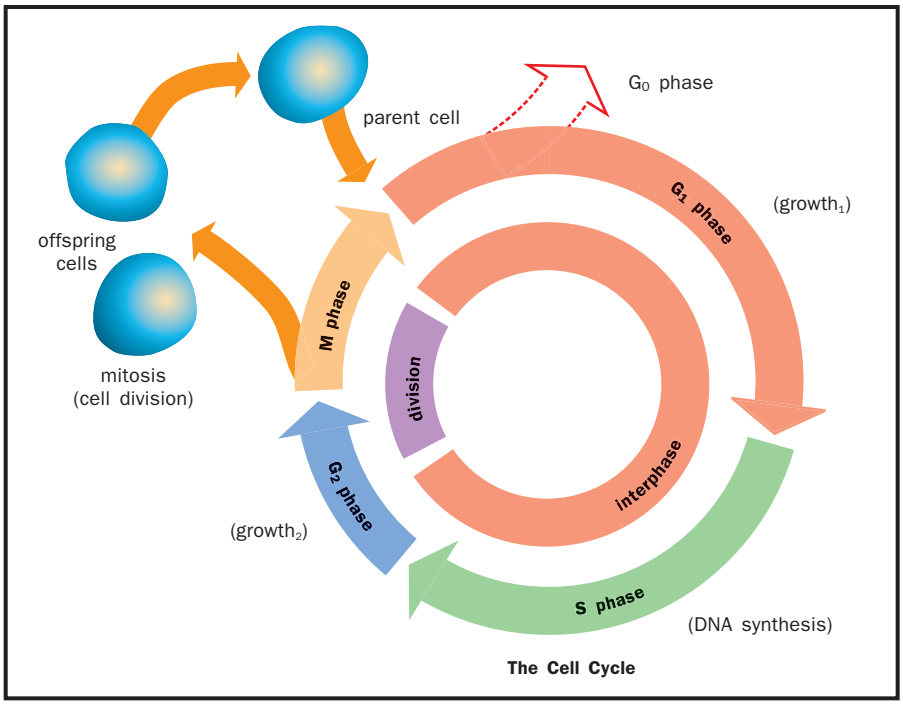
synchronously at the same time

Cytokinesis follows, in which the cytoplasm pinches apart and two new intact daughter cells are formed, each with the correct complement of chromosomes. G_1, a phase of cellular growth and preparation for DNA synthesis, occurs next. Thus a cell cycle proceeds from S to G_2 to M to G_1, and the two new cells' cycles continue to S and onward through the same series of stages. Cells that no longer undergo mitosis are said to be in G_0. Such cells include most **neurons** and mature muscle cells.

neuron nerve cell

Checkpoints

Both internal and external inputs trigger molecular events that regulate normal progress through the stages of the cell cycle. The precisely choreographed movements of chromosomes during mitosis provide one example



The Cell Cycle

Transition between stages is triggered by cyclin-dependent kinases (CDK).

of this intrinsically faithful, careful regulation. The apparent simplicity of the particular alignment, division, and locomotion of chromosomes in each normal cell division belies the many levels of regulation that guarantee such precision. For example, without complete and proper DNA replication, the events of mitosis are not initiated. This control of cell-cycle order is maintained through an **intracellular** "checkpoint" that monitors the integrity and completion of DNA synthesis before authorizing the initiation of mitosis. This S-phase checkpoint responds to various forms of DNA damage, such as single- and double-strand breaks in the DNA backbone or incorporation of unusual **nucleotides**, and halts the progression of the cell cycle until effective repairs have occurred. The S-phase checkpoint also responds to stalled DNA replication forks, making the cell cycle pause until replication is completed. Ted Weinert and Lee Hartwell were the first to report experimental evidence of such a cell-cycle checkpoint in 1988. Since then, checkpoints have been discovered that regulate many aspects of cell-cycle progression in all organisms studied. Initiation of DNA synthesis, assembly and integrity of the mitotic spindle, and chromosome attachment to the mitotic spindle are all regulated by checkpoints. Mutations in checkpoint genes can lead to cancer, because of the resultant deregulation of cell division.

intracellular within a cell

nucleotide the building block of RNA or DNA

Regulation by CDK Proteins

Remarkably, the coordinated transitions between cell cycle stages depend on one family of evolutionarily conserved **proteins**, called cyclin-dependent **kinases**. Cyclin-dependent kinases (CDKs) act as oscillating driving forces to direct the progression of the cell cycle. Each CDK consists of two parts, an **enzyme** known as a kinase and a modifying protein called a cyclin. Kinases are regulatory enzymes that **catalyze** the addition of phosphate groups to protein **substrates**. Adding one or more phosphate groups to a substrate protein can change that substrate's ability to do its cellular job: One partic-

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

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

enzyme protein that controls a reaction in a cell

catalyze aid in the reaction of

substrate the molecule acted on by an enzyme

ular substrate may be inhibited by such a modification, while a different substrate may be activated by the same type of modification. Cyclins, so named because their activity cycles up and down during the cell cycle, restrict the action of their bound kinase to particular substrates. Together, the two integral parts of a CDK target specific cellular proteins for **phosphorylation**, thereby causing changes in cell-cycle progression.

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

Each CDK, consisting of a particular kinase bound by a particular cyclin, directs a critical transition in the cell cycle. For example, one CDK controls the initiation of DNA synthesis, while another CDK controls the onset of mitosis. Inactivation of the mitotic CDK is necessary for a subsequent cell-cycle transition, when cells exit mitosis and proceed to G_1. CDKs are also the ultimate targets of most cell-cycle checkpoint activity. So that all cell-cycle events occur at the proper time during each cell cycle, CDK activity itself is tightly controlled by regulating the activity of every cyclin. Each cyclin is active only periodically during the cell cycle, with its peak of activity limited to the period during which it is needed. Regulated **transcription** of cyclin genes and regulated degradation of cyclin proteins provides this oversight.

transcription messenger RNA formation from a DNA sequence

Extrinsic Controls

In addition to intrinsic controls exerted by CDKs and checkpoints, many external controls affect cell division. Both normal and abnormal cell cycles can be triggered by such extrinsic controls. For example, the **hormone** estrogen affects the development of a wide variety of cell types in women. Estrogen exerts its effects on a receptive cell by binding to a specific receptor protein on the cell's nuclear membrane. By binding to an estrogen receptor, estrogen initiates a cascade of biochemical reactions that lead to changes in the cell-cycle program. Normally, estrogen moves cells out of a resting stage into an active cell cycle.

hormone molecule released by one cell to influence another

In a different context, however, even normal levels of estrogen encourage the growth of some forms of breast cancer. In these cases, estrogen increases the speed with which the cancerous cells complete their cell cycles, leading to more rapid growth of the tumor. The most effective current drug therapies for such breast cancers block the estrogen receptor's estrogen-binding ability, making cells unresponsive to estrogen's proliferation signal. Thus, while estrogen itself does not cause breast cancer, it plays an important role in stimulating the growth of some cancers once they initiate by other mechanisms, such as by an unregulated CDK or a defect in a cell-cycle checkpoint. SEE ALSO CONTROL MECHANISMS; GENETIC CONTROL OF DEVELOPMENT; HORMONES; ONCOGENES AND CANCER CELLS; SIGNALING AND SIGNAL TRANSDUCTION

Wendy E. Raymond

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Cell Division *See Cytokinesis, Mitosis*

Cell Evolution

Approximately 3.5 billion years ago, cellular life emerged on Earth in the form of primitive bacteria. Bacteria or "prokaryotes" organize their genes into a circular chromosome that lies exposed within the fluid environment of the cell. Within a billion years, bacterial cell types had flourished and diversified, evolving numerous ways of extracting energy from the environment. These types included first the fermenting **anaerobic** archaebacteria, then the oxygen-producing photosynthetic cyanobacteria, and finally respiring **aerobic** bacteria able to utilize the new oxygen-rich atmosphere. In addition some bacteria had become **motile**, such as the corkscrew-shaped wriggling spirochetes. All of these bacterial cell types have descendents living today.

Eukaryotes, whose deoxyribonucleic acid (DNA) is sequestered within a separate membrane-bound **nucleus**, first emerged perhaps 2 billion years ago. **Eukaryotic cells** also contain an extensive internal membrane system, a **cytoskeleton**, and different kinds of membrane-bound **organelle**, including **mitochondria** (the "power factories") and, in algae and plants, plastids (sites of photosynthesis). All multicellular life, including plants, animals, and fungi, are composed of eukaryotic cells; some microbes, such as unicellular algae and protozoa, are also eukaryotes. So how did this great diversity of eukaryotic organisms evolve from **prokaryotic** ancestors?

anaerobic without oxygen, or not requiring oxygen

aerobic with oxygen, or requiring it

motile able to move

nucleus membrane-bound portion of cell containing the chromosomes

eukaryotic cell a cell with a nucleus

cytoskeleton internal scaffolding in a cell, composed of protein

organelle membrane-bound cell compartment

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

prokaryotic without a nucleus

endosymbiosis symbiosis in which one partner lives within the other

symbiosis close relationship between two species in which at least one benefits

Serial Endosymbiosis

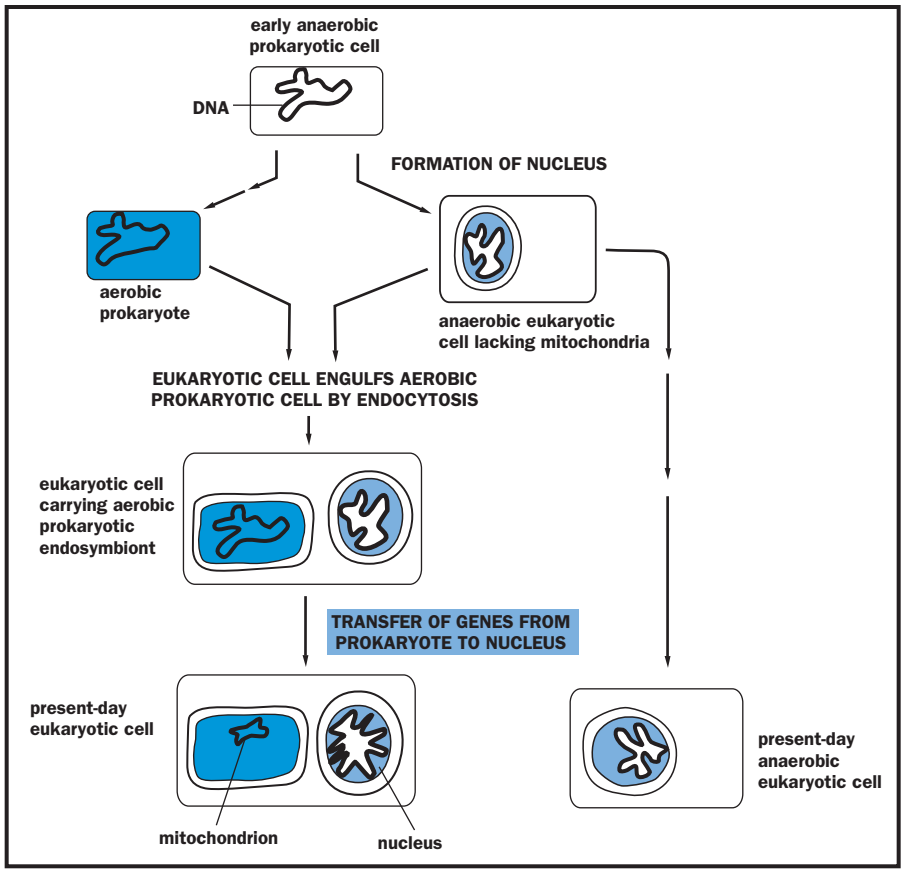
The most widely accepted explanation is known as the Serial **endosymbiosis** theory (SET), articulated and championed by scientist Lynn Margulis. In 1905 Russian scientist Konstantin Merezhkovsky proposed that new organs or organisms could form through **symbiosis** ("the living together of different kinds of organisms"). In the 1920s researcher Ivan Wallin suggested that organelles such as chloroplasts and mitochondria originated as symbiotic bacteria. His theory was rejected by his colleagues, leading him to abandon his laboratory investigations.

However, in 1967 the theory was resuscitated by Margulis to explain observations by geneticists of "cytoplasmic genes," DNA found outside the nucleus. Margulis proposed that cytoplasmic organelles with a bacterial origin were the source of the extranuclear genes. Margulis's SET begins with the merger of an archaebacterium, lacking a rigid cell wall, with motile spirochetes to form the first eukaryotic cell. The archeabacterium's flexible membrane pinched inwards to enclose the DNA within a double-membrane nucleus and the spirochetes provided cytoskeletal support, ultimately giving rise to motile structures known as microtubules.

This new cell type then engulfed an aerobic (needing oxygen) bacterium, which was retained within a membrane vesicle inside the host cell. Over many generations, this new cell component evolved into what scientists now call "mitochondrion" and allowed eukaryotes to thrive in an oxygen-rich environment by harnessing the metabolic capabilities of its newest partner. Over time, many of the proto-mitochondrion's genes were transferred to

MARGULIS, LYNN (1938–)

U.S. biologist famous for her widely accepted theory that a cell is a community of tiny organisms that have evolved to live together. A member of the prestigious National Academy of Science, Margulis has won the National Medal of Science for her outstanding work on "the development, structure, and evolution of living things, for inspiring new research in the biological, climatological, geological, and planetary sciences, and for her extraordinary abilities as a teacher and communicator of science to the public."



Suggested evolutionary pathway for the origin of mitochondria.

the host nucleus, making the mitochondrion dependent upon the host cell for its survival. In a similar fashion, some of these aerobic **nucleated** cells established symbiotic associations with **intracellular** cyanobacteria, leading to the evolution of photosynthetic eukaryotes.

nucleated having a nucleus

intracellular within a cell

The view that the eukaryotic cell evolved from an intimately associated consortium of bacteria initially met with sharp criticism. Some, including Margulis, argued that the discovery that both mitochondria and plastids contain bacteria-like circular chromosomes, the source of the "cytoplasmic genes," was evidence for the bacterial origins of these double-membrane-bound organelles. Others argued, however, that these organelles and their genes originated by pinching off from the nucleus.

Eventually researchers accumulated more and more supporting evidence for the main premise of SET: the symbiotic origin of mitochondria and plastids. The size, gene structure and sequences, biochemistry, and fission-style reproduction of these organelles all imply a closer evolutionary relationship to free-living aerobic bacteria and cyanobacteria than to the "host" archaebacteria-derived cell encoded by genes in the nucleus. The origin of microtubules from spirochete **symbionts**, however, is not as well supported and remains controversial. One of the reasons the theory met with such initial skepticism is that it challenged the prevailing ideas about how evolution occurs: that is, through slow accumulations of changes in vertically transmitted sets of genes, resulting in speciation events in which branches of the tree of life are forever splitting, never joining. SET describes the wholesale

symbionts organisms living in close association with another organism

fusion of two (three, four, or more) **genomes**, a process that joined previously diverging branches into one. SEE ALSO ARCHAEA; CELL; CHLOROPLAST; CYTOSKELETON; EUBACTERIA; MITOCHONDRION

Mary K. Montgomery

genome total genetic material in a cell or organism

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Cell Junctions

Cell junctions can be divided into two types: those that link cells together, also called intercellular junctions (tight, gap, adherens, and desmosomal junctions), and those that link cells to the extracellular **matrix** (focal contacts/adhesion plaques and hemidesmosomes). These junctions play a prominent role in maintaining the integrity of tissues in multicellular organisms and some, if not all of them, are involved in signal **transduction**.

matrix a network, usually of threadlike fibers

transduction conversion of a signal of one type into another type

focal at a point

substrate the molecule acted on by an enzyme

adhesion attachment; sticking to the surface of

cytoplasm material in a cell, excluding the nucleus

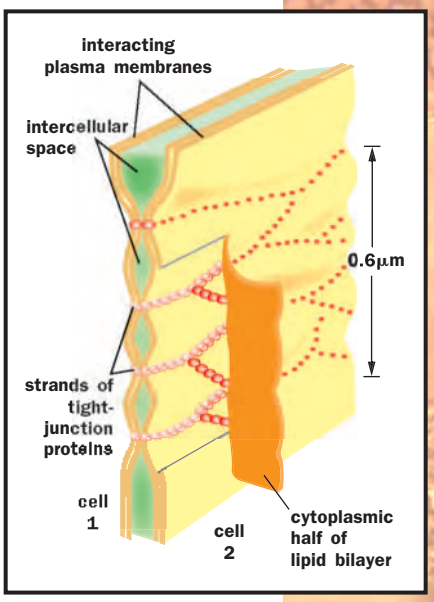
hexamer a structure composed of six parts

Intercellular junctions and hemidesmosomes were first identified in tissues examined by electron microscopy. In contrast, the **focal** contact was first observed in cultured cells in the light microscope by a technique called interference reflection. This procedure revealed specific sites where cells closely adhere to their **substrate**. These were called focal contacts or **adhesion** plaques.

Tight Junctions

The tight junction (also referred to as a zonula occludens) is a site where the membranes of two cells come very close together. In fact, the outer leaflets of the membranes of the contacting cells appear to be fused. Tight junctions, as their name implies, act as a barrier so that materials cannot pass between two interacting cells. The protein components of the tight junction are arranged like beads on a string that span the adjacent membranes of each tight junction.

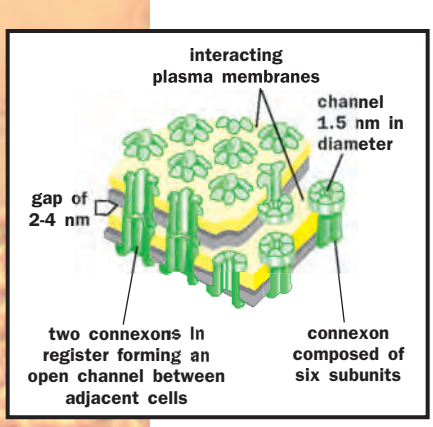
Tight junctions often occur in a belt completely encircling the cell. In a sheet of such cells, material cannot pass from one side of the sheet to the other by squeezing between cells. Instead, it must go through a cell, and hence the cell can regulate its passage. Such an arrangement is found in the gut, to regulate absorption of digested nutrients.



A model of a tight junction. It is thought that the strands that hold adjacent plasma membranes together are formed by continuous strands of transmembrane junctional proteins across the intercellular space, creating a seal.

Gap Junctions

In contrast to the tight junction, there is a channel between the membranes of contacting cells in the gap junction so that the **cytoplasm** of the two is connected. The basic building block of each gap junction is the connexin subunit. Six of these in each of the membranes of two neighboring cells come together, and then the group of six connexins in one cell interact with a comparable **hexamer** in the other cell resulting in the formation of a channel. This channel allows direct cytoplasmic communication among the cells; small molecules of 1,500 daltons or less can pass through the channel of



Model of a gap junction. The lipid bilayers are penetrated by protein assemblies called connexons. Two connexons join across the intercellular space to form a continuous aqueous channel that links the two cells.

each gap junction whose opening or closing can be controlled locally in the cell. Gap junctions unite muscle cells in the heart to help coordinate their contraction.

Adherens Junctions and Focal Contacts

Adherens junctions (sometimes called zonula adherens) are found at sites of cell-cell interaction. Focal contacts mediate association of cells with the extracellular matrix. Both associate with the actin **cytoskeleton** and both are involved in adhesion (sticking cells together or sticking cells to surfaces). Focal contacts possess specific transmembrane receptors of the integrin family that link the cell to the extracellular matrix on the outside of the cell and the microfilament system on the inside. Conversely, members of a family of calcium ion-dependent cell adhesion molecules, called cadherins, mediate attachment between cells at adherens junctions. Adherens junctions and focal contacts not only tether cells together or to the extracellular matrix, but they also **transduce** signals into and out of the cell, influencing a variety of cellular behaviors including proliferation, migration, and differentiation. In fact some protein components of these junctions can shuttle to and from the nucleus where they are thought to play a role in regulating gene expression.

Desmosomes and Hemidesmosomes

Desmosomes (the macula adherens) and hemidesmosomes are distinguished by their association with the **keratin**-based cytoskeleton. Despite their names, desmosomes and hemidesmosomes are distinct at the molecular level. Both are primarily involved in adhesion. The desmosome, like the adherens junction, possesses calcium ion-dependent cell adhesion molecules that interact with similar molecules in the adjacent cell. Meanwhile, **integrins** at the core of the hemidesmosome mediate its interaction with the extracellular matrix. The hemidesmosome and, most likely, the desmosome are also sites of signal transduction. SEE ALSO CYTOSKELETON; EXTRACELLULAR MATRIX; PLASMA MEMBRANE

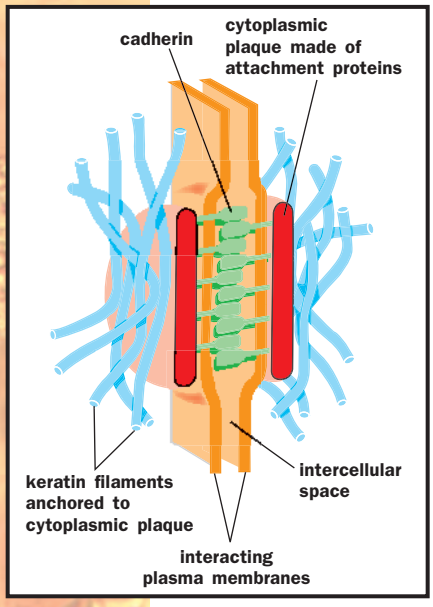
Jonathan Jones

cytoskeleton internal scaffolding in a cell, composed of protein

transduce to convert a signal of one type into another type

keratin a major structural protein

integrins a family of transmembrane linking proteins



Schematic drawing of a desmosome.

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Cell Motility

Cells exhibit a wide range of movement. These movements include migration of cells along a surface or through a tissue, or movement of components within cells. Specific examples of cell motility include:

- movement of cells from one location in an embryo to another during embryonic development
- migration of cells into a wound during wound healing
- contraction of a muscle cell that is the fundamental process responsible for muscle contraction
- separation of a cell into two daughter cells during cell division

- movement of membrane-bound **vesicles** into cells during **phagocytosis** or endocytosis
- movement of membrane-bound vesicle from the cell interior to the cell surface during **secretion**
- movement of **chromosomes** during **mitosis**

The first four bulleted points are examples of cell movement, while the last three bulleted points are examples of "intracellular motility." All of these movements have in common the fact that they are mediated by filamentous structures in the cell called the **cytoskeleton** and are powered by molecular motors that move along these filamentous structures. The simplest example is the movement of membrane-bound vesicles. These vesicles bind to a molecular motor just like a boxcar attaches to a railroad locomotive. The vesicle represents the cargo and the molecular motor represents the locomotive. The molecular motor then moves along the cytoskeletal filament as a locomotive moves along a railroad track. Most forms of **intracellular** movement occur using this mechanism.

A second mechanism is called contraction. This mechanism is responsible for contraction of muscle cells and the separation of daughter cells during cell division. Contraction works through the action of molecular motors pulling on the cytoskeletal filaments, drawing them toward each other. A third mechanism involves the rapid polyermization of the cytoskeleton. In this case the filamentous structures (usually the microfilament cytoskeleton) extend by the addition of subunits to the end. This growth of filaments then pushes out the membrane. This mechanism is responsible for protrusion of the front end of migrating cells.

Moving cells exhibit a special kind of directional movement called "chemotaxis." This mechanism accounts for the ability of cells to migrate in a specific direction. During chemotaxis, cells move in response to an external signal, most frequently a small molecule or short peptide, called a chemoattractant. Cells sense the concentration of the chemical and move in the direction of increasing concentration of the signal. This directional movement is responsible for much of the cell migration required for tissue formation and for wound healing. Wounded cells, for instance, release chemoattractants that attract immune system cells called macrophages and **connective tissue** cells called **fibroblast**.

For most **eukaryotic cells**, the process of cell movement occurs in several coordinated steps. First, cells extend a structure called a pseudopod ("false foot") using the polymerization mechanism. Next the pseudopod makes an attachment to the surface along which the cell is moving. This establishes the new front of the cell. A contraction-mediated process provides the force that moves the rest of the cell toward the front and leads to detachment of the trailing end of the cell. When cells are exhibiting chemotaxis they extend pseudopods in several directions, but only make the attachment to the surface in the direction of the highest concentration of the chemical signal.

In contrast, bacterial cells move by the action of an amazing rotary motor called a bacterial flagellum. This flagellum spins like a propeller propelling the cell forward. Bacteria undergo chemotaxis by a process called

vesicle membrane-bound sac

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

secretion release from the cell

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

mitosis separation of replicated chromosomes

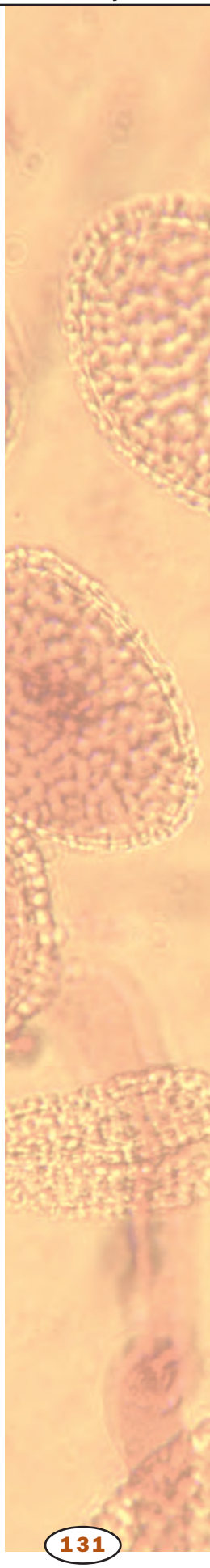
cytoskeleton internal scaffolding in a cell, composed of protein

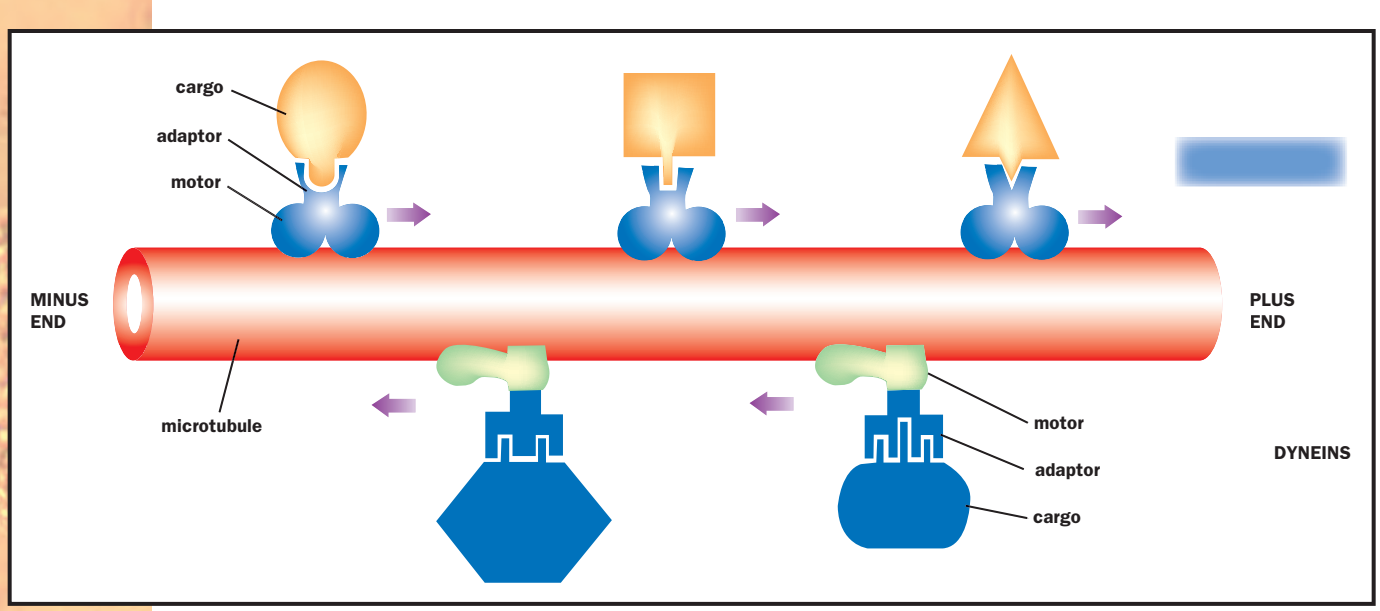
intracellular within a cell

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

fibroblasts undifferentiated cell normally giving rise to connective tissue cells

eukaryotic cell a cell with a nucleus





The motor proteins that move along microtubules. Kinesins move toward the plus end, whereas dyneins move toward the minus end.

"tumble and run." In this process, a bacterial cells tumbles end over end and then "runs," moving in a single (random) direction for a defined period of time. At the end of that period the cell stops, tumbles again, and measures the concentration of the chemoattractant. If the concentration of chemoattractant is higher than at the last sampling the cell runs for an increased distance. If the chemoattractant concentration is lower, the run distance is shortened and the cell tumbles more frequently. Through this biased process cells preferentially migrate in the direction of higher chemoattractants. SEE ALSO CONNECTIVE TISSUE; CYTOKINESIS; CYTOSKELETON; ENDOCYTOSIS; EXOCYTOSIS; IMMUNE RESPONSE; MITOSIS; MUSCLE

Rex L. Chisholm

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matrix a network, usually of threadlike fibers

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

ion an electrically charged particle

Cell Wall

With very few exceptions, all cells are enveloped by an extracellular **matrix** composed of **proteins**, **carbohydrates**, and other substances. Owing to its exceptional strength and its ability to control cell shape, the extracellular matrix of eubacteria, algae, fungi, and plants is called the cell wall. The composition of cell walls varies widely among these kingdoms and the species within them, but the central functions are similar for most organisms.

Cell walls provide rigidity and protection. For multicellular organisms, the cell wall also binds different cells together. Plants use their cell wall as part of their system for maintaining their shape and stiffness. The plant concentrates **ions** and other substances within the cell, which pulls in wa-

ter by **osmosis**. The cell swells, pressing tightly against the cell wall. The swelling increases rigidity, or **turgor**, while the wall keeps the cell from bursting.

Eukaryotic Cell Walls

Eukaryotic organisms, such as algae, fungi, and higher plants, have multilayered cell walls composed in large part of either **cellulose** or **chitin**. Cellulose and chitin are **polysaccharides**, meaning they are composed of many linked sugar molecules. Cellulose is a **polymer** of **glucose**, which contains only carbon, hydrogen, and oxygen, while chitin is a polymer of N-acetylglucosamine, a sugar that contains nitrogen as well. Both cellulose and chitin are linear, unbranched polymers of their respective sugars, and several dozen of these polymers are assembled into large crystal-like cables, called microfibrils, that spool around the cells.

Cellulose microfibrils form the scaffold of all plant cell walls. At least two types of primary walls are found among the species of flowering plants (angiosperms). In the Type I walls of **eudicots** and some monocots, the microfibrils are tethered together by sugars called xyloglucans, and this framework is embedded in a gel of **pectins**, another type of polysaccharide. The pectins establish several of the wall's physical characters, such as electrical charge, density, porosity, **enzyme** and protein distribution, and cell-to-cell **adhesions**. Pectins are used commercially to thicken jellies and jams. The Type II walls of cereal grains and other monocot relatives tether the microfibrils with different sugars, and is relatively pectin-poor. The hardness of wood comes from **lignin**, which is impregnated between the cellulose microfibrils. Lignin is a phenolic compound, chemically related to benzene.

The cell walls of fungi are diverse among the taxonomic groups, but most contain chitin microfibrils embedded in a polysaccharide matrix and covered with a loose coating of additional molecules combining sugars and peptides (amino acid chains). However, the cell walls of the Oomycetes contain cellulose instead of chitin. Different groups of fungi can be distinguished partly by the composition of their cell wall components.

Cellulose forms a substantial part of the microfibrillar framework of most algae, although some contain other polysaccharides instead. These microfibrillar networks are embedded in a thick gel of polysaccharides of immense diversity. Three important classes of algae, the Chlorophyceae (green), Rhodophyceae (red), and Phaeophyceae (brown), can be distinguished to a certain extent based on their polysaccharide constituents. Alginic acid and fucans are found in brown algae, whereas agarose and carrageenan are found predominately in red algae. Several of these polysaccharides are used as thickening and stabilizing agents in a variety of foods.

Bacterial Cell Walls

In eubacteria, the cell wall is composed of one or more layers of a peptidoglycan, called murein. A peptidoglycan is a combination of peptides and sugars. Murein is composed of the sugars N-acetylglucosamine and N-acetylmuramic acid. To murein are linked peptide extensions that are cross-linked to form the netlike wall. The antibiotic penicillin shuts down the enzyme that creates these cross-links, thus preventing bacterial growth.

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

turgor internal pressure

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

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

polysaccharide carbohydrate composed of many individual units of sugar

polymer molecule composed of many similar parts

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

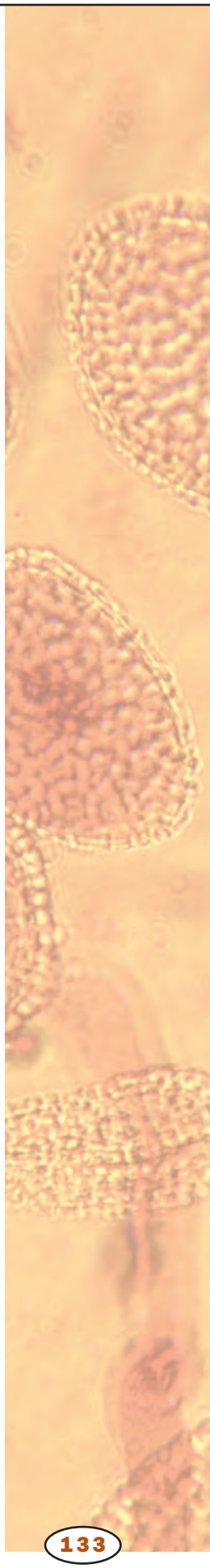
eudicot "true dicot"; plants with two seed leaves that originated from the earliest of flowering plants

pectin carbohydrate in plants that forms crosslinks to stabilize cell walls

enzyme protein that controls a reaction in a cell

adhesion attachment; sticking to the surface of

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



polypeptide chain of amino acids

complex carbohydrates molecules formed by linking simpler carbohydrates such as sugars

Many bacteria produce a capsule to the exterior of the murein wall, composed of a diverse selection of molecules, including **polypeptides** and several **complex carbohydrates,** which may include cellulose. Bacteria with this outer capsule do not absorb a particular dye, called Gram stain, and therefore known as Gram-negative bacteria. Bacteria lacking the outer capsule do absorb the dye and are called Gram-positive bacteria. The Gram stain is a basic tool for identifying bacteria. *Escherichia coli* bacteria in the human large intestine are Gram-negative bacteria.

In contrast to eubacteria, archaea possess a pseudomurein wall, with a different set of sugars, no D-amino acids, and exterior layers of proteins, glycoproteins, and polysaccharides similar to those found in higher organisms. SEE ALSO AMINO ACID; ANGIOSPERMS; ARCHAEA; EUBACTERIA; EXTRACELLULAR MATRIX; FUNGI, PLANT; HOMEOSTASIS; PROTISTA

Nicholas C. Carpita

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Cellular Respiration

See Glycolysis, Krebs Cycle, Oxidative Phosphorylation

Central Nervous System

motor neuron nerve cell that controls a muscle or gland

ventral to toward the belly side

dorsal to to the back of

efferent conducting outward or directing away from

The central nervous system (CNS) consists of a brain and spinal (nerve) cord. Most invertebrates and all vertebrates have sensory and **motor neurons** that are linked by way of a CNS. Most invertebrates have a CNS that is organized into a brain and a longitudinal nerve cord that is **ventral to** the digestive system, whereas chordates have a spinal cord that is hollow and **dorsal to** the digestive system. The CNS processes input from the internal and external environments, integrates information, and controls the body's responses through **efferent** pathways to the body.

The brain is protected by the skull in vertebrates. The head is usually first to make contact with changes in the environment (for example, changes in light through the eyes, sound through the ears, and olfactory encounters through the nose), so it is beneficial to have the information-processing tissues of the nervous system concentrated there.

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

neuron nerve cell

The nerve cord, or spinal cord, serves as a connection between the **peripheral** nerves and the brain. It receives sensory information from the periphery, relays it to the brain for interpretation and feedback, and coordinates many reflexes. It also contains the cell bodies of many of the **neurons** that control the body's glandular and muscular responses by way of the peripheral nervous system. SEE ALSO BRAIN; NERVOUS SYSTEMS; NEURON; PERIPHERAL NERVOUS SYSTEM; SPINAL CORD

Barbara Cocanour

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Chemoreception

The detection of chemicals by smell, taste, or other means is generally known as chemoreception. A phenomenon that occurs widely in nature, chemoreception is found in the simple chemotaxis of a **motile** bacterium toward food as well as the more complex interpretative pathways associated with an animal's ability to smell and taste.

motile able to move

Chemicals detected by chemoreception are small molecules that can readily diffuse through a fluid. Airborne odor molecules must be small enough to become **volatile** (less than 400 molecular mass), and taste molecules are generally soluble in **aqueous** solutions. Detection of a specific molecule occurs on the outer surface of a receptor cell at a plasma membrane **protein** known as chemoreceptor. Generally, a chemoreceptor will detect just a single chemical or a small range of structurally similar chemicals. Detection elicits a series of biochemical changes inside the receptor cell. The response of the receptor cell may signal yet other cells in multicellular organisms such as animals or cause a response unique to the sensing cell.

volatile easily vaporized

aqueous watery or water-based

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

Chemotaxis

Chemoreception that leads to movement of a cell or organism is known as chemotaxis. For example, a simple motile bacterium responds by swimming toward food molecules released by a decomposing organism. In this example of chemoattraction, the bacterium follows an increasing concentration of food molecules to their source. Conversely, the same bacterium might swim away from repellant chemicals released from an unfavorable environment.

In other cases a cell's movement may simply be a change in its shape. For example, in the mating of the single-celled yeast, the nonmotile yeast cells of opposite mating types respond to their mutual detection of **complementary pheromones** by elongating toward each other. Chemotaxis also plays an important role in chemically directed movement of cells during mammalian development and in human immune cells as they migrate toward invading bacteria near the site of an infected wound.

complementary matching opposite

pheromone molecule released by one organism to influence another organism's behavior

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

Smell

The ability to smell odor molecules is known as olfaction. Scientists have estimated that humans can sense over ten thousand different types of smells and that their detection can influence mood, memory, emotions, mate choices, and the immune and **endocrine** systems.

epithelium one of four tissue types found in the body, characterized by thin sheets and usually serving a protective or secretory function

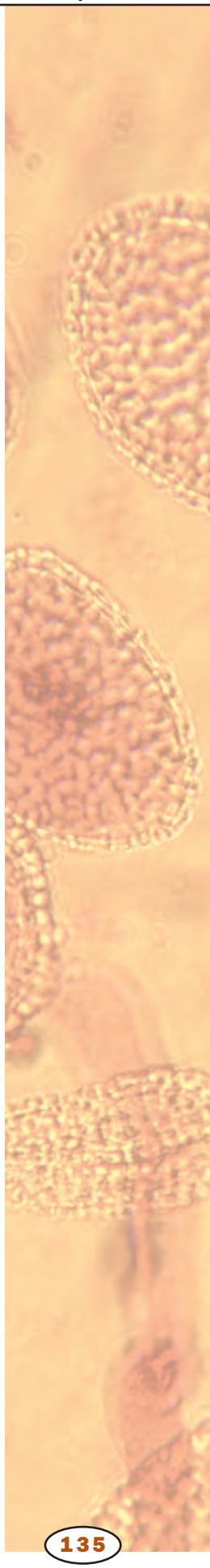
secretion material released from the cell

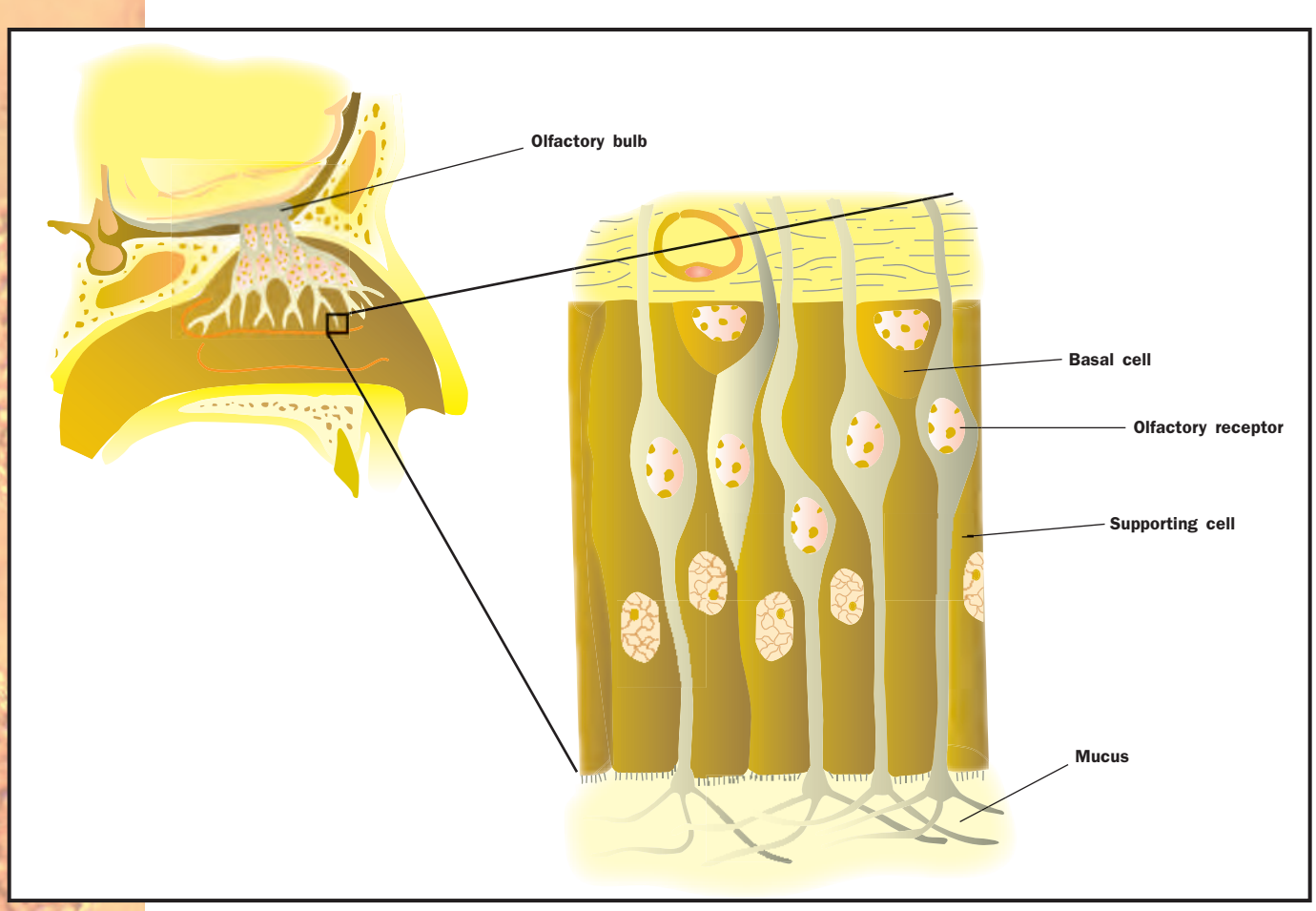
hydrophobic "water hating," such as oils

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

axon long extension of a nerve cell down which information flows

Olfaction begins with the extremely sensitive detection of odor molecules by one or more of the 12 million receptor cells that line the nasal cavity. Covering this olfactory **epithelium** is a mucous **secretion** that may hold some of the more **hydrophobic** odors to be detected. The chemoreceptors of the olfactory receptor cells are located on nonmotile **cilia** projecting into the mucous layer. At the other end of these receptor cells are **axons** that project up through the skull and terminate in the two olfactory bulbs near the front and base of the cerebral hemispheres. From there, olfactory nerve tracts project to the limbic system (an ancient region of the brain concerned





The olfactory epithelium.

with motivation, emotion, and certain kinds of memory) and to the thalamus and then to the frontal cortex for recognition of the odor.

Taste

Gustation is the sense of taste. The tongue is the major organ associated with gustation, and it is the tongue's taste buds that sense the majority of chemicals dissolved in saliva. During gustation receptor cells in taste buds and elsewhere respond and make synaptic contact with **cranial** nerves VII (serving the **anterior** two-thirds of the tongue), IX (serving the **posterior** one-third of the tongue), or X (serving parts other than the tongue, for example, the epiglottis and **pharynx**). From there cranial nerve fibers project to the thalamus and then the primary gustatory cortex in the lower parietal lobe of the cerebrum. It is at this final location that the taste is recognized. Commonly recognized tastes are salty, sweet, bitter, sour, and umami (a meaty taste). The flavor of food and drink, often associated solely with taste, is actually a combination of the gustatory and olfactory processes. SEE ALSO BRAIN; IMMUNE RESPONSE; SIGNALING AND SIGNAL TRANSDUCTION

Michael L. Gleason

cranial related to the cranium, or brain cavity

anterior toward the front

posterior toward the back

pharynx throat

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Chloroplast

Chloroplasts are the source of virtually all of the world's food and fuel and much of its oxygen supply, and as such life on Earth depends on them. They are a vital component of all photosynthetic cells in plants and algae, and are unique to them. What makes them so important is that they are the sites of photosynthesis, from the absorption of light by chlorophyll through to the production of the first simple sugars. It is chlorophyll that gives them their characteristic green color. They are present in all green-colored cells of a plant; not only in leaves, but also in green stems and green parts of a fruit (for example, in an apple peel).

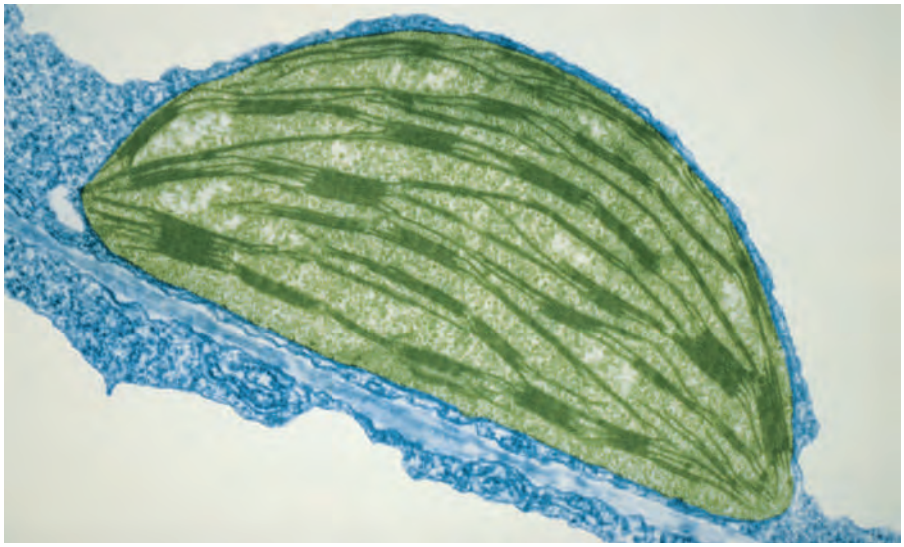
Chloroplasts are approximately 4 to 6 micrometers in diameter and shaped like a satellite dish with the concave face toward the light. This shape, together with their alignment along the inner surface of the cell, maximizes their ability to capture light. Depending on the plant species there can be as many as two hundred chloroplasts in a cell.

A chloroplast is enclosed by two membranes, which together are termed the "envelope." Inside are two distinct features: a complex organization of folded and interconnecting membranes, called the thylakoids, and a **protein**-rich fluid region called the stroma. The proteins and pigments (chlorophyll and carotenoids) involved in the light reactions of photosynthesis are located on the thylakoid membranes. The **enzymes** involved in the conversion of carbon dioxide to simple sugars (the "dark reactions") are found in the stroma. Together these reactions convert carbon dioxide and water to sugars and oxygen.

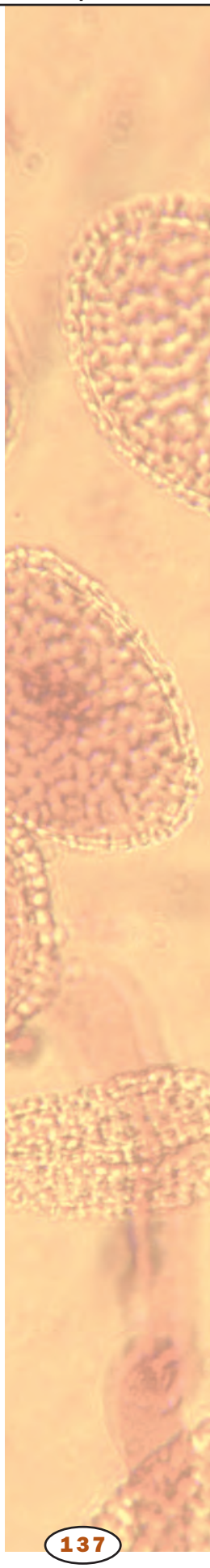
protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

enzyme protein that controls a reaction in a cell

As well as in making sugars, chloroplasts are important in making other essential plant products, such as fats, oils, scents, and proteins. They can



A false-color transmission electron micrograph of a chloroplast from a tobacco leaf.



even make many of the proteins needed to produce another chloroplast. They are thought to have been originally free-living, single-celled photosynthetic bacteria, which became engulfed in a nonphotosynthetic host cell. At first, the two cells lived symbiotically, where each was an individual organism that derived some benefit from the other. Eventually, through evolution, the bacteria lost more and more of their ability to live independently and became the chloroplasts we recognize today.

Many pieces of evidence support the endosymbiotic theory. Chloroplasts, for example, contain deoxyribonucleic acid (DNA), the entire sequence of which has been determined in a number of species. Chloroplast DNA codes for a number of essential chloroplast proteins. Over time, large parts of the DNA of the original bacterium have found their way into the **nucleus** of the host cell, giving it control over many of the functions and features of the chloroplast. **Genes** involved in controlling the division, and hence "reproduction," of the chloroplast are now present in the nucleus. The composition of the DNA and the way in which it is translated resembles that of bacterial cells, adding further support to the endosymbiotic origin of chloroplasts. SEE ALSO CELL EVOLUTION; LEAVES; PHOTOSYNTHESIS

nucleus membrane-bound portion of cell containing the chromosomes

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

Alyson K. Tobin

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Chordata

Chordata is a large and diverse group of animals, with roughly 50,000 living species included. The majority of chordates belong to a group called Vertebrata. Vertebrates have backbones that are composed of vertebrae. Some examples of vertebrates are sharks, fish, dinosaurs, and human beings.

A second group of chordates, called Urochordata, consists of animals found mostly in oceans. Urochordates include sock-shaped pyrosomes that grow up to 10 meters (32.8 feet) long, sack-shaped sea squirts that live attached to the seafloor, and tadpole-shaped larvaceans that build their floating houses out of mucus.

All of these assorted chordates are united because they are descended from a common ancestor that had three features that were passed on to all of its descendants. These three characteristics can be used to distinguish chordates from other animals.

First, chordates have a collection of nerve fibers, called a nerve cord, which runs down their back sides connecting the brain to the organs and muscles. The second characteristic is a notochord, which is a stiffened rod that runs underneath the nerve cord. The notochord is used by many chordates as an aid for swimming. Muscles pull the notochord one way and then it springs back, propelling the chordate forward through the water.

Finally, all chordates have pharyngeal slits, a set of openings behind the head that connect directly to the throat. Some chordates use their pharyngeal slits to filter food out of water sucked in through their mouths. Other chordates have modified pharyngeal slits, called gills, that are used to get oxygen out of water. Human beings, like other land-dwelling chordates, only have pharyngeal slits as an embryo. During a baby's development they are modified into parts of the inner ear. SEE ALSO ANIMALIA; TAXONOMY

Allen G. Collins

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Chromosome Aberrations

Chromosome aberrations are departures from the normal set of chromosomes either for an individual or from a species. They can refer to changes in the number of sets of chromosomes (ploidy), changes in the number of individual chromosomes (somy), or changes in appearance of individual chromosomes through mutation-induced rearrangements. They can be associated with genetic diseases or with species differences.

Trisomy

Chromosome number, size, and shape (X-shaped or V-shaped) are fixed for each species. In most animals, chromosomes are present in pairs, called **homologous** pairs, carrying similar genes. Each chromosome pair carries a distinctive set of genes. Genes code for **proteins**, and the amount of protein produced in a cell from a particular gene is proportional to the number of functional gene copies present.

homologous similar in structure

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

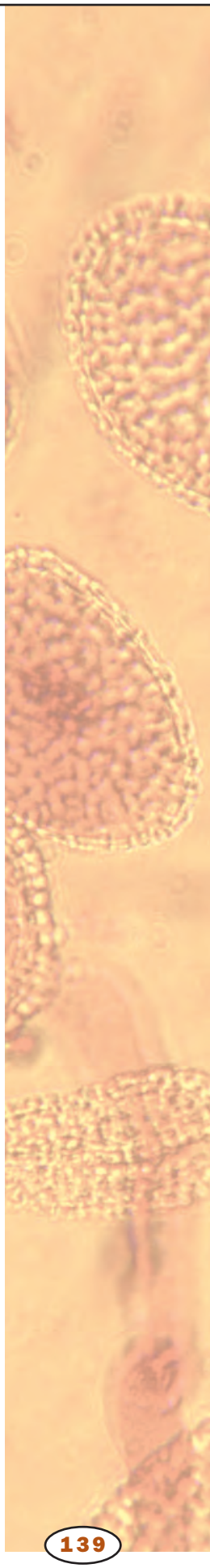
Trisomy refers to having three copies of one chromosome. It arises through the chromosomal accident of nondisjunction during **meiosis**, which sends two copies of a particular chromosome into a sperm or egg, rather than one. An individual with a trisomy who survives to be born produces more of the gene products encoded on the trisomic chromosome. The resulting genic imbalance almost always severely impairs growth. Trisomy of the twenty-first chromosome, the smallest in humans, is the cause of Down syndrome, which is associated with mental retardation, **congenital** heart disease, accelerated aging, and characteristic facial features. Trisomy that occurs after **fertilization**, during fetal development, results in a "mosaic" individual with only some trisomic cells in the body. Such individuals may display some but not all of the features of the syndrome.

meiosis cell division that forms eggs or sperm

congenital present at birth; inherited

fertilization union of sperm and egg

Trisomics for different chromosomes result in different abnormal characteristics. In humans, trisomies 13 and 18 are associated with different birth defects. While these individuals do not live long after birth, trisomies for



any of the other non-sex chromosomes die before birth. Monosomies (having only one copy) for any chromosome also do not survive fetal existence, except for the sex chromosomes X and Y. Sex chromosome trisomies and monosomy for the X chromosome are associated with less severe effects on the **phenotype**.

phenotype observable characteristics of an organism

Translocations

Translocations are the result of a chromosomal-level mutation, with two different (nonhomologous) chromosomes breaking and rejoining, placing the genes from one part of the one chromosome with part of the second chromosome, and vice versa. The number of genes is unchanged. Occasionally, the breakpoint mutation interrupts and inactivates the gene located at that chromosomal site. In other cases, the juxtaposition of new deoxyribonucleic acid (DNA) sequences from the other chromosome next to a gene at the breakpoint results in inappropriate expression. This action may activate an **oncogene**, for example. The "Philadelphia chromosome" is a translocation that fuses parts of chromosomes 9 and 22, which produces a new gene product that functions as an oncogene called Abl, which is implicated in chronic myelogenous leukemia.

oncogene gene that causes cancer

Inherited translocations are passed through generations in a codominant fashion. Since one copy of each chromosome remains normal, both parent and **progeny** with such a translocation are **heterozygous**, or "balanced" carriers. Half their **gametes** will include one copy of each gene, either on the translocated chromosomes or their normal homologs. The other half, however, are unbalanced with some combination of translocated and normal homologs. The result is that the gamete has two copies of some genes, but no copies of other genes, from the translocated chromosomes. Such an "unbalanced" gamete, if it takes part in fertilization, often disrupts development so greatly that the individual does not survive to be born. If the number of unbalanced genes is low, however, children may be born, but often they have growth defects and mental retardation. Couples with recurrent spontaneous abortions may have one partner carrying a balanced translocation. Thus, gene copy number determines the specific phenotypes associated with a translocation, or with any chromosome aberration. Extreme examples of the importance of gene number are triploidy (3n = 69 for humans) and tetraploidy (4n = 92). These individuals nearly always die early in fetal life and are detected only in the remains of early spontaneous abortions. However, intolerance of polypoidy may be a mammalian phenomenon. It is common among plants, and frogs that are triploid are both viable and fertile.

progeny offspring

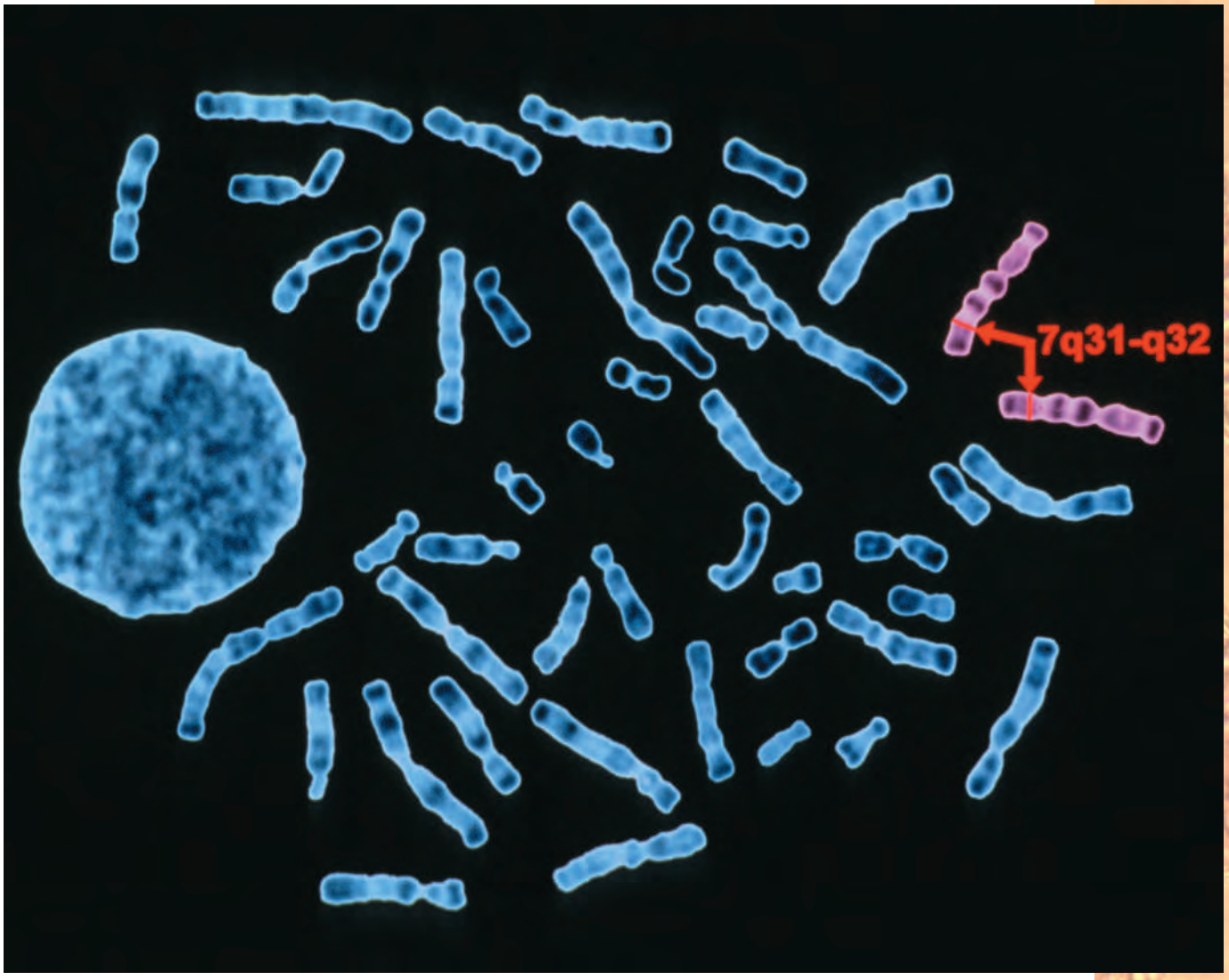
heterozygous characterized by possession of two different forms (alleles) of a particular gene

gamete reproductive cell, such as sperm or egg

Robertsonian translocations are a special class that result from the fusion of two V-shaped chromosomes at their **centromere** ends to form a single X-shaped chromosome. Individuals who are balanced for this translocation have forty-five chromosomes, but are otherwise normal. However, during gamete formation, some gametes will become unbalanced, and their progeny are at risk for being aneuploid (without the correct set of genes). If the two fused chromosomes are homologs, then the risk is 100 percent that the **zygote** will be aneuploid since it will either have too few or too many genes. If nonhomologs are fused, the risk is usually 50 percent. About 5 percent of Down syndrome cases are caused by Robertsonian translocations.

centromere region of the chromosome linking chromatids

zygote fertilized egg



A photomicrograph of human chromosomes showing a mutation on gene 7, which is responsible for cystic fibrosis.

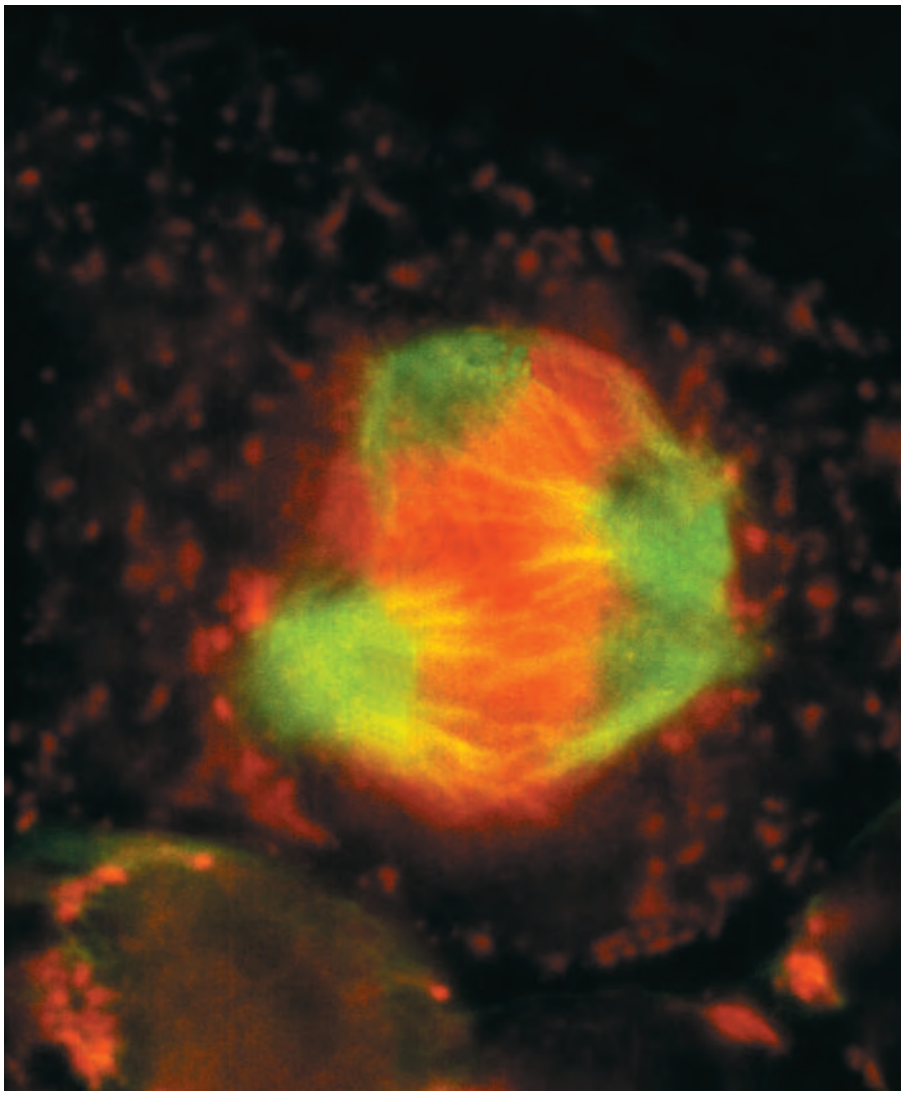
Chromosome fusions or exchanges at the centromere position can often be correlated with differences between closely related species. The great apes (chimpanzees and gorillas) have forty-eight chromosomes, for example. Their chromosome constitution differs from humans only in having one fewer small X-shaped chromosome pair and two additional small V-shaped pairs. At some point in our past, the V-shaped pairs fused at the centromeres to form the X-shaped pairs. Using DNA sequences that are conserved among vertebrate species as position markers, it is possible to create comparative maps of conserved blocks of genes. All mammalian X chromosomes are alike in the genes present, for instance. Thus, changes visible at the chromosome level are useful markers to follow the evolutionary relatedness of different species. Further comparison of conserved sequences suggests the vertebrate **genome** is a tetraploid (four-copy) version of the invertebrate genome.

genome total genetic material in a cell or organism

Polyploidy

Changes in ploidy are of evolutionary importance in the flowering plants (angiosperms). Tetraploid plants often grow faster and larger than the **diploid** plants they derive from, and tend to be selected for agriculture. Alfalfa, cof-

diploid having pairs of chromosomes in the nucleus



A digital image of multipolar and bipolar spindles from T84 colonic cancer cell cultures.

fee, wheat, peanuts, and potatoes are some examples. Commercially grown strawberries are octaploids (eight chromosome sets). Triploid plants, formed by crossing tetraploid with related diploid species, are almost always sterile because their aneuploid seeds abort. Seedless watermelons and bananas are examples of this technique used to improve fruit for human consumption.

An example of plant polyploidy that affected human civilization and history is the origin of wheat. Modern bread wheat, cultivated for about eight thousand years, is a hexaploid with 2n = 42, formed by sequential **hybrids** formed among three related grass species, each with 2n = 14. To complete the circle, modern hybridizers have created a new species, *Triticale*, by crossing the ancestral Emmer wheat (2n = 28) with rye (2n = 14) and then doubling the chromosome number to 42 to take advantage of strong wheat growth with the high **lysine** content of rye. DNA analysis is scrutinizing the hybrid origins of many cultivated plants to identify their ancestors. SEE ALSO ANGIOSPERMS; CHROMOSOME, EUKARYOTIC; GENE; GENETIC DISEASES; MUTATION; ONCOGENES AND CANCER CELLS; PATTERNS OF INHERITANCE

John Merriam

hybrid combination of two different types

lysine an amino acid

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Chromosome, Eukaryotic

The deoxyribonucleic acid (DNA) of eukaryotic cells carries the blueprint for the biosynthesis of cellular **proteins** and the control of cellular assembly and regulation. If all the DNA in a single human cell were stretched out straight and the strands representing all the chromosomes laid end-to-end, they would extend for well over 1 meter (3 feet). This meter of DNA must fit into a **nucleus** whose diameter is on the order of 10 **microns** (10^{-5} meter)! The dual problem of how to store this large amount of **genetic** information but also to keep it accessible for use and for faithful maintenance, copying, and distribution to daughter cells during cell division, is solved by using proteins to package the DNA into chromosomes.

During the **cell cycle**, the cell grows (during G1 phase), replicates its DNA (during S phase), prepares for cell division (during G2 phase), and divides by **mitosis** (during M phase). During M phase, each chromosome is duplicated, and each replica remains attached to its original at the **centromere** portion of the chromosome. The two identical strands, called **chromatids**, wind up and become visible under the microscope at the beginning of mitosis. During the portion of mitosis known as **metaphase**, spindle fibers (which attach to the centromeres) jostle the chromatid pairs to the middle of the cell. The two chromatids are then pulled apart and segregated into different daughter cells, ensuring that each new cell has identical genetic information. The cells then enter G1 phase again. The combination of G1, S, and G2 is known as interphase. During interphase, the genes carried on the chromosomes are **transcribed**, to form proteins needed by the cell.

Various proteins act to stabilize DNA in interphase, while additional proteins are required to condense the chromosomes over a thousandfold to form the compact chromosomes required for mitosis and cell division. The sections that follow summarize key concepts concerning the structure of eukaryotic chromosomes.

Histones and Nucleosomes

Nearly all of the DNA in eukaryotic cells is complexed with a set of small basic proteins called **histones**. (As its name suggests, DNA is acidic, and is attracted to the basic histones.) The complexes form a repeating unit, the nucleosome, which consists of an **octomeric** disc of histones with about two turns of DNA wrapped around the outside. Thus, chromosomal DNA is organized as a string of nucleosome beads with a small amount of DNA connecting each bead. This first level of organization helps to compact the DNA so it can fit into the nucleus while still affording the necessary flexibility to fold the chromosome further; for example, in the **condensation** of chromosomes at metaphase.

The structure of the nucleosome is known at the atomic level through **X-ray crystallography**. The histone proteins interact extensively with one

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

nucleus membrane-bound portion of cell containing the chromosomes

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

genetic of, relating to the portion of DNA that codes for a protein or RNA molecule

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

mitosis separation of replicated chromosomes

centromere region of the chromosome linking chromatids

chromatid a replicated chromosome before separation from its copy

metaphase intermediate stage in cell division, in which chromosomes line up before separating

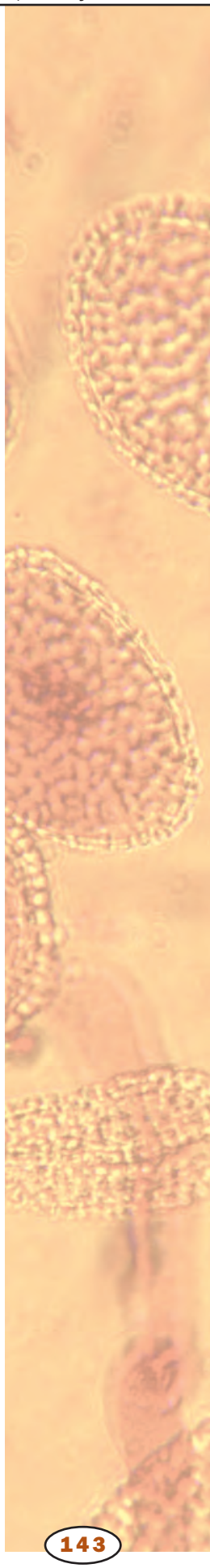
transcribe creation of an RNA copy of a DNA gene

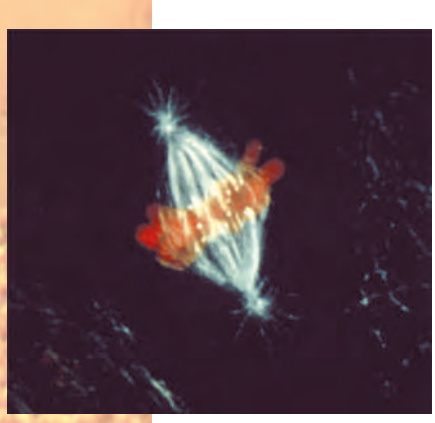
histone protein around which DNA wraps to form chromosomes

octomeric composed of eight parts

condensation compaction of chromosome strands into a tight structure

X-ray crystallography use of X rays to determine the structure of a molecule





An immunofluorescence photomicrograph of the mitosis metaphase in an animal cell.

another to form the compact central disc of the nucleosomes, while specific amino acids have been identified that hold the DNA tightly onto the nucleosome surface. However, about fifteen to twenty-five amino acids at the end of each histone extend outside the compact limits of the central protein core. These tails are invisible in the X-ray structure of the nucleosome, indicating that they are relatively unstructured. (X-ray crystallography can only utilize structures with a high degree of order.) This indicates they can accommodate dynamic interactions with DNA or with adjacent nucleosomes in living chromosomes.

The sequence information encoded in DNA must be accessible to ribonucleic (RNA) polymerases in order to be useful as a **template** for **transcription**. Since the binding of DNA by histones interferes with this access, cells have evolved specific mechanism to destabilize nucleosomes in chromosome regions that must be transcribed. While the details of this important process are still being deciphered, it is clear that there are enzymes in eukaryotic nuclei that can modify nucleosome structure or the structure of individual histones to loosen the histone-DNA contacts, thereby making the DNA available for transcription.

template master copy

transcription messenger RNA formation from a DNA sequence

catalyze aid in the reaction of

acetylation addition of an acetyl group, $CH^{3-}CHOO-$

lysine an amino acid

RNA polymerase enzyme complex that creates RNA from DNA template

promoter DNA sequence to which RNA polymerase binds to begin transcription

One class of enzyme believed to modify nucleosomes for transcription is the histone acetyltransferases, which **catalyze acetylation** of specific **lysines** in the N-terminal tails of histones. Acetylation of lysines reduces the overall positive charge of the histone protein; since DNA has a net negative charge, histone acetylation may reduce the electrostatic forces holding the DNA on the nucleosome. This is thought to make the DNA more accessible to other DNA-binding proteins such as **RNA polymerase**.

In addition, some transcription regulatory proteins bind more easily to their DNA target sites if the nucleosomes associated with those sites are acetylated. A critical part of the transcription activation mechanism in eukaryotic cells appears to be the specific recruitment of nucleosome remodeling enzymes, such as histone acetyltransferases to **promoters**, thus allowing those promoters to be used more efficiently by RNA polymerase. Histone acetylation, therefore, can increase the transcription rate for a gene. Conversely, cells also possess histone deactylases. Histone deacetylases may be specifically recruited to shut off genes when they are no longer required.

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

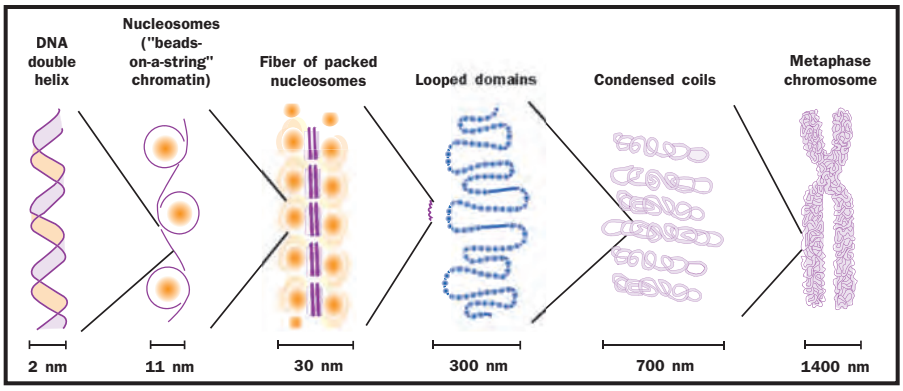
Another type of histone modification is addition of a phosphate group called **phosphorylation**. Phosphorylation typically causes significant changes in protein structure and activity. Increased histone phosphorylation is correlated with chromosome condensation at the onset of mitosis. The mechanism by which phosphorylation promotes condensation is unclear, but may involve nucleosome-nucleosome interactions, or the binding of nonhistone proteins to nucleosomal DNA as part of the folding of chromosomes for metaphase.

30 Nanometer Fiber

genome total genetic material in a cell or organism

solenoid cylindrical coiled structure

The nucleosomal organization of DNA in chromosomes cannot fully account for the degree of compaction necessary to fit the **genome** into the compact nucleus. The nature of these additional levels of DNA folding is controversial, but is believed to include the coiling of nucleosome arrays to form a **solenoidal** structure. Such solenoids have been visualized in elec-



DNA is highly organized and has a structure that allows tight compaction while still allowing access for gene expression.

tron micrographs of eukaryotic chromosomes as fibers of 30 **nanometers** (a nanometer equals one billionth of a meter) in diameter, in contrast to the 10-nanometer diameter of the nucleosome particle itself. In **somatic** nuclei, the 30-nanometer fiber appears to be stabilized by a specific histone, histone H1, which interacts with the DNA-linking adjacent nucleosomes.

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

somatic nonreproductive; not an egg or sperm

Domains and Higher Order Structures

Early electron micrograph images of eukaryotic metaphase chromosomes gave the impression of looped fibers extending out from the central axis of each chromatid. Subsequent analysis by microscopic and biochemical techniques suggests that stretches of chromosome approximately forty thousand to eighty thousand **nucleotide** pairs long may be anchored to a nuclear scaffold or **matrix**. These points of anchorage may serve to organize or spatially restrict chromosomes during interphase. These same anchor points may coalesce at metaphase to condense chromosomes for mitotic segregation.

nucleotide the building block of RNA or DNA

matrix a network, usually of threadlike fibers

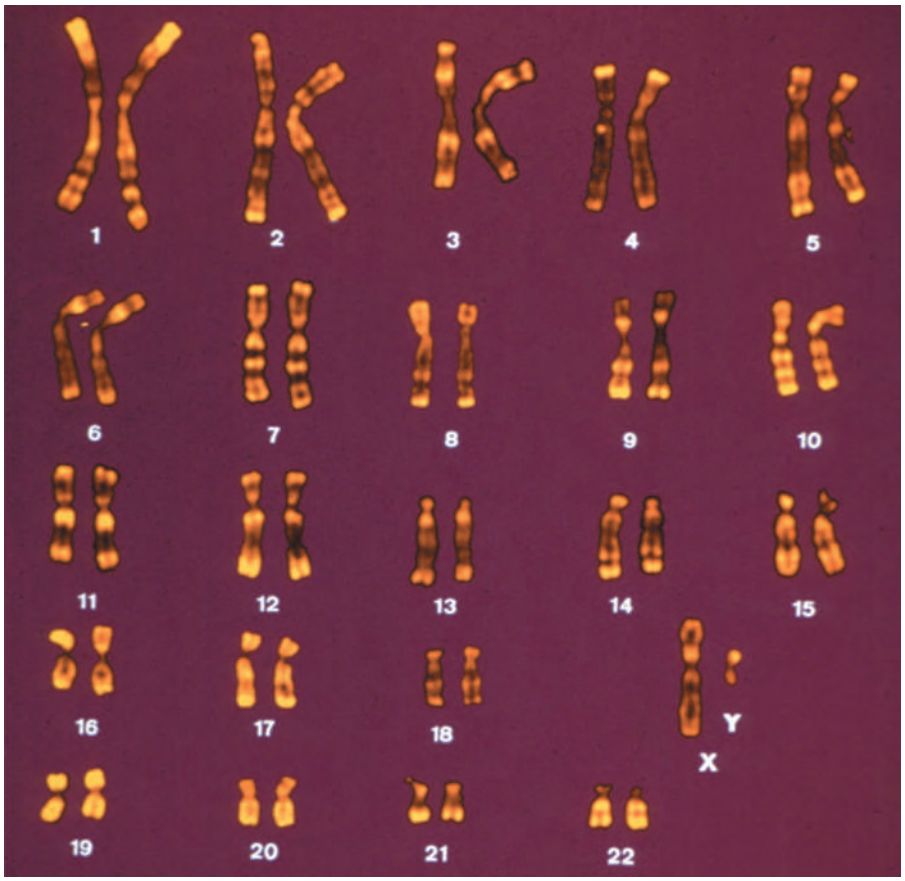
Chromosomes exist to hold genes, of course, and some structural features of the chromosome may serve to separate genes from one another to help regulate transcription. Gene transcription in higher eukaryotes is controlled by regulatory elements that, in some cases, are located hundreds of thousands of nucleotides away from their target promoters. How can such elements be prevented from activating other nearby promoters? Experiments suggest that there are DNA sequences that act as boundaries or barriers to prevent the distant regulatory elements from one gene from contacting the promoters of genes located elsewhere on the same chromosome. In some cases, these genetic domain borders may be equivalent to the nuclear scaffold/matrix anchorage points, but in other cases these activities appear separable.

An average human chromosome contains approximately 240 million base pairs.

Telomeres, Telomerase, and Cancer

In his studies of chromosome structure, geneticist Herman Muller recognized that the natural ends of chromosomes were peculiar in that they could not be placed at internal sites in chromosomes, and that if they were detached (by breakage with **ionizing radiation**), the resulting chromosome behaved abnormally. He recognized the special properties of chromosome ends by giving them a special name: "telomeres." Scientists now know that the ends of chromosomes have a unique structure and are maintained by a unique mechanism.

ionizing radiation high-energy radiation that destroys chemical bonds



A karyotype of human male chromosomes (XY karyotype) with G banding.

The chromosomes of eukaryotic cells are linear DNA molecules. Because of this fact, and because of the mechanics of normal DNA replication by DNA-dependent DNA polymerases, a small amount of DNA at each end of every chromosome fails to be replicated with every cell cycle in somatic cells. If this loss occurred in the **germ line** as well, all eukaryotes would become extinct after a few generations, as important genes located near the chromosome ends would eventually be lost by the gradual chipping away at the ends. The major way that living cells offset this loss is by adding extra DNA onto one strand using a special enzyme for this purpose called "telomerase." Telomerase is a **ribonucleoprotein** complex, consisting of an RNA-dependent DNA polymerase (also known as a **reverse transcriptase**) and an RNA molecule that serves as a template for DNA synthesis, giving rise to the characteristic repeated DNA sequence of most eukaryotic telomeres. (The fruit fly *Drosophila* is a notable exception to this; it uses transposable elements to maintain its telomeres.)

germ line cells creating eggs or sperm

ribonucleoprotein combination of RNA and protein

reverse transcriptase enzyme that copies RNA into DNA

Telomerase activity in **metazoans** is found primarily in germ cells and at low levels in a few somatic tissues (stem cells that give rise to blood and skin cells that have to be replenished constantly throughout adult life). Normal animal somatic cells that are cultured **in vitro** usually lack telomerase activity. Such cells typically can divide only a finite number of times before they stop proliferating, go into a quiescent state, and eventually die, a process called senescence. Sencescence in cultured cells is correlated with loss of telomeric repeats. In general, cancer cells escape senescence and often can proliferate indefinitely in culture; this phenomenon, called immortalization,

metazoans animals other than sponges

in vitro "in glass"; in lab apparatus, rather than within a living organism

is accompanied by the activation of telomerase activity. Although cancer cells are often found to have unusually short telomeres, the length of their telomeres remains stable as the cells continue to proliferate. It is believed that telomerase activation in cancer is essential to continuous tumor growth and **metastasis**. Since most somatic cells have low or undetectable telomerase activity, drugs that specifically inactivate telomerase activity should be potent anticancer drugs with minimal side effects on healthy normal tissue.

metastasis breaking away of cancer cells from a solid tumor to travel elsewhere in the body

Condensation and Decondensation

While chromosomes undergo cycles of condensation and decondensation with entry into and exit from mitosis during the cell cycle, some regions of chromosomes remain condensed throughout most of interphase. This chronically condensed material in the nuclei of all eukaryotic cells was recognized by German cytogeneticist Emil Heitz, who named it "heterochromatin" (in contrast with the "euchromatin," or "true chromatin"), which disperses with the onset of interphase. The regions surrounding most eukaryotic centromeres is composed of heterochromatin.

Heterochromatin is distinguished from euchromatin by other properties. It replicates late in S phase while euchromatin replicates early in S, and it has the ability to silence euchromatic genes. Biochemical analysis shows that the DNA in heterochromatin is less accessible to a variety of DNA-binding proteins, suggesting that heterochromatin condensation inactivates regions of chromosomes by interfering with the accessibility of DNA for transcription. In mammalian females, one X chromosome is inactivated by heterochromatinization. This is thought to ensure that both males (who have only one X) and females (who have two) have equal "doses" of the many genes carried on the X chromosome.

In mealybugs, the entire paternal genome set is inactivated by heterochromatinization early in development, and therefore mealybugs express only maternally derived genes.

Classes of DNA

The chromosomes of higher eukaryotes contain classes of DNA sequences that differ in the number of times they are presented in the genome. Much of the DNA in higher eukaryotes is unique, in the sense that the exact linear sequence of nucleotides is found only once per **haploid** chromosome complement. But some DNA sequences are found in a few dozen or a few hundred identical or nearly identical copies in each haploid chromosome set. These are considered "moderately repetitive" DNA sequences, and in most higher eukaryotes include the genes encoding the histones and the ribosomal RNA (rDNA), as well as certain classes of transposable elements. In the case of the repeated histone and rDNA, having many copies of these genes may be important at certain stages of development to allow biosynthesis of large amounts of histone proteins (during S phase) and ribosomal RNA (during ribosomal synthesis) in a short period of time.

haploid having single, non-paired chromosomes in the nucleus

The third broad class of DNA found in higher eukaryotic chromosomes is represented in many thousands of copies, and is thus termed "highly repetitive." Because of the relative abundance and sequence homogeneity of highly repetitive DNA sequences, they were initially isolated from fragmented eukaryotic DNA as "sattelites" easily separated from the main mass of DNA. This satellite DNA includes tandem arrays—many copies, one right after another—of a 171-nucleotide pair repeat called "alphoid satellite." Alphoid satellite DNA is found in tandem arrays of thousands of copies

Extra X chromosomes, as in XXY males or XXX females, are also condensed, to leave only one active X chromosome.

in the centromeres of all human chromosomes. The alphoid repeats are sufficient to confer centromeric properties on artificial human chromosomes. (The centromere region forms the "pinched waist" so characteristic of metaphase chromosomes, and is the site to which the spindle fibers attach to separate daughter chromatids in mitosis.

The function of other types of highly repetitive sequence DNA is unknown; indeed, some repetitive DNA sequences are thought to be "junk DNA," present in chromosomes simply because there is no evolutionarily efficient way to eliminate it. Approximately 500,000 copies of a 300-nucleotide-pair sequence called an "Alu sequence" are found in the human genome. Unlike the alphoid satellite, Alu sequences are interspersed throughout all human chromosomes. Alu sequences are **homologous** to portions of the 7SL RNA, a structural component of the signal recognition particle that targets **ribosomes** to the **endoplasmic reticulum**. Alu sequences are probably relics of **reverse transcription** of this RNA into 7SL DNA, which then recombined randomly into chromosomes. Such dispersed repeated DNA sequences are potential sites for **homologous recombination**, not only between noncorresponding positions on the same chromosome or on different chromosomes. Indeed, recombination between Alu elements is probably responsible for some deletion or rearrangement of mutations leading to inherited human diseases, since Alu sequences are often found at deletion/rearrangement breakpoints.

homologous similar in structure

ribosome protein-RNA complex in cells that synthesizes protein

endoplasmic reticulum network of membranes within the cell

reverse transcription creation of DNA from an RNA template

homologous recombination exchange of DNA segments between chromosomes

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

Throughout all chromosomes of all living organisms, short, simple sequence repeats may be found. For example, short stretches of guanosine-cytosine **base pairs**, alternating adenosine-thymidine and cytosine-guanosine, occur randomly, both within and outside of protein-coding sequences, and are sometimes referred to as "microsatellite repeats." In such regions, there is a higher tendency for the DNA polymerase to make errors by skipping a nucleotide or adding a couple of nucleotides. Such errors create sites of mismatched bases, which could lead to mutation—and cancer—if they are inherited by daughter cells after cell division. Most living cells have a way of detecting and correcting such mismatches shortly after they occur, using a mechanism termed "mismatch repair." Patients that lack one of the components of the mismatch repair machinery have a much higher chance of being victims of certain types of cancers.

Hereditary nonpolyposis colon cancer is associated with defects in mismatch repair.

Identifying Chromosomes

Numbers and sizes of chromosomes vary widely in eukaryotes, and neither correlates with genome size. The classification of chromosomes within a given species was made possible initially by the used of stains that revealed variation in the DNA sequence composition along the length of the chromosome, resulting in a banded staining pattern characteristic for each chromosome. Using the criteria of overall chromosome length, relative centromere position and banding pattern, chromosomes of any species can be identified as a characteristic ordered set called a karyotype. With advent of **molecular hybridization** and extensive molecular cloning of unique-sequence DNAs, DNA sets representing sequences unique to individual chromosomes have been identified. By coupling the cloned DNA to fluorescent dyes and hybridizing the fluorescently labeled DNA directly to chromosomal preparations or whole cells, fluorescent *in situ* hybridization

molecular hybridization base-pairing among DNAs or RNAs of different origins

(FISH) enables rapid, efficient, and reliable identification of whole chromosomes or chromosome fragments. FISH has found widespread clinical application in the identification of chromosome rearrangements underlying inherited disease and many tumors.

Cytosine Methylation and Gene Regulation

When cellular DNA is first replicated, it consists of four nucleotide subunits: deoxyadenosine, deoxycytidine, deoxyguanosine, and thymidine. Following DNA replication, though, chemical modifications can occur to DNA. One of the most commonly encountered modifications found in the DNA of mammalian cells is the **methylation** of cytidine at carbon number 5 of the cytosine base. In human cells, about 3 to 5 percent of the cytosines are so methylated. The distribution of methylated sites is not uniform, but occurs only at cytosine residues that precede a guanosine (so-called CpG motifs, where the "p" symbolizes the intervening phosphate in the sugar-phosphate DNA backbone). Clusters of CpG dinucleotides—called CpG islands—preferentially occur near the promoters of many mammalian genes. When the cytosines in such islands are extensively methylated, the gene associated with that island is usually found to be transcriptionally silent. Thus, cytosine methylation is inversely correlated with **gene expression**. The mechanism of methylation-dependent silencing involves proteins that specifically recognize and bind to methylated DNA

Rett syndrome is a rare genetic disorder resulting from defects in a methylcytosine-binding protein, MeCP2. Rett syndrome affects girls, and causes slowed development, mutism, and seizures.

methylation addition of the methyl group CH_3

gene expression use of a gene to create the corresponding protein

Cytosine methylation is also found in plants, where it is also inversely correlated with gene activity. Interestingly, many fungi and insects have no detectable DNA methylation at all, yet they seem to be able to regulate their genes adequately. One theory is that DNA methylation arose in evolution as a secondary mechanism to ensure faithful gene silencing in organisms that undergo many cell divisions in development between **fertilization** and adulthood. It may also have evolved to inactivate certain types of viruses. SEE ALSO CELL CYCLE; CHROMOSOME ABERRATIONS; CONTROL OF GENE EXPRESSION; DNA; GENE; NUCLEOTIDES; ONCOGENES AND CANCER CELLS; SEX CHROMOSOMES; TRANSPOSON

fertilization union of sperm and egg

Joel C. Eissenberg

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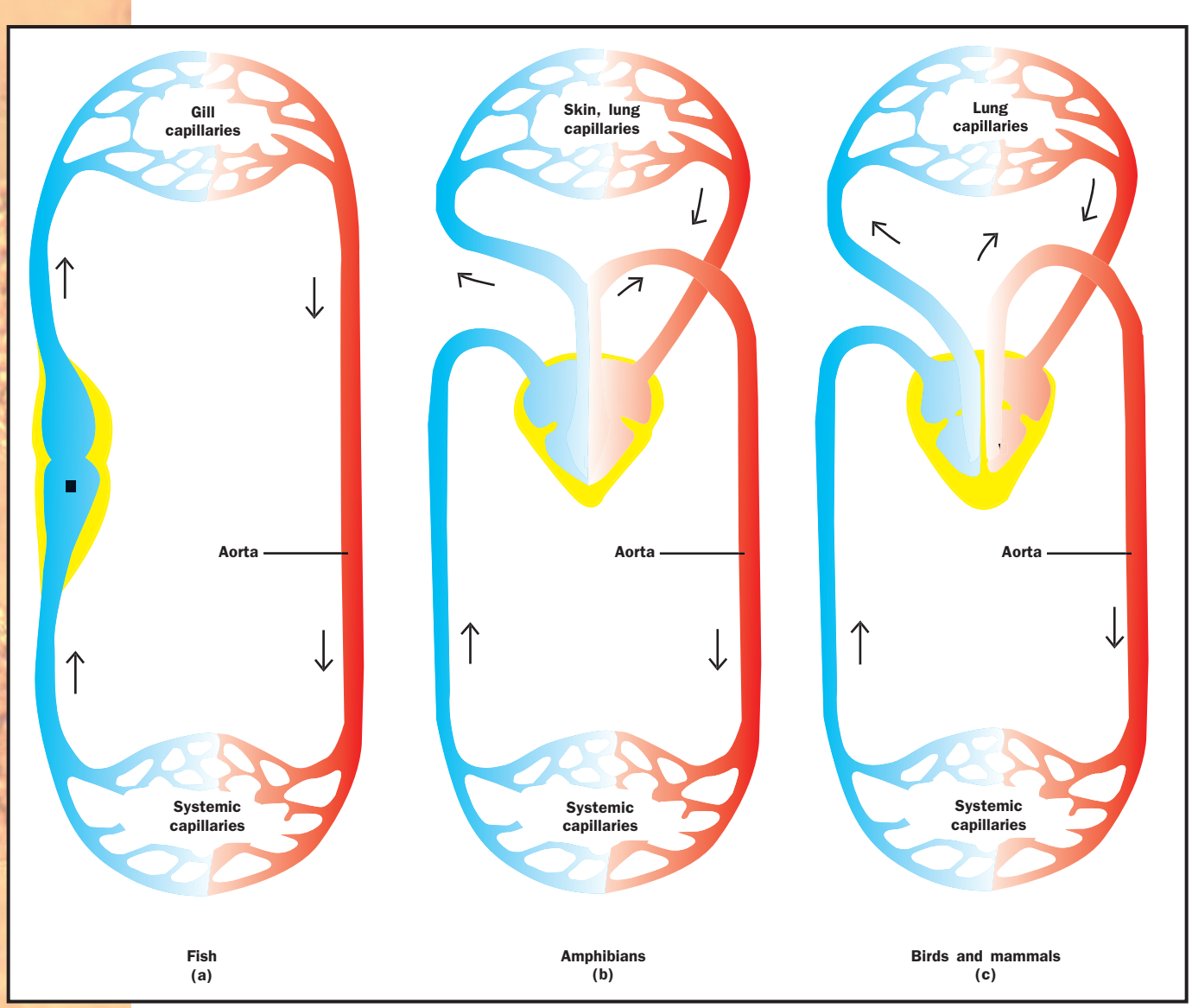
Circulatory Systems

Animal circulatory systems consist of a blood or a bloodlike fluid, a system of tubular blood vessels, and one or more pulsating hearts that pump the blood through the vessels. Animals that are only a few cell layers thick do not need or possess circulatory systems, because they can rely on diffusion through the body surface to exchange materials with the environment. Larger animals, however, require a circulatory system to transport nutrients



Vertebrate circulatory systems. Oxygen-rich blood is shown as red and oxygen-poor blood as blue. (a) In fish, the heart has one atrium (A) and one ventricle (V). Blood oxygenated in the gill capillaries flows directly to the capillaries of the systemic circulation without first returning to the heart. (b) In amphibians, the single atrium is divided into two separate chambers. Oxygen-rich blood from the lungs enters one atrium, and oxygen-poor blood enters the other. Oxygen-rich blood is pumped from one ventricle to the body tissues, while oxygen-poor blood is sent from the lungs to the skin, which is a major respiratory organ in amphibians. (c) In birds and mammals, the atrium and ventricle are divided into two separate chambers, forming two hearts. One pumps oxygen-rich blood through the body, and one pumps oxygen-poor blood through the lungs.

hormone molecule released by one cell to influence another

and oxygen to their tissues, remove wastes, transport **hormones**, equalize body temperature, and maintain homeostasis.

Circulatory systems are classified as open or closed. In an open circulatory system, the heart pumps a fluid through arteries that empty into a large space, the hemocoel. The fluid bathes the organs in the hemocoel, and returns through veins to the heart. Since there is no distinction between blood and tissue fluid in such a system, the fluid is called hemolymph. Open circulatory systems are found in most mollusks and **arthropods**.

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

In a closed circulatory system, blood never leaves the blood vessels, and is thus separated from the tissue fluid. Blood flows away from the heart by

way of arteries and returns to the heart by way of veins. Arteries are connected to veins by tiny, thin-walled capillaries. Arteries and veins have a wall made of elastic and muscular tissue, and an inner lining of thin **epithelium** called endothelium. Capillaries are made of endothelium only. This thin wall allows for exchange of substances between the blood and tissue fluid.

epithelium one of four tissue types found in the body, characterized by thin sheets and usually serving a protective or secretory function

Closed systems have a relatively high blood pressure. This enables nutrients and oxygen to be delivered quickly to their tissues and supports the high metabolic rate associated with the relatively high mobility of some animals. Squids, for example, have closed circulatory systems with three hearts, one to serve each gill and one for the rest of the body. Earthworms, although not highly mobile, have a closed circulatory system with five pairs of hearts.

Vertebrates independently evolved closed circulatory systems in close association with the respiratory systems. In fish, blood flows from the heart to the gills for gas exchange, then to the rest of the body, and finally back to the heart. This is called a single circulation since the blood flows through the heart only once during each complete trip around the body. Amphibians evolved a double circulation; blood flows from the heart to the gills or lungs for gas exchange, then back to the heart to be repressurized before flowing to the rest of the body. The vessels that serve the respiratory organs are called the branchial circuit (for gills) or pulmonary circuit (for lungs). Vessels that serve the rest of the body are called the **systemic** circuit.

systemic throughout the body

The amphibian heart and most reptilian hearts have only three chambers—two **atria** and one **ventricle**—and there is some mixing of oxygen-rich and oxygen-poor blood in the single ventricle. **Endothermic** vertebrates, the birds and mammals, have higher metabolic rates and require stricter separation of the pulmonary and systemic blood. Thus, they have four-chambered hearts. Oxygen-rich blood flows through the other ventricle to the systemic circuit. SEE ALSO ARTHROPODS; BLOOD; BLOOD VESSELS; HEART AND CIRCULATION; TISSUE

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

ventricle fluid-filled chamber

endothermic characterized by regulation of body temperature through metabolic activity

Barbara Cocanour

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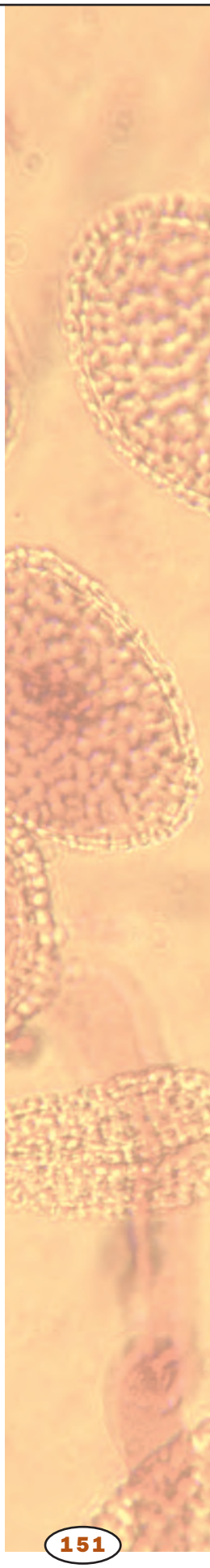
Clinical Trials

A clinical trial is a prospective study of the effectiveness of a new treatment, such as a drug, surgical technique, or medical device. The term prospective indicates that there is a well-defined starting point from which the subjects are tracked for some definite period of time. Before a clinical trial is conducted, laboratory experimentation and animal trials on the proposed treatment is performed.

Clinical trials must meet strict government guidelines established by the U. S. Food and Drug Administration (FDA) to assure the safety of subjects and the scientific validity of the trial. Prior to admission to a clinical trial, subjects must meet the study requirements and be sufficiently informed re-



garding the purpose of the trial. A new treatment may have major benefits but may also have significant side effects for the type of patient that it could help. Careful screening and examination help select persons who meet the trial's design and intent. Informed consent, required of all participants, will alert the subjects not only to the purpose and design of trial with its potential benefits but to any known or suspected side effects or complications.

A phase I trial is a small-scale test in healthy volunteers to determine the general safety of the treatment with human subjects. Phase II tests the safety and effectiveness of the new treatment in a small group of patients who might benefit. A phase III trial is a large-scale study to scientifically document the value of the proposed drug, technique, or device. Phase IV studies allow the long-term follow-up of patients to determine side effects and continued effectiveness after a treatment reaches the market.

The expense involved in clinical trials is due to the extensive development and research costs, initial laboratory testing, and their large-scale nature. Conducted at multiple sites around the country, clinical trials have significant infrastructure for record-keeping, follow-up, dissemination, and safety.

Craig Clifford

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Clone

The word "clone" has several different meanings in biology. As a noun, a clone is an identical genetic copy of either a piece of deoxyribonucleic acid (DNA), a cell, or a whole organism. Identical twins are clones, as are two daughter cells produced by **mitosis**. As a verb, "to clone" means to produce identical genetic copies of either pieces of DNA, cells, or whole organisms.

mitosis separation of replicated chromosomes

Cloning DNA

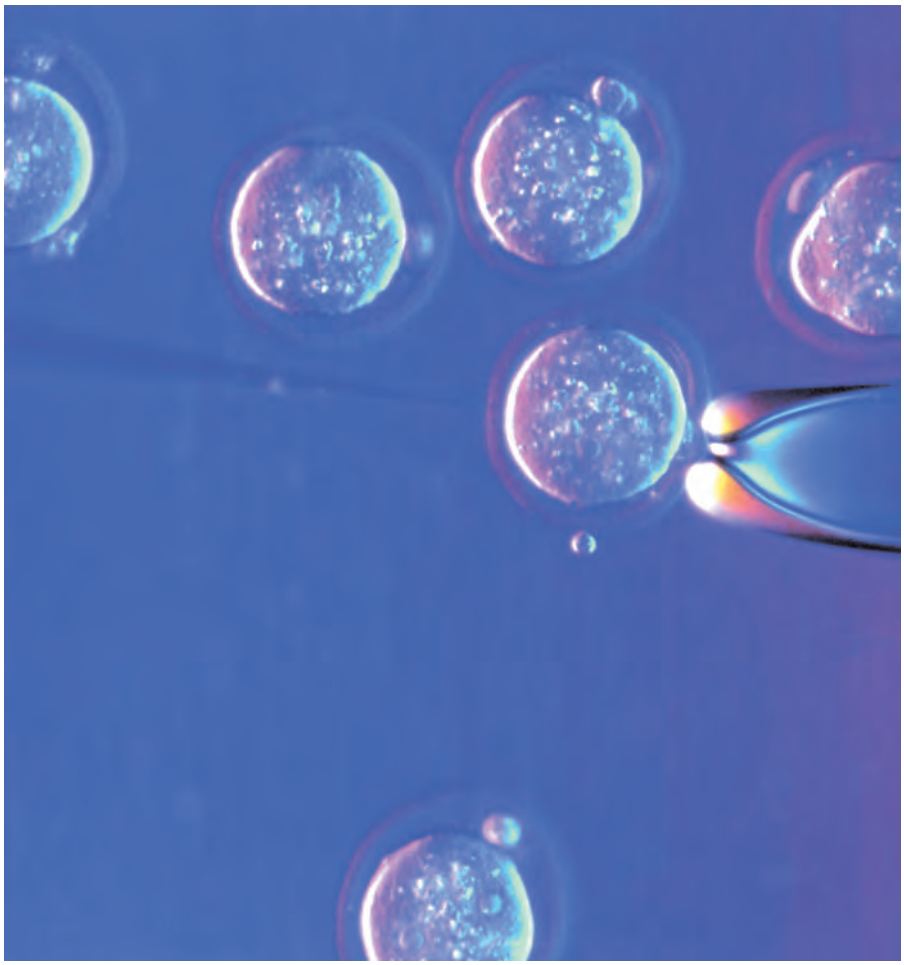
DNA cloning is usually performed for one of two reasons: either to produce a lot of identical DNA for further study, or to use the DNA in an intact organism to produce useful **proteins**. In the first case, for example, a researcher might want to determine the DNA sequence of the gene or study the factors that control its expression (transcription). In the second case, one might want to produce large amounts of a medically useful protein, such as insulin or growth **hormone**.

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

hormone molecule released by one cell to influence another

Large quantities of identical DNA can be produced via the polymerase chain reaction (PCR), but only if the DNA pieces are rather short (less than about 40 **kilobases** [kb], and usually closer to 1 kb). For larger pieces, or for protein production, DNA is almost always cloned in bacteria.

kilobase one thousand DNA bases; a measure of size of a piece of DNA



A micro injection of foreign genes into animal cells. Similar techniques are used to insert an entire nucleus into a host egg cell.

Techniques for cloning change rapidly, but the overall picture is as follows, using the insulin gene as an example:

- Isolate and purify all the DNA from a sample of human cells. Break apart the cells and then wash, centrifuge, and use other purification techniques.
- Cut the DNA into millions of small fragments using **restriction enzymes**. Each DNA piece may be as large as 10 kb, but is more commonly 1 to 5 kb.
- Mix the DNA fragments with **plasmids** that have been cut with the same restriction enzymes. Add DNA ligase, an **enzyme** that joins the human DNA fragments to the plasmids and seals the circles up again. By using the right ratio of plasmid to fragment, a researcher can ensure that each plasmid harbors at most one human DNA fragment. With luck, one DNA fragment will contain the insulin gene.
- Cause a bacterial culture to take up the plasmids. This can be done by ionic shock. Again, adjusting the ratio can ensure one plasmid per bacterium. The plasmid used usually carries a gene for antibiotic resistance.
- Grow the bacteria on antibiotic-containing **agar** plates, spread very thinly. The antibiotic will kill bacteria that didn't take up the plas-

restriction enzyme enzyme that cuts DNA at a particular sequence

plasmid small ring of DNA found in many bacteria

enzyme protein that controls a reaction in a cell

agar gel derived from algae

mid. Single bacteria give rise to colonies, which will appear as small spots on the plate. The resulting bacterial colonies are called a genomic library.

- To find which of the colonies includes the human insulin gene, use a probe. This is typically a radioactive segment of DNA whose sequence is **complementary** to part of the insulin gene, allowing it to bind. Apply the probe, and see where it sticks.
- Isolate that colony, and let it multiply in a rich broth. Each bacterium will replicate the insulin gene, providing many copies to work with. Including the appropriate **promoters** and other regulatory factors will prompt the bacteria to synthesize the human insulin protein, which can then be purified for medical use.

complementary matching opposite

promoter DNA sequence to which RNA polymerase binds to begin transcription

Several modifications of this technique allow cloning of even larger DNA fragments. Cloning into the bacterial virus bacteriophage **λ** allows use of fragments up to about 20 kb. In this scheme, the bacteriophage infects cultured bacteria and directs production of the gene of interest. Cosmid **vectors** can package about 44 kb. These are plasmids containing special sequences from bacteriophage (λ) that promote very efficient sealing of the plasmid circle. Bacterial artificial **chromosomes** (BACs) can contain up to 300 kb, and yeast artificial chromosomes (YACs), grown in yeast cells, can handle up to 2,000 kb, or 2 megabases.

λ the Greek letter lambda

vector carrier

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

nucleus membrane-bound portion of cell containing the chromosomes

genome total genetic material in a cell or organism

Cloning an Animal

Since the **nucleus** of virtually every animal cell contains the entire **genome** of the animal, it might seem easy enough to clone an animal by placing the nucleus in an egg cell from which the nucleus has been removed. While this was tried many times, it was never successfully accomplished until 1996, in the creation of the sheep Dolly by Ian Wilmut and colleagues in Scotland. Dolly was the first mammal created using the nucleus from a cell of a mature adult mammal. Prior to this feat, it had been thought that normal mammalian development caused irreversible changes in some portion of the DNA that prevented it from acting as embryonic DNA does.

Amphibians have long been cloned from adult cells, but they invariably die in the tadpole stage. Adult amphibians, though, have been successfully cloned for many years from embryo nuclei. In this technique, nuclei from cells of an early embryo are extracted using a very fine glass **pipette** and placed in egg cells that have been shed by a female amphibian such as a frog (after removing the unfertilized egg cell nucleus). In 1998, mice were cloned from adult **somatic** cell nuclei, using the same technique as was used for Dolly. This technique may become especially important for producing large numbers of **transgenic** animals, for use in research or production of specialized proteins. However, cloned mammals are generally not very healthy. Apparently development is not quite normal when it begins with a nucleus that has already existed in another animal, compared to a genome derived from a sperm and an egg. SEE ALSO Bacterial Viruses; Genetic Control of Development; Polymerase Chain Reaction; Reproductive Technology

Richard Robinson

pipette lab instrument for precise measurement and transfer of small volumes of liquids

somatic nonreproductive; not an egg or sperm

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

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Cnidarian

The Cnidaria (pronounced ny-DARE-ee-ah) are a **phylum** of simple animals including the hydras, jellyfish, sea anemones, and corals. Any swimmer who has suffered a jellyfish sting has painfully encountered the feature for which the phylum is named: the venomous, stinging **organelles** called nematocysts or cnidae (pronounced NID-ee). Nematocysts are used for defense and to sting and paralyze prey, ranging from **plankton** to fish.

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

organelle membrane-bound cell compartment

plankton microscopic floating organisms

Cnidarians have a simple body plan with two epithelial cell layers: the epidermis and gastrodermis, separated by a gelatinous mesoglea ("middle glue"). The mesoglea ranges from a thin, gluelike layer in the freshwater hydras to a thick, gelatinous layer in the jellyfish. The simple body wall encloses a water-filled space, the gastrovascular cavity, responsible for the digestion of food and the distribution of digested nutrients.

Many cnidaria have a life cycle that alternates between a **sessile** polyp stage and a swimming medusa. The polyp may consist of a single stalklike body, attached to the **substrate** below and with a mouth surrounded by a ring of tentacles above; or it may be a branching colony, easily mistaken for a plant until one looks at it under the microscope. The medusa (jellyfish) is typically umbrella shaped, with a mouth-bearing stalk where the handle of the umbrella would be, and stinging, nematocyst-laden tentacles around the margin. Hydras, corals, and sea anemones, however, have only the hydroid stage, and some medusae have no polyp stage in the life cycle. SEE ALSO ANIMALIA; CORAL REEF; OCEAN ECOSYSTEMS; PLANKTON

sessile attached and remaining in one place

substrate surface for attachment

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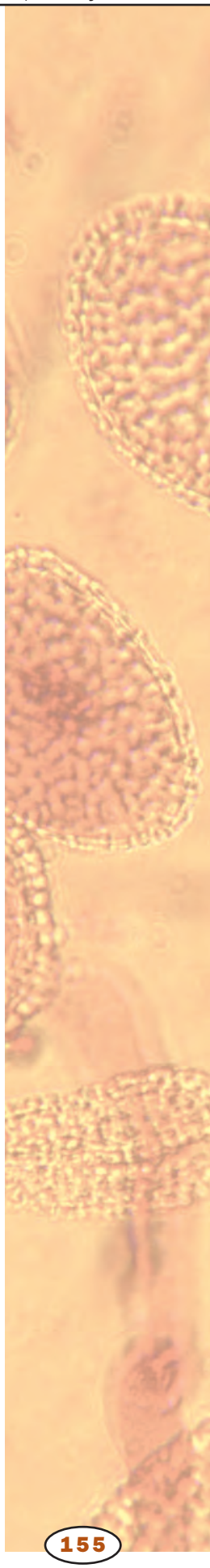
Coffee, Botany of

Coffee is made from the bean of the coffee plant, *Coffea arabica* or *Coffea canephora*, in the Rubiaceae family. It is native to the forest understory of the east African highlands. It grows best with frequent rains, warm but not extreme temperatures, and hilly ground 600 to 1,200 meters (2,000 to 4,000 feet) above sea level and therefore has been cultivated in high tropical regions around the globe.

The coffee plant is a woody shrub, and it grows in the wild as high as 12 meters (39 feet), but cultivated trees are pruned to 2 meters (6.5 feet) to make harvesting easier. Small, white flowers give rise to a red, fleshy fruit, the "coffee cherry," which contains a pair of beans. A single coffee tree pro-



duces enough beans for about forty cups of coffee per year. Because fruit does not all set at once, most coffee cherries are harvested by hand, rather than by machine. The bean is removed from the fruit for drying. Dried beans can be stored for a year or more before roasting. Once roasted, the bean begins to lose flavor and is best used within several weeks.

Though native to Africa, the majority of coffee is now grown in South and Central America, with Brazil being the single largest producer. In 2000 world coffee production was more than 6 billion kilograms (6.6 million tons), almost all of which was exported, making coffee one of the largest commodities traded on the international market. Almost one-quarter of the world's coffee is imported by the countries of North America.

Desire to increase yield has led some growers to cut back the forest trees under which most coffee is grown. This has the undesirable effect of reducing biodiversity, especially of birds, and increasing soil erosion. Some coffees are labeled as "shade-grown" to alert consumers to its more environmentally sensitive origins. SEE ALSO AGRICULTURE; BEER-MAKING, BIOLOGY OF; BIODIVERSITY; WINE-MAKING, BOTANY OF

Richard Robinson

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College Professor

College and university professors have satisfying careers because they work in an intellectually stimulating environment and with people who want to learn more about the world around them. Professors need to have many qualities and skills such as excellent teaching abilities, inquisitive minds, a love of learning, and a willingness to dedicate their lives to their profession.

Science professors need to have a great deal of education. A bachelor's degree (bachelor of science or bachelor of arts) is earned after completing a minimum of four years of college. A master's degree can be earned in about two years of study. To teach in a college or university, the minimum requirement is a doctor of philosophy (Ph.D.) degree in one of the sciences, such as biology, chemistry, or geology. The doctorate is primarily a research degree, which takes three to five years to complete, depending on the topic which is chosen for research. The research topics in science are sharply focused and require experimental study in the field or a laboratory on a subject that has previously never been explored.

In addition to these three degrees, it is common for professors to have post-doctoral ("post-doc") experience doing research full time for one or more years before they are accepted for a position as a professor.

A professor may teach a variety of courses, which is for many the most exciting part of this career. Usually professors teach two to four courses per semester. Each course requires a great deal of preparation by reading much material about the subject, especially new discoveries, and designing ways

to teach the materials so that the students understand it well. Professors are expected to advise students about courses and careers available to them. Faculty members are required to conduct research and publish the results in journals. However, not everything that is written by a faculty member gets published in a journal.

Faculty members make decisions on a wide variety of subjects, such as the curriculum, the selection of new faculty members, the cultural events on the campus, the supervision of athletic programs, and many more topics. Often, faculty members provide service to their professional organizations and to the community by serving on boards and councils.

Students can prepare themselves to be a professor by doing extremely well in school, reading and studying a great deal, and getting to know professors and their work. SEE ALSO HIGH SCHOOL BIOLOGY TEACHER

Orin G. Gelderloos

Community

An ecological community is a collection of organisms occurring together in a location and interacting to varying degrees. A community is often defined by the most common or prominent species found in it (a beech-maple forest) or by its environment (a wetland community).

Species Diversity

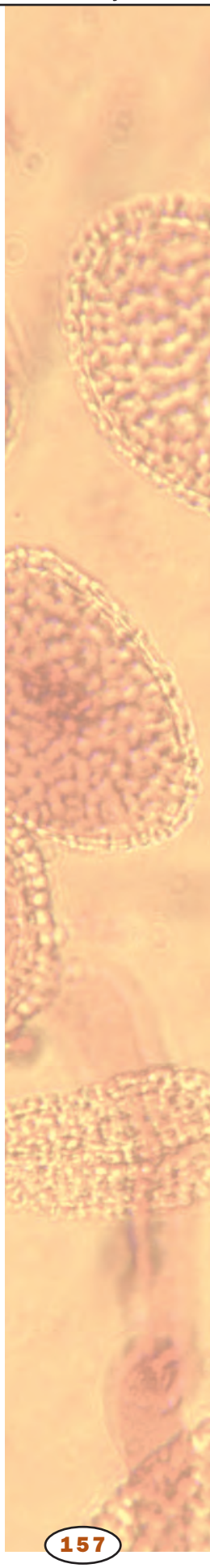
Community ecologists study what determines membership in communities and how and why communities change in space and time. One of the most important characteristics of an ecological community is species diversity. Species diversity is a measure that combines the number of species in a community with the relative abundances of those species. Understanding why some species are more abundant than others is particularly important because communities that are strongly dominated by one or a few species often have low species diversity overall. Differences in species diversity among communities occur because of differences in environment, differences in the kinds and strengths of species interactions, or both.

Interactions

There are many kinds of species interactions in communities, all of which affect species diversity. Predation, parasitism, and herbivory are interactions in which one species benefits at the expense of another. Competition involves a mutually negative interaction among species. **Mutualism** involves an interaction in which both species derive benefit.

mutualism symbiosis between two organisms in which both benefit

Some of these interactions may lower diversity, while others increase diversity. In addition, the strengths of these interactions change as the environment changes. For example, competition may be more intense when resources are severely limited. In streams, for instance, different species of fish compete for insect prey. When prey are scarce, competition among fish species is strong, and when prey are abundant, competition is weak.



A second-growth birch forest with an evergreen understory in northern Wisconsin. One of the most important characteristics of an ecological community is species diversity.

Ecological communities are complex because many different factors affect species interactions in communities. Moreover, the different types of interactions among species in communities interact. For example, high predation rates can reduce competition among prey species. Because of this complexity, ecologists are keenly interested in understanding the complex web of interactions among the various plants, herbivores, carnivores, and decomposers in a community.

In fact, one of the challenging questions in community ecology is whether the web of interactions in a community is controlled primarily by resources or by top predators. Human activities are changing the abundance of resources in the environment, which in turn changes the types and strengths of interactions among species in communities. Ultimately, these changes could alter species interactions and patterns of species diversity.

Disturbance and Succession

Ecological communities are dynamic. An ecological community may change as a result of species interactions, but other phenomena, such as dispersal or the movement of an individual from one place to another, also cause communities to change. Dispersal is important because it means that a community in one area can influence community composition some place far away.

In the Caribbean, for example, the composition and abundance of lizards on islands change suddenly and dramatically following hurricanes. Flooding during hurricanes kills animals on some islands while some animals float from one island to another during and after the storm. Hurricanes are an example of ecological disturbance, an event that destroys living organisms and frees space for new individuals to colonize. Disturbances—including

CLEMENTS, FREDERICK (1874–1945)

American plant ecologist who defined early-twentieth-century ecology by introducing the concept of climax communities. In the 1910s, before many paved roads existed, Clements and his wife drove across the American West describing and photographing every major ecosystem in North America.

fires, floods, and volcanoes—are natural occurrences, and they are one of the primary forces that create change in ecological communities.

The study of how disturbances affect communities is an important aspect of community ecology. Many disturbances, like forest fires, may appear harmful or destructive, but they are natural phenomena that initiate change. **Succession** is the change in species composition at a site over time. Primary succession occurs in previously unoccupied habitats, such as the lava produced by a volcano. Secondary succession, which is much more common, occurs following a disturbance in an area that was previously occupied by a community. Successional change occurs as species disperse to a newly disturbed site and interact over time. Eventually, the rate of community change during succession decreases.

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

Stability is a measure of a community's ability to return to a condition that existed before disturbance. The question "Does diversity increase stability?" is hotly debated by ecologists. Some think that diversity increases stability because when many different species occupy an area, they use the resources more fully. In doing so, the diverse community is resilient because when the abundance of one species declines, for example during a drought, the abundance of a more drought-tolerant species increases.

Other ecologists think there is little relationship between diversity and stability. Rather, they believe that any response is really a function of the dominant species in the community. This issue is not likely to be resolved for some time.

Ecological communities are complex assemblages of organisms that undergo a rich array of interactions. These interactions affect the kinds and abundances of species found in a community. Understanding how species coexist and why communities change over time are exciting and challenging questions in ecology. Knowledge about community ecology becomes increasingly valuable as human activity alters the global environment. Thus, as the human population increases, ecologists will provide key information needed to help manage and conserve species diversity and ecological communities. SEE ALSO COMPETITION; ECOSYSTEM; PREDATION AND DEFENSE; SYMBIOSIS

Scott Collins and Margaret Palmer

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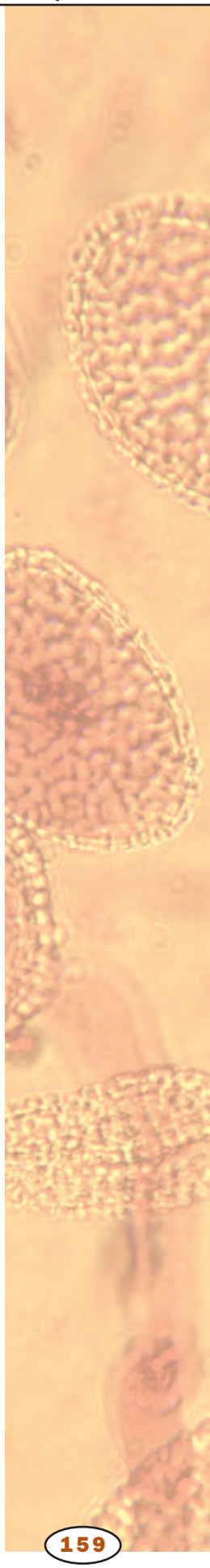
Competition

Competition is a negative interaction that occurs among organisms whenever two or more organisms require the same limited resource. All organisms require resources to grow, reproduce, and survive. For example, animals require food (such as other organisms) and water, whereas plants require soil nutrients (for example, nitrogen), light, and water. Organisms, however, cannot acquire a resource when other organisms consume or defend that



resource. Therefore, competitors reduce each other's growth, reproduction, or survival.

Interference and Exploitation

Biologists typically recognize two types of competition: interference and exploitative competition. During interference competition, organisms interact directly by fighting for scarce resources. For example, large aphids (insects) defend feeding sites on cottonwood leaves by kicking and shoving smaller aphids from better sites. In contrast, during exploitative competition, organisms interact indirectly by consuming scarce resources. For example, plants consume nitrogen by absorbing it into their roots, making nitrogen unavailable to nearby plants. Plants that produce many roots typically reduce soil nitrogen to very low levels, eventually killing neighboring plants.

Within Species and Between Species

Competition can occur between individuals of the same species, called intraspecific competition, or between different species, called interspecific competition. Studies show that intraspecific competition can regulate population dynamics (changes in population size over time). This occurs because individuals become crowded as a population grows. Since individuals within a population require the same resources, crowding causes resources to become more limited. Some individuals (typically small juveniles) eventually do not acquire enough resources and die or do not reproduce. This reduces population size and slows population growth.

Species also interact with other species that require the same resources. Consequently, interspecific competition can alter the sizes of many species' populations at the same time. Experiments demonstrate that when species compete for a limited resource, one species eventually drives the populations of other species extinct. These experiments suggest that competing species cannot coexist (they cannot live together in the same area) because the best competitor will exclude all other competing species. Why then do communities seem to have many competing species that coexist in the same area?

The Competitive Exclusion Principle

To explain how species coexist, in 1934 G. F. Gause proposed the competitive exclusion principle: species cannot coexist if they have the same niche. The word "niche" refers to a species' requirements for survival and reproduction. These requirements include both resources (like food) and proper habitat conditions (like temperature, **pH**). Gause reasoned that if two species had identical niches (required identical resources and habitats) they would attempt to live in the exact same area and would compete for the exact same resources. If this happened, the species that was the best competitor would always exclude its competitors from that area. Therefore, species must at least have slightly different niches in order to coexist.

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

Peter Grant and colleagues tested Gause's principle by studying seed-eating finches (birds) that live on the Galapagos Islands in the Pacific Ocean. They found that different finch species can coexist if they have traits that allow them to specialize on particular resources. For example, two finch species, *Geospiza fuliginosa* and *Geospiza fortis*, vary in a key trait: beak size.

Beak size is a critical trait because it determines the size of a seed that a finch can eat: Individuals with small beaks eat small seeds, individuals with intermediate sized beaks can eat intermediate size seeds and individuals with large beaks can eat large seeds. *G. fuliginosa* and *G. fortis* do compete for intermediate sized seeds because each species has some individuals with intermediate sized beaks. However, *G. fuliginosa* specializes upon smaller seeds because it has more individuals with small beaks. Conversely, *G. fortis* specializes upon larger seeds because it has more individuals with large beaks. Thus, these species niches differ slightly because a specific trait, beak size, allows them to specialize upon a particular seed size.

Joe Connell also tested Gause's principle by studying barnacles (shelled marine organisms) that live on rocks along European coastlines. In 1961, Connell found that two barnacle species, *Balanus* and *Chthamalus*, can coexist because they differ in two traits: growth rate and vulnerability to **desiccation**. *Balanus*'s growth is rapid, which allows it to smother and crush the slower-growing *Chthamalus*. *Balanus*, however, dies close to shore because it gets too dry during low tide. In contrast, *Chthamalus* tolerates these dry conditions. Consequently, even though *Balanus* is a better competitor for space, these barnacles coexist because *Chthamalus* can survive in areas that *Balanus* cannot survive. These and many other examples support the competitive exclusion principle: Species can only coexist if they have different niches.

desiccation drying out

Character Displacement

Competition can cause species to evolve differences in traits. This occurs because the individuals of a species with traits similar to competing species always experience strong interspecific competition. These individuals have less reproduction and survival than individuals with traits that differ from their competitors. Consequently, they will not contribute many offspring to future generations. For example, the finches previously discussed can be found alone or together on the Galapagos Islands. Both species' populations actually have more individuals with intermediate-sized beaks when they live on islands without the other species present. However, when both species are present on the same island, competition is intense between individuals that have intermediate-sized beaks of both species because they all require intermediate sized seeds. Consequently, individuals with small and large beaks have greater survival and reproduction on these islands than individuals with intermediate-sized beaks.

Studies show that when *G. fortis* and *G. fuliginosa* are present on the same island, *G. fuliginosa* tends to evolve a small beak and *G. fortis* tends to evolve a large beak. The observation that competing species' traits are more different when they live in the same area than when competing species live in different areas is called character displacement. For the two finch species, beak size was displaced: Beaks became smaller in one species and larger in the other species. Studies of character displacement are important because they provide evidence that competition plays a very important role in determining ecological and evolutionary patterns in nature. SEE ALSO ADAPTATION; COMMUNITY; EVOLUTION; EXTINCTION; NATURAL SELECTION; POPULATION DYNAMICS; SYMBIOSIS

J. P. Cronin and Walter P. Carson

A ground finch on Santa Cruz Island in the Galapagos. Different finch species can coexist if they have traits—for instance, beak size—that allow them to specialize on particular resources.

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Conifers

The conifers are a group of about 588 species of trees and shrubs that include many of the best-known plants in the world. All conifers bear seeds inside cones, woody protective structures. There are seven families of conifers. The largest is the Pine family (232 species), which includes such familiar trees as pine, spruce, fir, and larch. Most plants in this family have needlelike foliage and bear their seeds in a cone formed of papery or woody scales whorled about a central axis. The Pine family includes the oldest known trees, the bristlecone pines, many of which are known to be more than four thousand years old.

The next largest family (147 species) is the Podocarps. Most Podocarps are tropical trees, many of them native to the Southern Hemisphere. Generally, they have broad leaves and bear their seeds in a structure similar to a berry. Nonetheless, their flowers, the anatomy of their wood, and the details of seed development all show that Podocarps are closely related to the Cypress family (141 species).

Most trees in the Cypress family bear scalelike foliage and have cones that have only a few scales. Besides cypress, this diverse family includes juniper, a common tree or shrub in desert areas; giant sequoia, which is the world's largest tree; and coast redwood, the tallest tree in the world. The remaining 68 species of conifers include a wide variety of less well-known trees, such as the yews, which are common garden plants, and the araucarias, which are important timber trees in some tropical countries.

Although the 588 species of conifers are not a very abundant group compared with the 250,000 species of flowering plants, the conifers are ecologically and economically one of the most important plant groups. A few species in the Pine family form the most extensive forest on Earth, the boreal forest, which covers thousands of miles across Russia, Canada, and Scandinavia. One species, the Siberian larch, is the most numerous and widespread of all trees.

ecosystem an ecological community and its environment

Almost all conifers are trees, and so they create forests that provide habitat for wildlife and a wide variety of insects, fungi, and smaller plants. Some conifer forests support extremely complex **ecosystems** with very high levels of biodiversity. Conifers are also very important economically because they provide wood and wood products that are used to make buildings, furniture, and paper. Before petroleum was widely used, conifers were also the

All conifers bear seeds inside cones, woody protective structures.

source of many important **organic** chemicals used to make paint and other finishes, solvents, and oils used by industry. Native peoples have used conifers to make houses and necessary implements, and some peoples have even used them for clothing (from woven bark) and food (seeds).

organic composed of carbon, or derived from living organisms

Conifers are one of the oldest groups of plants, with araucaria-like trees first appearing about 290 million years ago, and primitive representatives of most of the conifer families appearing during the Mesozoic era, from 230 to 68 million years ago. Therefore, conifers, and other types of **gymnosperms**, are generally regarded as being more evolutionarily primitive than angiosperms. SEE ALSO FOREST, BOREAL; GYMNOSPERMS; WOOD AND WOOD PRODUCTS

gymnosperms "naked seed" plants, including conifers

Christopher J. Earle

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Connective Tissue

The human body is composed of just four basic kinds of tissue: nervous, muscular, epithelial, and connective tissue. Connective tissue is the most abundant, widely distributed, and varied type. It includes fibrous tissues, fat, cartilage, bone, bone marrow, and blood. As the name implies, connective tissues often bind other organs together, hold organs in place, cushion them, and fill space.

Connective tissue is distinguished from the other types in that the extracellular material (matrix) usually occupies more space than the cells do, and the cells are relatively far apart. Fat is an exception, having cells in close contact with each other; but with large, nonliving, **intracellular lipid** droplets, fat contains much more nonliving material than living material.

The **matrix** of connective tissue typically consists of fibers and a featureless ground substance. The most abundant fiber in connective tissues is a tough **protein** called collagen. Tendons, ligaments, and the white stringy tissue (fascia) seen in some cuts of meat are composed almost entirely of collagen, as is leather, which consists of the connective tissue layer (dermis) of animal skins. Collagen also strengthens bone and cartilage. Elastic and **reticular** fibers are less abundant connective tissue proteins with a more limited distribution.

The ground substance may be liquid, as in blood; gelatinous, as in **areolar** tissue; rubbery, as in cartilage; or calcified and stony, as in bone. It consists mainly of water and small dissolved **ions** and **organic** molecules, but the gelatinous to rubbery consistency of some tissues results from enormous protein-carbohydrate complexes in the ground substance. The hard consistency of bone results mainly from calcium phosphate salts in the ground substance.

Some of the cells of connective tissue are **fibroblasts** (which produce collagen fibers and are the only cell type in tendons and ligaments); adipocytes (fat cells); leukocytes (white blood cells, also found outside the

intracellular within a cell

lipid fat or waxlike molecule, insoluble in water

matrix a network, usually of threadlike fibers

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

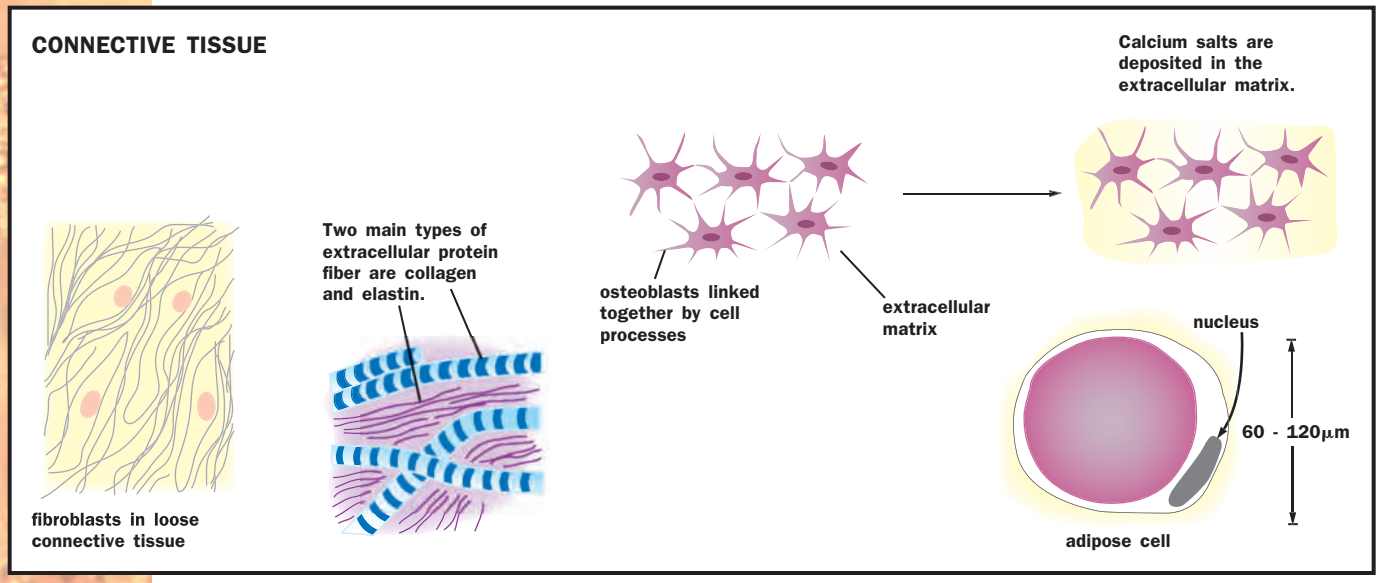
reticular netlike

areolar related to a small space within a tissue

ion an electrically charged particle

organic composed of carbon, or derived from living organisms

fibroblast undifferentiated cell normally giving rise to connective tissue cells



Connective tissue type and characteristics	Functions	Locations
Areolar (loose) connective tissue. Loose array of random fibers with a wide variety of cell types	Nourishes and cushions epithelia, provides arena for immune defense against infection, binds organs together, allows passage for nerves and blood vessels through other tissues	Under all epithelia; outer coverings of blood vessels, nerves, esophagus, and other organs; fascia between muscles; pleural and pericardial sacs
Adipose tissue (fat). Large fat-filled adipocytes and scanty extracellular matrix.	Stores energy, conserves body heat, cushions and protects many organs, fills space, shapes body	Beneath skin; around kidneys, heart, and eyes; breast; abdominal membranes (mesenteries)
Dense irregular connective tissue. Densely spaced, randomly arranged fibers and fibroblasts.	Toughness; protects organs from injury; provides protective capsules around many organs	Dermis of skin; capsules around liver, spleen, and other organs; fibrous sheath around bones
Dense regular connective tissue. Densely spaced, parallel collagen fibers and fibroblasts.	Binds bones together and attaches muscle to bone; transfers force from muscle to bone	Tendons and ligaments
Cartilage (gristle). Widely spaced cells in small cavities (lacunae); rubbery matrix.	Eases joint movements; resists compression at joints; holds airway open; shapes outer ear; moves vocal cords; forerunner of fetal skeleton; growth zone of children's bones	External ear, larynx, rings around trachea, joint surfaces and growth zones of bones, between ribs and sternum, intervertebral discs
Bone (osseous tissue). Widely spaced cells in lacunae; much of matrix in concentric onionlike layers; hard mineralized matrix.	Physically supports body, provides movement, encloses and protects soft organs, stores and releases calcium and phosphorus	Skeleton
Blood. Erythrocytes, leukocytes, and platelets in	Transports nutrients, gases, wastes, hormones,	Circulates in cardiovascular system

bloodstream in fibrous connective tissues); macrophages (large phagocytic cells descended from certain leukocytes); erythrocytes (red blood cells, found only in the blood and bone marrow); chondrocytes (cartilage cells); and osteocytes (bone cells).

The table above lists representative locations and functions of the major types of connective tissue. Further details on connective tissue can be found in textbooks of **histology** and human anatomy. SEE ALSO BLOOD; BONE; MUSCULOSKELETAL SYSTEM; ORGAN; SKIN; TISSUE

histology study of tissues

Kenneth S. Saladin

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Conservation

Biological diversity throughout the world is being threatened by human activity: species are being driven to the edge of extinction; biological com-

munities are being degraded, fragmented, and destroyed; and the genetic variation within species is being lost as populations are reduced in size and lost. Conservation biology is a multidisciplinary science that has developed in response to this biodiversity crisis. Conservation biology has three goals: (1) to investigate and describe the diversity of the living world; (2) to understand the effects of human activities on species, communities, and **ecosystems**; and (3) to develop practical interdisciplinary approaches to protecting and restoring biological diversity.

ecosystem an ecological community and its environment

Conservation biology arose because none of the applied disciplines, such as forestry, fisheries and wildlife management, zoo and park management, and agriculture, were comprehensive enough individually to address the critical threats to biological diversity. In general, these applied disciplines have developed methods for managing a small range of species for the marketplace and recreation. Conservation biology complements these applied disciplines by providing a broader approach and by having the long-term preservation of biological diversity as its primary goal, with economic factors often secondary. The academic disciplines of population biology, ecology, taxonomy, landscape ecology, and genetics constitute the core of conservation biology, with increasing inputs from economics, law, philosophy, anthropology, and other related fields.

Origins in the United States

The need for the conservation of biological diversity has been recognized for centuries in North America, Europe, and other regions of the world. Religious and philosophical beliefs concerning the value of protecting species and wilderness are found in many cultures. In the United States, philosophers such as Ralph Waldo Emerson and Henry David Thoreau saw wild nature as an important element in human moral and spiritual development. Wilderness advocates such as John Muir and Aldo Leopold argued for preserving natural landscapes and maintaining the health of natural ecosystems.

The influential forester Gifford Pinchot developed the idea that commodities and qualities found in nature, including timber, clean water, wildlife, species diversity, and even beautiful landscapes, can be considered as natural resources, and that the goal of management is to use these natural resources to obtain the greatest good for the greatest number of people for the longest time. In the twenty-first century, the concepts of ecosystem management and sustainable development have extended these ideas by emphasizing management practices that maintain ecosystem health and wild species now and for future generations.

Conservation at Many Levels

All levels of biological diversity are necessary for the continued survival of species and natural communities, and all are important for people. The diversity of species includes the full range of organisms on Earth, from bacteria and protists, through the multicellular kingdoms of fungi, plants, and animals. The diversity of species provides people with resources and resource alternatives.

The polluted Swazambhunath River in Kathmandu, Nepal. Sewage, industrial waste, and agricultural runoff can severely damage aquatic communities.

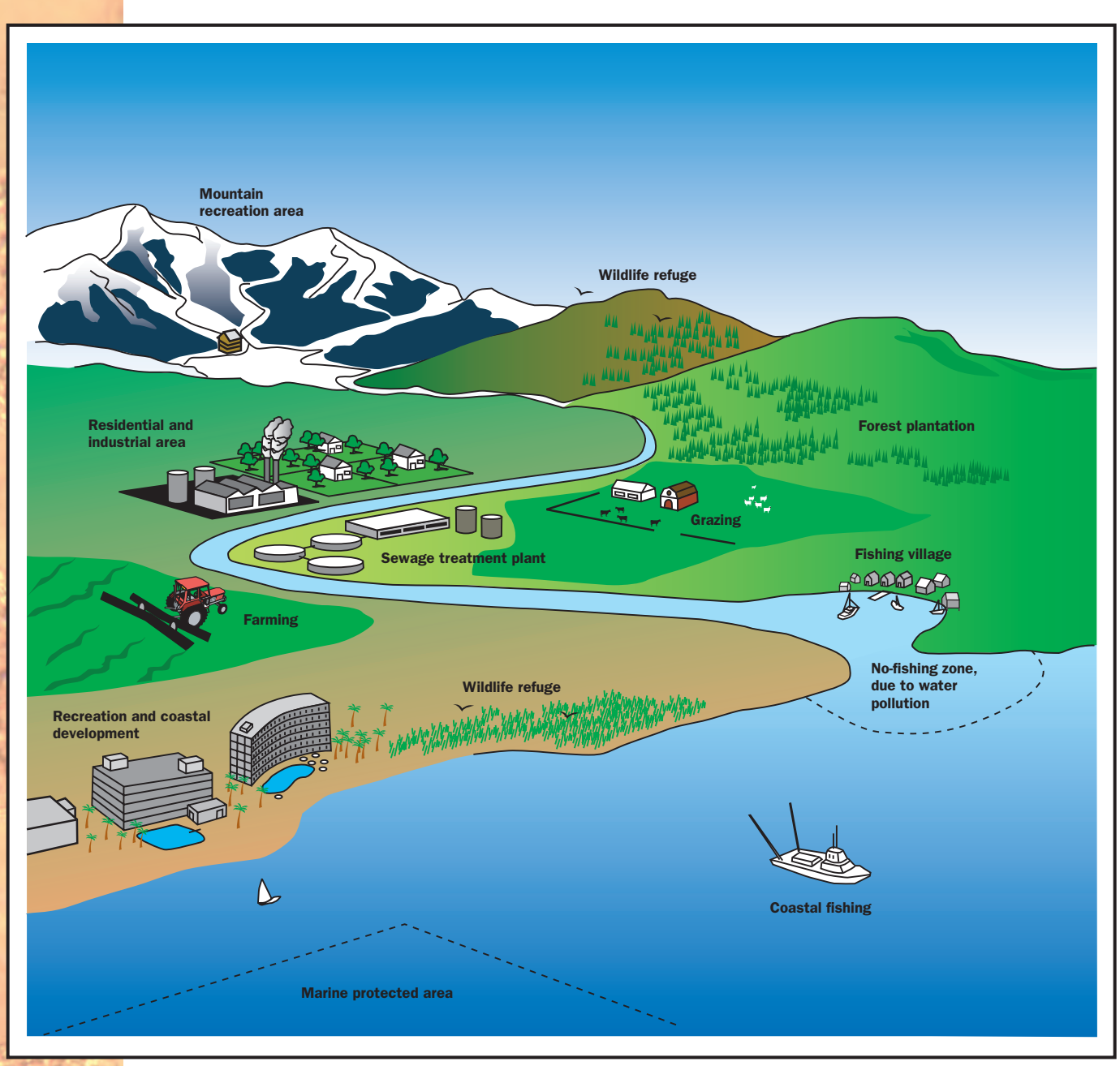
At the finest scale, genetic variation within species allows species to survive in the face of a changing environment; this genetic variation is also crucial for the continued efforts to improve domestic plants and animals, and for the rapidly developing biotechnology industry. On a larger scale, biological diversity includes the range of biological communities in which species live, and the ecosystem-level interactions with the physical and chemical environment. Biological communities provide beneficial services such as flood control, protection from soil erosion, the production of new plant material, and the filtering of air and water. As each one of these levels of biological diversity is degraded and destroyed, the natural fabric of the living world unravels and its value to people also diminishes.

Threats to Biological Diversity

The major threats to biological diversity are all caused directly or indirectly by an ever-increasing use of the world's resources by the exponentially expanding human population. Because more people require more resources for their livelihood, many scientists have argued that controlling human numbers is the key to protecting biological diversity. A more equitable distribution of natural resources throughout the world, and reducing the excessive consumption of natural resources by wealthy countries, such as the United States, are also important targets for conservation efforts.

The major threat to biological diversity is loss of habitat, and the most important means of protecting biological diversity is habitat preservation. Eighty-one percent of the endangered species in the United States are threatened by habitat destruction. Tropical rain forests, wetlands, coral reefs, and temperate grasslands are all being eliminated by human activity. Even when habitat still remains, it is increasingly fragmented by roads, power lines, fences, farms, ranches, residences, and other human activities that restrict wildlife movement and alter the local environment.

Air and water pollution can also eliminate susceptible species, even where the basic habitat structure remains. Sewage, industrial waste, and agricultural runoff can severely damage aquatic communities.



Land-use planning is a critical component of conservation. A well-planned community provides sufficient resources for a variety of uses, while preserving large areas for conservation.

Biological communities can be harmed when exotic species are transported by people to a new place deliberately or accidentally. In many areas of the world introduced sheep, cattle, pigs, and goats have driven native plants to extinction; introduced invasive grasses, agricultural weeds, and ornamental plants have escaped into the surrounding landscapes, replacing the native species. Diseases spreading from one continent to another are a significant threat decimating important tree species in North America and birds in Hawaii.

Global climate change is an emerging threat to biological diversity. If Earth's climate continues to change and warm as scientists predict, many species will not be able to migrate or adapt and will go extinct.

Numerous bird, mammal, and fish species continue to be overharvested. Entire communities of large animals have been removed for consumption or sale resulting in "empty" forests, lakes, and oceans. Certain species have been targeted by collectors and represent special conservation problems, such as shellfish, butterflies, tropical and coral reef fish, orchids, and cacti and other succulent plants.

Conservation Efforts

The single most important method to protect biological diversity is to establish national parks, nature reserves, and other protected areas. Such efforts to protect biological diversity in their natural habitats are referred to as *in situ* or on-site conservation. Approximately 6 percent of the world's land surface is designated as protected, with more national parks being designated each year. Many new marine reserves are being established to protect the nursery grounds for commercial fish species and maintain high-quality areas for recreation and tourism.

To be effective at preserving biological diversity, protected areas must be well-designed, be as large as possible, and contain a variety of vegetation types and water sources. Management practices—such as regulating hunting, removing exotic species, and employing controlled burning to maintain habitat diversity—need to be developed and put into practice. One of the most rapidly developing areas of conservation management involves restoring native biological communities on degraded lands, often by planting the original species. Protected areas must be periodically monitored to make sure they are meeting their objectives.

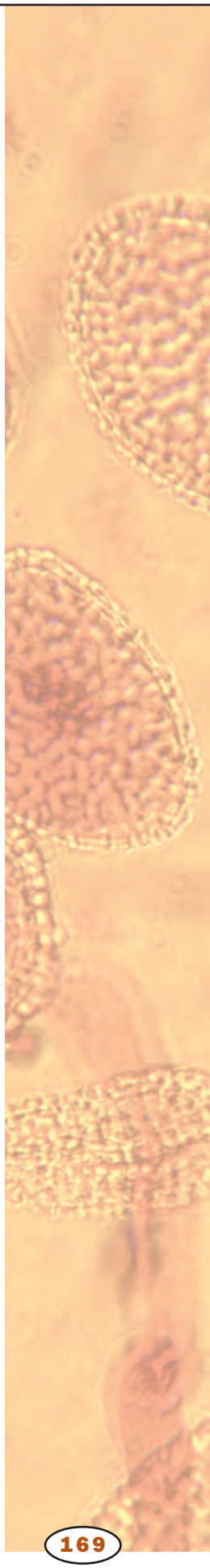
Where species can no longer live in the wild due to continuing threats, they can be maintained in zoos and botanical gardens. In such places, information can be gathered about the biology of the species and the public can be educated about conservation issues. The goal of such captive breeding programs is to return species back into their original habitat, known as "reintroductions," once the original threat to the species has been identified and eliminated.

The greatest challenge involves developing projects in which conservation efforts are integrated with rural economic development. If local people benefit from conservation efforts through obtaining jobs, improved **infrastructure**, or new business and education opportunities, they will contribute to conservation objectives. But if local people perceive that the establishment of a protected area is harming their livelihood, they may actively oppose conservation efforts and damage the area.

infrastructure roads, phone lines, and other utilities that allow commerce

Since the 1980s, conservation biology has become one of the most vibrant subject areas within biology. Enormous interest has led to whole new fields of knowledge being developed. However, conservation biologists are not simply content with developing new knowledge. The field of conservation biology will only be judged a success if this knowledge is used in a practical way to protect and restore the world's fragile biological diversity. SEE ALSO BIODIVERSITY; ENDANGERED SPECIES; EXTINCTION; GLOBAL CLIMATE CHANGE; INVASIVE SPECIES

Richard B. Primack



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Control of Gene Expression

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

All cells contain a set of genes, which can be thought of as a set of instructions for making each of a very large number of **proteins**. The creation of a protein from its gene is called gene expression. However, for a given cell not all of these instructions are actually used, and among those that are, some are used more than others or only under certain circumstances. Controlling gene expression is critical to a cell because it allows it to avoid wasting energy and raw materials in the synthesis of proteins it does not need. Thus, it allows a cell to be a more streamlined and versatile entity that can respond to changing conditions by adjusting its physiology.

transcription messenger RNA formation from a DNA sequence

To understand the control of gene expression, two key concepts should be understood. First, gene expression requires **transcription**, the process of making a messenger ribonucleic acid (mRNA) copy of the deoxyribonucleic acid (DNA) gene. Transcription can only occur if RNA polymerase first attaches, or binds, to the DNA. Controlling this binding process is the major way that gene expression is controlled, and proteins are the major controllers of binding.

RNA polymerase enzyme complex that creates RNA from DNA template

The second important concept is that a protein molecule that helps regulate binding can itself be regulated. This usually occurs when some other molecule binds to the protein, causing the protein to undergo a structural change, in other words, to change shape. In some cases this shape change will help **RNA polymerase** to bind to DNA, and in other cases it will prevent it from doing so.

Control in Prokaryotes

Negative Control. The concept that gene expression could be controlled originated with studies done in the 1950s by French scientists François Jacob and Jacques Monod. They were studying the **metabolism** of a sugar, called lactose, by the *E. coli* bacterium. **β**-Lactose metabolism requires three proteins. Galactosidase and lactose permease are both involved directly in lactose metabolism; *β*-galactosidase **hydrolyzes** lactose into galactose and **glucose**, and lactose permease transports lactose across the bacterial cell membrane. The physiologic role of the third protein, thiogalactoside acetylase, is unclear. Jacob and Monod found that the amount of the three proteins all increased when *E. coli* were cultured in lactose-containing medium

metabolism chemical reactions within a cell

β the Greek letter beta

hydrolyze to split apart using water

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

(a nutrient source). This led to the hypothesis that the three genes were regulated together as a single unit.

This type of multigene unit was dubbed an "operon" and consists of the structural genes, which encode proteins, plus regulatory sequences lying upstream on the DNA. The structural genes in an operon are **transcribed** as a single mRNA, and the mRNA is thus polygenic (or polycistronic). An elegant series of experiments showed that transcription was begun when a lactose derivative, Allolactose, caused a repressor to be removed from the transcription initiation site. Thus, lactose regulates the synthesis of the **enzymes** necessary for its own metabolism by releasing the transcriptional repression imposed upon them. This type of regulation is called negative regulation, since it employs a repression to prevent transcription. The use of activator proteins in the positive control of gene expression is also common in **prokaryotes**. In this system, the activator protein promotes transcription.

transcribe creation of an RNA copy of a DNA gene

enzyme protein that controls a reaction in a cell

prokaryote single-celled organism without a nucleus

Positive Control. Positive control of gene expression is illustrated by the transcriptional activator, catabolite gene activator protein (CAP). CAP activates transcription of the lac operon, in addition to many other **inducible** operons. Because glucose is a preferred food source, the lac operon is not activated in *E. coli* cells cultured in medium containing both glucose and lactose until the glucose is used up. However, since lactose is present, one might expect the lac operon to be derepressed and hence active. But experiments have shown that glucose itself represses the activity of the lac operon, such that only when lactose is the only source of energy is it activated. This glucose repression is observed for a number of other operons that encode enzymes for the utilization of alternative energy sources. Glucose repression occurs via a positive mechanism. As glucose is consumed, its level in the cell drops. Low glucose levels stimulate the production of a small molecule called cyclic-**AMP** (cAMP), which then binds CAP. CAP undergoes a structural change that allows it to bind DNA and activate transcription. Thus, regulation of the lac operon is achieved by a collaboration between the negative control of the lac repressor and the positive control of CAP.

inducible able to be switched on

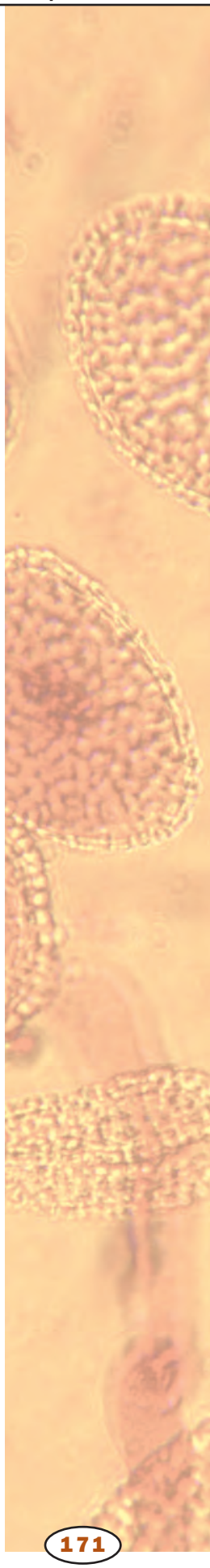
AMP adenosine monophosphate, form of ATP after removal of two phosphate groups

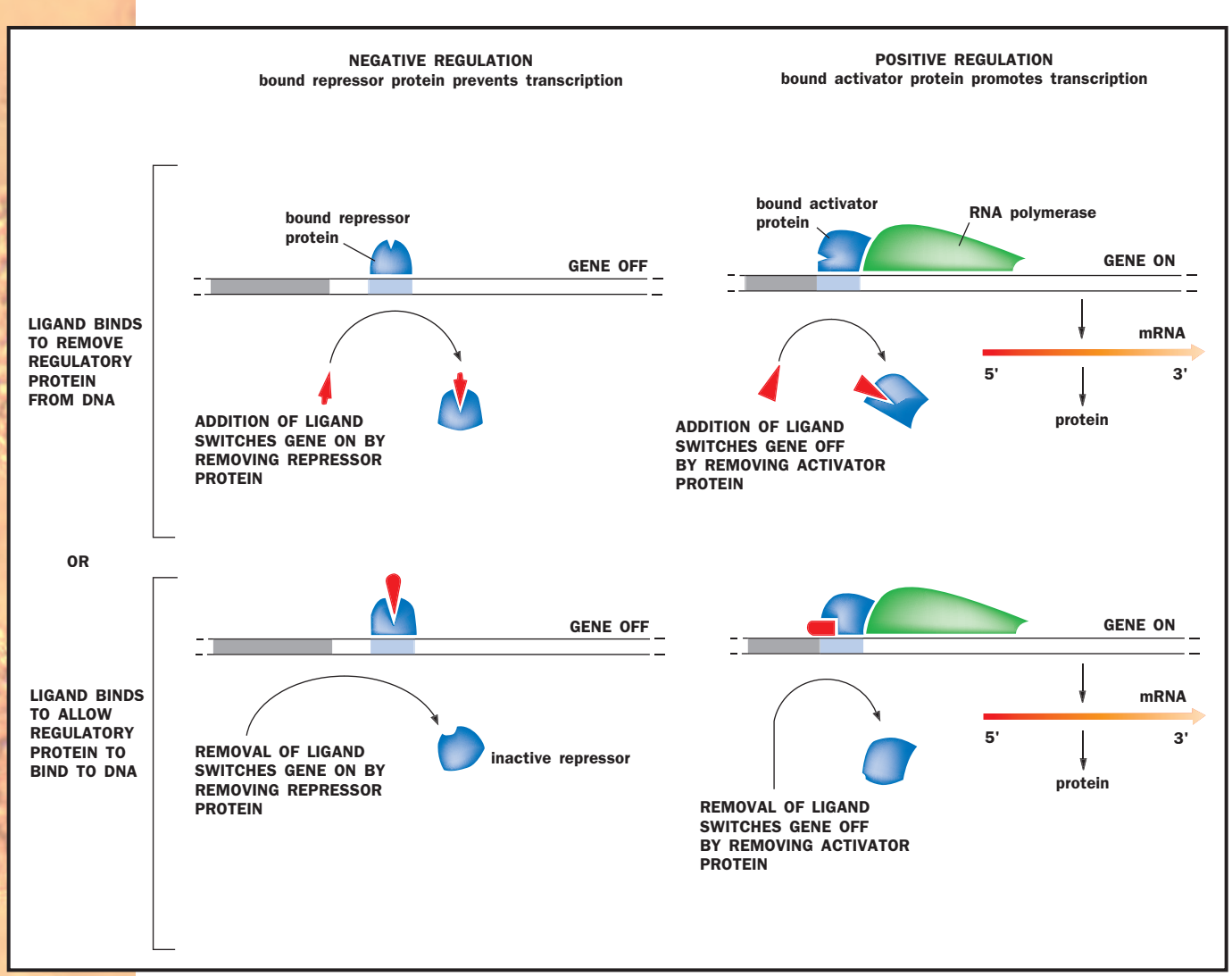
The lac repressor and CAP are examples of regulators of initiation of transcription. Although most regulators act at this level, some act at the level of elongation of the mRNA, after transcription has started. The tryptophan operon (trp operon) consists of five structural genes necessary for the biosynthesis of the **amino acid** tryptophan. It is regulated at the level of initiation via a negative regulatory scheme much like that for the lac operon; however, an additional mechanism, called transcriptional **attenuation**, is also at work. Part of the mRNA generated from the trp operon spontaneously folds into a stem-loop structure that exposes a termination sequence, causing transcription to terminate prematurely. However, when tryptophan is lacking, the **ribosome** works more slowly (since tryptophan is needed to make protein). This allows time for the formation of a different structure, the stem-loop, which hides the termination sequence, with the result being that transcription continues and a full-length transcript is produced. Thus, the end product of the operon, tryptophan, actively participates in the regulation of its own synthesis. This is a common theme in prokaryotic transcriptional regulation. Transcriptional attenuation can occur in prokaryotes

amino acid a building block of protein

attenuation lessening over time

ribosome protein-RNA complex in cells that synthesizes protein





The mechanisms by which gene regulatory proteins control gene transcription in prokaryotes. A ligand is a small molecule that binds to a protein.

because **translation** of an mRNA begins before its synthesis is complete. In eukaryotes it does not occur because transcription and translation are completely separate processes that do not occur simultaneously.

Eukaryotic Transcription

Regulation of transcription is by necessity far more complex in eukaryotic cells (cells with a **nucleus**) than in prokaryotic cells. Not only are eukaryotic cells larger and more highly compartmentalized, but multicellular eukaryotes pass through a number of developmental stages, each requiring different proteins, on the road to their final differentiated state. Also, multicellular organisms contain many different cell types, each of which expresses distinct sets of proteins.

Certain basic features of transcriptional regulation are shared between prokaryotes and eukaryotes; in both cases it involves an interplay between activators and repressors that bind cis-acting sequences on DNA. However, one major difference is that, unlike prokaryotic DNA, eukaryotic **chromosomes** are wrapped around proteins called **histones**, to form a condensed form of DNA called **chromatin**. This tends to repress gene transcription,

translation synthesis of protein using mRNA code

nucleus membrane-bound portion of cell containing the chromosomes

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

and several transcriptional activators have been found to function by relieving chromatin-induced repression. Another feature that distinguishes eukaryotic from prokaryotic transcription is that RNA polymerase does not bind directly to DNA but instead binds via a set of proteins called the basic **transcription factor**. Thus, in many cases the role of activators is to recruit these transcription factors to the **promoter** site rather than to directly recruit the polymerase itself. Finally, whereas prokaryotic genes are often controlled by only one or two regulatory proteins, eukaryotic genes are typically controlled by a multiplicity of factors. This added complexity allows for the fine-tuning of gene activity in response to multiple stimuli.

histone protein around which DNA wraps to form chromosomes

chromatin complex of DNA, histones, and other proteins making up chromosomes

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

promoter DNA sequence to which RNA polymerase binds to begin transcription

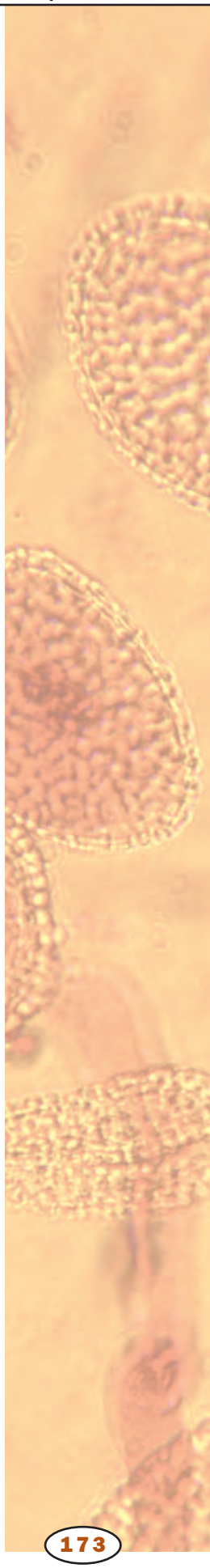
Structure of Transcriptional Activators

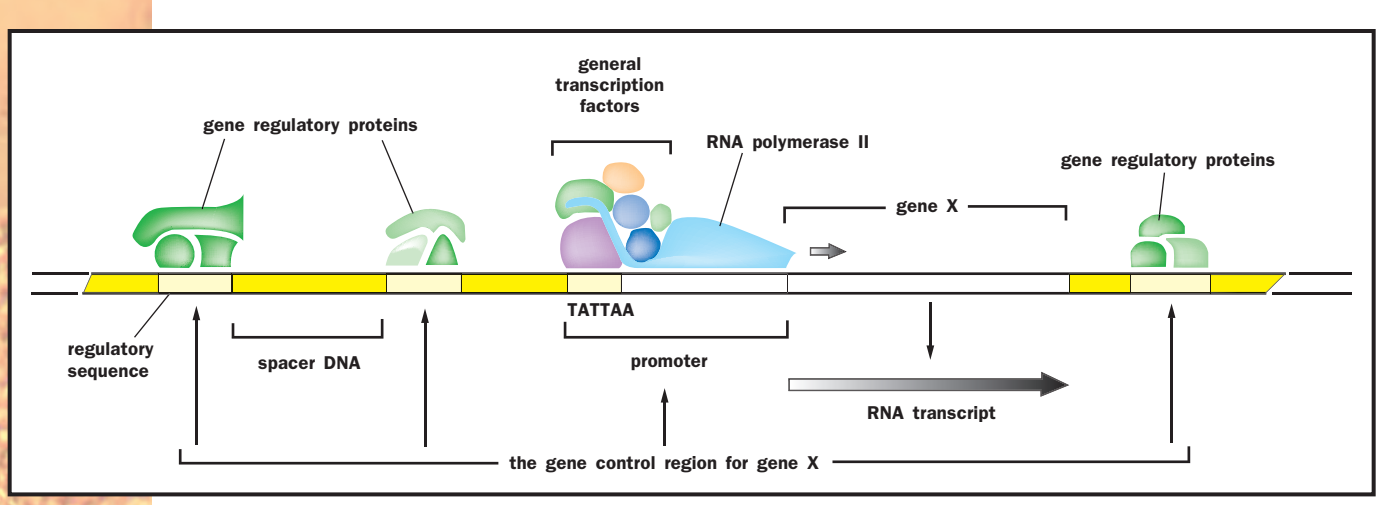
Many transcriptional activators are essentially modular in structure in that the DNA-binding domain and the transactivation (or activation) domain can almost be thought of as two distinct proteins that are physically linked. The DNA-binding domain is the part of the molecule that contacts DNA at the promoter site. The transactivation domain is the part that recruits other factors to the promoter such that the rate of transcription of the gene increases. Although transcription factor DNA-binding domains vary in amino acid sequence, many can be placed into structural categories based on their three-dimensional structures. Among these are the zinc finger, helix-loop-helix,

REGULATION OF THE LAC OPERON

E. coli with defects in the regulation of the lac operon were found to have mutations in one of two loci, called *o* and *i,* located upstream of the structural genes. Mutations in *o* yielded cells that constitutively (continually) expressed the lac operon, whereas mutations in *i* fell into two categories; one in which the lac operon was constitutively expressed, and the other in which it was uninducible (could not be expressed). Subsequent experiments showed that *i* was a gene for a diffusible protein that was the repressor of the lac operon, whereas *o* was a DNA sequence to which a repressor bound.

This was consistent with the mutant results: A mutation in *o* would disrupt the binding of the repressor protein, leading to constitutive expression of the lac operon, and a mutation in *i* would either prevent the repressor from binding to *o,* resulting in constitutive activation, or render the repressor unresponsive to the inducer, lactose, which would cause uninducibility. Because *i* was diffusible (could move within the cell) and could interact with any piece of DNA containing its target sequence, it was called a trans-acting factor (*trans* means "across"). In contrast, *o* only affects the genes to which it is physically linked and so has been called a cis-acting factor (*cis* means "together"). These elegant genetic studies paved the way for biochemical studies carried out in the 1960s by Walter Gilbert and Benno Müller-Hill. They purified *the lac repressor,* encoded by *i,* and found that it bound to a 30 base-pair region of DNA spanning the transcription initiation site, consistent with the location of *o.* In addition, they found that the lac repressor released its hold on *o* when bound to allolactose, a derivative of lactose.





The gene control region of a eukaryotic gene.

and helix-turn-helix classes. Although the three-dimensional structures within a class are similar, each individual binding domain can recognize a different DNA sequence due to specific amino acid differences and different amino acid–DNA contacts. Many transcriptional activation domains can also be placed into categories, the most common of which is the **acidic** activation domain category. Others include the glutamine-rich and proline-rich classes.

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

Regulation of Transcriptional Activators

Regulation of transcription sometimes occurs via the simple presence or absence of transcription factors. An example of this is in the regulation of the immunoglobulin (an immune protein, also called **antibody**) heavy chain gene, which is expressed in B lymphocytes (white blood cells that make antibodies) but not other cell types. This gene's enhancer (a region distant from the promoter) contains at least nine binding sites for regulatory proteins. The enhancer is acted on by activators present in **B lymphocytes**, while in nonlymphocyte cells repressors are present that inhibit transcription. This limits expression of the gene to lymphocytes.

antibody immune system protein that binds to foreign molecules

B lymphocyte white blood cell that makes antibodies

Often, however, regulation does not occur at the level of presence or absence of a regulatory protein but rather by modulation of its activity. Thus, many transcription factors are always present in the cell, awaiting the specific signals that will convert them from an inactive to an active form. How is this achieved? The three most common mechanisms are regulation of nuclear localization, regulation of DNA binding, and regulation of transactivation.

Regulation of Nuclear Localization. In many cases a protein is kept in the **cytoplasm**, well away from its target genes, until a stimulus signals it to enter the nucleus and activate transcription. This mode of regulation works because transport into the nucleus is regulated, such that only proteins possessing a special tag are allowed to enter. The transcription factor NF-κB, which regulates a number of genes in immune cells that help fight infections, is regulated in this way. NF-κB is present in the cytoplasm of unstimulated immune cells as a complex with an inhibitory protein called iκB. Upon receiving a stimulus, such as a viral infection, iκB becomes **phosphorylated** and is sub-

cytoplasm material in a cell, excluding the nucleus

phosphorylate add a phosphate group to

sequently degraded, leaving NF-κB free to enter the nucleus and activate its target genes to help fight infection. Interestingly, one of these target genes is the iκB gene, and thus inhibition of NF-κB is reestablished shortly thereafter. This kind of negative **feedback** mechanism, bringing the cell back to its unstimulated state, is common among inducible genes. In addition, NF-κB activation illustrates another common feature of transcription factor regulation in eukaryotes: **phosphorylation** is often used as a switch that interconverts a transcription factor back and forth between inactive and active forms.

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

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

Regulation of DNA Binding. A second common mechanism by which the activity of a transcription factor is controlled is through alteration of its DNA-binding ability. The **steroid hormone** receptor family is a good example of this. This family of transcription factors has many members, all related in structure, yet binding to distinct steroid hormones on the one hand, and activating distinct sets of genes on the other. Some of these hormone receptors reside in the cytoplasm and others in the nucleus, but all are unable to bind their target DNA sequence until they first bind to their corresponding steroid hormone. This causes them to undergo a conformational change that increases their **affinity** for DNA, allowing them to bind. It is through their action on hormone receptors and DNA that steroid hormones exert their powerful effects on the body's cells.

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

affinity attraction

Another way to increase the DNA-binding ability of a transcription factor is to induce it to multimerize. Many factors are inactive by themselves, but when induced to bind other factors, they can bind their target sequences and activate transcription. The other factors can either be identical molecules of the same factor, thus forming homo-multimers, or different proteins, forming hetero-multimers. An example of this occurs with heat shock factor (HSF) in mammalian cells, which upon stimulation forms homotrimers. The DNA-binding affinity of a single molecule of HSF for its binding site is too low to be physiologically significant; however, a complex of three molecules binds the target site very tightly, making HSF one of the most inducible transcription factors known.

Regulation of Transactivation. Finally, some transcriptional activators are already bound to their target sites in gene promoters but remain transcriptionally inactive until they are stimulated. In yeast, HSF is already trimerized and bound to some of its target genes in unstimulated cells. Heat shock (a rise in temperature) results in phosphorylation of HSF at multiple sites, which induces a structural change in the protein that unleashes the transactivation domain.

The aforementioned examples illustrate a number of ways in which a transcriptional activator may be regulated. However, it should be kept in mind that many are regulated in more than one way. For example, both nuclear localization and DNA-binding ability of an activator may be controlled. Thus, even if a few molecules should happen into the nucleus by mistake, they would not be able to bind and activate their target genes. This kind of tight control is important because sometimes even small levels of a protein can set off a cascade of reactions that can dramatically change the physiology of the cell. It is critical to avoid these types of false alarms in order for the cell not to waste valuable energy and resources, and so that it remains poised to respond to a genuine stimulus.

In the laboratory the DNA-binding domain and the transactivation domain—the two functional domains—can be mixed and matched between different transcription factors to yield hybrid molecules that still function, albeit differently from the original proteins. This feature has been exploited experimentally. For example, the relative strengths of various activation domains can be assessed by fusing each to the same DNA-binding domain and determining the rate at which each promotes transcription.

Transcriptional Repression

Transcriptional repressors, like activators, bind cis-acting sequences in the genes they regulate and are modular in structure, possessing distinct DNA-binding and repressor domains. However, as their name implies, their role is in the repression of gene activity rather than their activation. Some repressors function by simply binding upstream regions of genes and blocking the binding of either activator proteins or the polymerase itself, much like the repressor in the lac operon. Some extremely versatile proteins can function either as repressors or activators, depending on the proteins with which they interact. An example is the Mcm1 protein in yeast. Yeast can be one of two mating types, called ***α*** and ("alpha"), each of which expresses mating type-specific sets of genes. Mcm1 **dimerizes** with one protein to repress the a-specific genes in ***α*** cells, and with another to activate the α-specific genes.

α the Greek letter alpha

dimerizes forms a pair

The Role of Chromatin

Although transcriptional repressors often participate in gene regulation, it must be kept in mind that the very nature of DNA in eukaryotic cells tends to keep genes in the repressed state. Eukaryotic DNA is wrapped around protein complexes called histone octamers, which has the effect of packaging the DNA into a compact form such that it fits inside the nucleus. However, this also limits access of regulatory factors to their target sites. As the mechanisms of transcriptional activators are being uncovered, more and more are being found that act by relieving chromatin-induced repression. An example is the Swi/Snf protein complex, first identified in yeast. Mutations in components of the complex resulted in decreased activity of certain target genes. It was later found that mutations in the histone genes restored normal activity to those target genes; in other words, the mutations in the histone genes somehow compensated for the mutations in Swi/Snf. This was an indication that histones and Swi/Snf interact in some way and suggested that Swi/Snf might function by disrupting histone binding to DNA. Biochemical experiments carried out later on showed that this was indeed the case. Although Swi/Snf does not completely **dissociate** histones from DNA, it loosens them, which is sufficient to allow many activators to bind. Swi/Snf is only involved in activating a subset of genes, and the question of why it functions at some promoters and not others is a topic of intense research.

dissociate break apart

Mutations in the MeCP2 cause Rett syndrome, an X-linked dominant disorder marked by seizures, abnormal movements, and mutism.

A second mechanism by which chromatin-induced repression is relieved is by histone **acetylation**. Histones are positively charged proteins and hence interact tightly with DNA, which is negatively charged. Acetylation of histones reduces their net positive charge, which loosens their interaction with DNA and increases transcription factor binding. Several transcription factors in a variety of organisms have now been found to be acetyltransferases; in effect, they can acetylate histones.

In addition, some transcriptional repressors in yeast and mammals have been found to be histone deacetylases. In fact, the protein MeCP2, which binds to methylated DNA, has been found to function in a complex with a histone deacetylase. Thus, **methylation** would lead to binding of this complex, causing deacetylation of histones and a more condensed chromatin structure. Methylated DNA has long been known to be associated with tran-

acetylation addition of an acetyl group, CH_3-CHOO-

methylation addition of the methyl group CH_3

scriptionally inactive genes, and inroads into the study of histone acetylation have finally provided an explanation for this. SEE ALSO CHROMOSOME, EUKARYOTIC; CONTROL MECHANISMS; DNA; GENE

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Control Mechanisms

The cell possesses an extraordinary array of **enzymes**, each specialized to carry out an important function in the cell. However, in many cases it is critical that the enzymes only be active at certain times and not others. For example, the digestive enzymes secreted by cells lining the stomach and intestine must only be active once they have been secreted and not before. If they were active prior to secretion they would degrade the **proteins** within the very cells that synthesized them. Or consider the enzymes that carry out the many activities of cell division. If these are not held in tight control, a cell will divide inappropriately and may become cancerous.

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

Thus, it is critical for the cell to be able to control the activities of many of its enzymes, and a number of intricate mechanisms have evolved to do just that. In most cases the activity of an enzyme is achieved via changes in its conformation, or shape, and the four most common ways of achieving this are regulation by small molecules; regulation by **phosphorylation**; regulation by protein-interactions; and regulation by proteolytic cleavage.

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

Regulation by Small Molecules

Regulation of an enzyme can occur by the binding of a small molecule to a site distant from the **active site**, which is the binding site for the enzyme's **substrate**. This is called allosteric regulation (from the Greek *allo*, meaning "other," and *steric*, meaning "site"). Because the small molecule does not bind the active site, it does not function by blocking access to the substrate. Instead, it acts by changing the conformation of the protein. A classic example of this occurs with an enzyme called aspartate transcarbamoylase (ATCase) from the bacterium *E. coli*.

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

substrate the molecule acted on by an enzyme

ATCase is the first enzyme in a series of enzymes whose end product is cytidine triphosphate (CTP), which is used to make ribonucleic acid (RNA) and deoxyribonucleic acid (DNA). CTP has been found to bind to ATCase and inhibit its activity. The binding of CTP to ATCase changes the conformation of the active site such that the **affinity** for substrates is decreased by up to 90 percent. Thus, the buildup of CTP shuts the entire pathway off, thereby maintaining a fairly constant supply. This type of inhibition, in which the end product of a reaction inhibits its own synthesis, is called feedback inhibition and is a common regulatory mechanism in biologic pathways. In a more extreme case, the **amino acid** tryptophan goes so far as to inhibit the synthesis of the mRNAs encoding the **biosynthetic**

affinity attraction

amino acid a building block of protein

biosynthetic forming a complex molecule from simpler ones

enzymes that synthesize it. Thus, in that case, the enzymes themselves are not even synthesized until they are needed.

Although G-proteins have intrinsic GTPase activity, this activity can often be further stimulated by a protein called a GTPase activating protein (GAP).

An important class of proteins regulated by small molecules are the G-proteins. They are called G-proteins because they bind and are activated by guanosine triphosphate (GTP). G-proteins have intrinsic GTPase activity, meaning they convert the bound GTP molecule to GDP (guanosine diphosphate). Typically, when GDP is bound, the conformation of the protein is such that the molecule is inactive. A protein called a GTP exchange factor (GEF) stimulates the exchange of GDP for GTP, thus reactivating the G-protein.

The ras protein is a G-protein found in a number of different organisms. Research has shown that ras activates proteins involved in cell growth and division. It was first discovered in a virus that causes tumors in mice. It causes tumors when it is mutated such that its GTPase activity is defective. This causes the protein to always be bound to GTP (instead of GDP) and hence it remains active. Thus, overactive ras causes uncontrolled cell proliferation and cancer. It has since been found that up to 15 percent of human cancers involve a mutation in ras that inhibits its GTPase activity, making it an important protein in human disease. The normal protein is only activated when stimulants outside the cell, such as growth factors, signal it to grow and proliferate. Following a short period of activity, inherent GTPase activity of the ras returns it to the inactive form.

Interestingly, in the fruit fly, *Drosophila melanogaster*, ras serves a different function. The structure and regulation of ras in *D. melanogaster* is similar to that in mammalian cells, but instead of participating in a pathway signaling cell proliferation, it is involved in a pathway leading to the differentiation of a certain type of cell in the eye, the photoreceptor cell. The regulation of protein activity by a GTP-GDP switch is apparently evolutionarily ancient and has been adapted to serve a variety of different cellular functions.

Regulation by Phosphorylation

Phosphorylation means the addition of a phosphate group, PO_4^{3-}. Phosphorylation of certain amino acids in a protein can occur via the action of a group of proteins called **kinases**. Kinases are classified into two broad classes based on the amino acid they phosphorylate: the serine/threonine class and the tyrosine class. All three of these amino acids contain a **hydroxyl** (-OH) side chain, to which a phosphate group can be attached. Phosphorylation often occurs on more than one amino acid in a protein, and the result is a conformational change that affects the protein's activity. A second class of proteins, called phosphatases, reverses the activity of kinases by removing the phosphates, returning the proteins to their original forms. Phosphatases are also categorized by their substrate specificities, either serine/threonine or tyrosine, however, a few have the ability to dephosphorylate all three amino acid side chains. In the example of regulation by phosphorylation described below, dephosphorylation leads to activation. This is not always the case, and equally as many proteins are activated by phosphorylation.

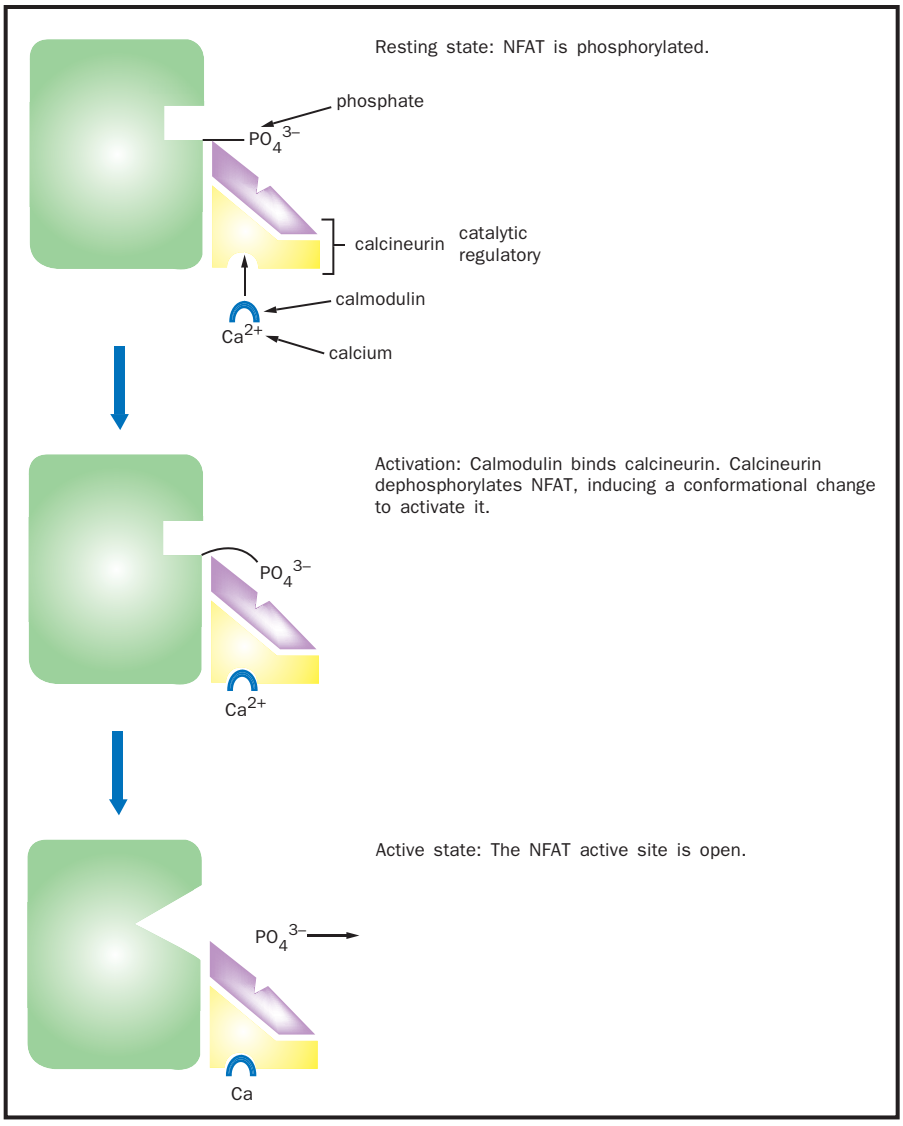
kinase enzyme that adds a phosphate group to another molecule, usually a protein

hydroxyl chemical group consisting of -OH

Nuclear factor of activated **T cells** (NFAT) is a protein regulated by phosphorylation. NFAT is a **transcription factor** that is found in the

T cell white blood cell that controls the immune response

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



cytoplasm and is phosphorylated in resting cells. Dephosphorylation causes a conformational change that allows it to be transported to the **nucleus**, where it binds other transcription factors to activate **gene transcription**. NFAT was first found to activate genes in T cells (an immune cell); however, it has since been found in a number of other cell types as well.

The phosphatase that dephosphorylates and activates NFAT is called calcineurin, which is of the serine/threonine class. Even when inactive, calcineurin is bound to NFAT, ensuring a rapid response upon activation. Stimulation by an inducer such as a viral infection or perhaps an organ transplant causes the activation of calcineurin, which then makes additional contacts with NFAT via its active site and dephosphorylates it. This activates NFAT, aiding the immune response by the T cell.

cytoplasm material in a cell, excluding the nucleus

nucleus membrane-bound portion of cell containing the chromosomes

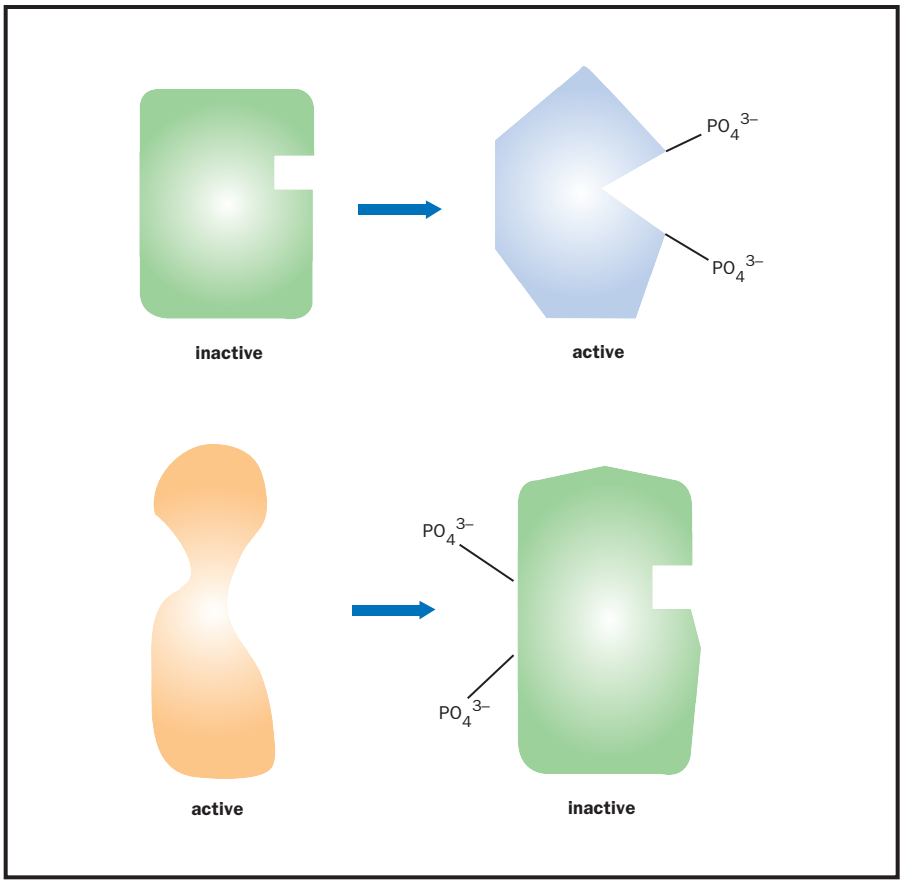
gene portion of DNA that codes for a protein or RNA molecule

transcription messenger RNA formation from a DNA sequence

Regulation by Protein-Protein Interactions

Many enzymes are regulated by binding to another protein. For example, transcription factors, such as heat shock factor (HSF), can be activated by

Phosphorylation or dephosphorylation causes a conformational change that affects the protein's activity.



binding to other copies of itself (homomultimerization). In addition, inactivation of a protein can also occur by protein-protein interactions.

Although HSF activation occurs by binding of identical molecules to one another, often regulation by protein-protein interactions occurs between different proteins. For example, calcineurin, the phosphatase that activates NFAT, is itself regulated by protein-protein interactions. Calcineurin is composed of two **polypeptide** subunits, one catalytic and one regulatory. The catalytic subunit contains the active site and is the part of the enzyme that dephosphorylates NFAT. The regulatory subunit binds the catalytic subunit and keeps it inactive by blocking the active site until a stimulus is detected.

polypeptide chain of amino acids

The stimulus for calcineurin activation is increased cytoplasmic calcium levels. Calcium, together with a small protein called calmodulin, binds calcineurin, which results in the displacement of the regulatory subunit, exposing the active site and allowing it to dephosphorylate NFAT. Thus, calcineurin is an example of an enzyme that is regulated by both small molecules (calcium) and proteins (the regulatory subunit and calmodulin).

Another example of this occurs with a kinase called cAMP-dependent protein kinase, which in resting cells consists of a complex of two catalytic and two regulatory subunits. As with calcineurin, the regulatory subunits keep the kinase inactive until cyclic AMP (cAMP), a small molecule derived from adenosine monophosphate (**AMP**), binds and activates the kinase. In this case, however, the regulatory subunits completely **dissociate**

AMP adenosine monophosphate, form of ATP after removal of two phosphate groups

dissociate break apart

from the catalytic subunits, rather than simply shifting their position as in calcineurin.

Regulation by Proteolytic Cleavage

A number of proteins are activated by **proteolytic** cleavage, that is, they are synthesized as a longer protein that is inactive and are later cleaved into a smaller, active form. The inactive precursor is called a zymogen, or proenzyme. For example, the **hormone** insulin is derived from proinsulin by proteolytic cleavage, as are many of the proteins involved in blood clotting. In addition, many digestive enzymes are activated by cleavage. Trypsinogen is a zymogen that upon cleavage becomes the digestive enzyme trypsin. Trypsinogen is made in the pancreas and secreted into the duodenum (the small intestine) where it is cleaved by an enzyme called enteropeptidase. The small amount of trypsin made by enteropeptidase then goes on to cleave other molecules of trypsinogen to make more trypsin as well as cleaving the other pancreatic zymogens into their active forms, and thus trypsin can be thought of as a master switch in the digestive process.

proteolytic breakdown of proteins

hormone molecule released by one cell to influence another

Calcineurin is the target of immunosuppressive drugs used to treat patients following an organ transplant.

Unlike the other control mechanisms described above, proteolytic cleavage is irreversible, and thus once cleavage has occurred the enzyme cannot be returned to its inactive form. Thus, enzymes activated in this way may need to be turned off via other mechanisms. In the case of trypsin, there exists a small protein called pancreatic trypsin inhibitor that binds to trypsin's active site and inhibits its activity. It binds the active site so tightly that even very harsh conditions used to dissociate proteins in the laboratory are ineffective at removing it. This extremely effective inhibitor has probably evolved to target trypsin because of its role as a master switch in the regulation of digestion in the small intestine. Once trypsin has been inactivated, proteolytic soon ceases, and digestion comes to a halt. SEE ALSO CELL CYCLE; CONTROL OF GENE EXPRESSION; DIGESTION; DIGESTIVE SYSTEM; ENZYMES; ONCOGENES AND CANCER CELLS; SIGNALING AND SIGNAL TRANSDUCTION

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Convergent Evolution

Convergent evolution is the process by which unrelated or distantly related organisms evolve similar adaptations. Organisms displaying these similarities usually live in similar environments, and the force driving convergence is natural selection. Similar environments pose similar challenges to survival, and traits that aid in survival are selected for in each environment. Convergent evolution is seen in the fusiform (tapering toward the end) shapes and similar countershading coloration of sharks and dolphins, both of which are adapted to marine environments. Their shape facilitates rapid and effi-

A sand skink in Polk County, Florida. Some of the most striking examples of convergent evolution are found in desert lizards throughout the world.

cient movement through water, and their light underbelly and a gray upper surface make them less visible from both below and above.

Convergent Evolution in Desert Lizards

Some of the most striking examples of convergent evolution are found in desert lizards throughout the world. Australian and North American deserts each support a cryptically colored lizard species that is specialized to eat ants and is protected by sharp spines. The Australian species, the thorny devil (*Moloch horridus*, Agamid family) is only distantly related to the American species, the desert horned lizard (*Phrynosoma platyrhinos* Iguanid family), as shown by sequencing deoxyribonucleic acid (DNA). They are much more similar anatomically than either is to its closest living relatives. Clearly, the desert environment has posed strong challenges for survival, which have been met by evolution of similar external characteristics.

Open sandy deserts pose severe problems for their inhabitants: (1) windblown sands are loose and provide little traction; (2) surface temperatures at midday rise to lethal levels; and (3) open sandy areas offer little food or shade or shelter for evading predators. Even so, natural selection over eons of time has enabled lizards to cope fairly well with such sandy desert conditions. Subterranean lizards simply bypass most problems by staying underground and actually benefit from the loose sand because underground locomotion is facilitated. Burrowing is also made easier by evolution of a pointed, shovel-shaped head and a countersunk lower jaw, as well as by small limbs and muscular bodies and tails.

diurnal active during the daytime

During the hours shortly after sunrise, but before sand temperatures climb too high, **diurnal** lizards scurry about above ground in such sandy desert habitats. Sand-specialized lizards provide some of the most striking examples of convergent evolution. Representatives of many different families of lizards scattered throughout the world's deserts have found a similar solution for getting better traction on loose sand: enlarged scales on the toes, or lamellae, have evolved independently in six different families of lizards: skinks, lacertids, iguanids, agamids, gerrhosaurids, and geckos.

A skink (*Scincus philbyi*), appropriately dubbed the "sand fish", literally swims through sandy seas in search of insect food in the Sahara. These sandy desert regions also support lacertid lizards (*Acanthodactylus*) with fringed toes and shovel noses. Far away in the Southern Hemisphere, on windblown dunes of the Namib desert of southwestern Africa, an independent **lineage** of lacertids has evolved a similar life form, *Meroles anchietae*. Such organisms that fill similar ecological **niches** in different regions have undergone convergent evolution and are called "ecological equivalents."

lineage ancestral line

niche the habitat supplying the right environment for a particular species

In North America, this body form has been adopted by members of the iguanid genus *Uma*, which usually forage by waiting in the open and eat a fairly diverse diet of various insects, such as sand roaches, beetle larvae, and other burrowing **arthropods**. They also listen intently for insects buried in the sand and dig them up. Sometimes they dash, dig, and paw through a patch of sand and then watch the disturbed area for movements.

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

All of these lizards have flattened, duckbill-like, shovel-nosed snouts, which enable them to make remarkable "dives" into the sand even while running at full speed. The lizards then wriggle along under the surface, sometimes for over a meter. SEE ALSO ADAPTATION; DESERT; EVOLUTION; NATURAL SELECTION

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Coral Reef

A coral reef is a living community built around the accumulated mineralized remains of coral animals, which belong to **phylum** Cnidaria. The hardened calcium carbonate **secretion** from coral animals, with mineralized algal cells and other secretions, create nooks and crannies that shelter up to sixty thousand species, including hundreds of types of corals, as well as eels, lobsters, sea slugs, sea horses, sea urchins, turtles, and a huge variety of fishes. A coral reef houses some permanent occupants, and others that come and go. Often life lives within life. For example, snapping shrimp dwell in sponges that occupy crevices in layers of coral.

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

secretion material released from the cell

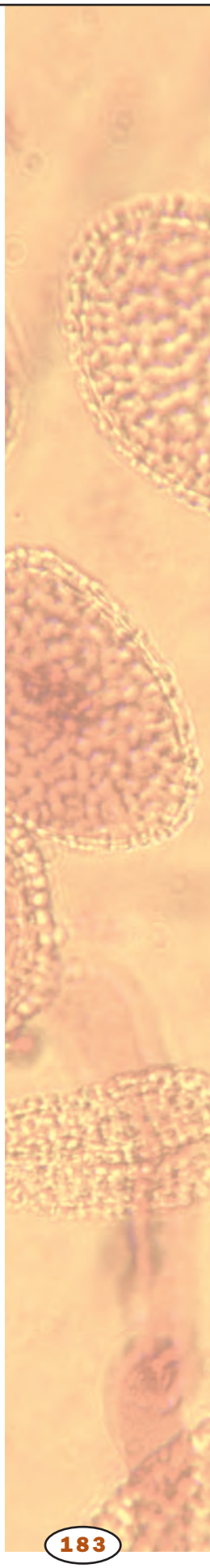
A living coral animal, called a polyp, is small and soft. Polyps collect atop their preserved ancestors, using their waving tentacles to capture prey that floats by. The sticky calcium carbonate **exoskeletons** that polyps secrete meld them to each other and to the graveyard below.

exoskeleton external skeleton

The tides deliver nutrients to coral polyps. Algal and dinoflagellate **symbionts** live inside the corals and actively photosynthesize, providing nutrients to their hosts and contributing the vibrant colors that give coral reefs their rainbow hues. These guests remove wastes from polyps and maintain water **pH** at a level that stimulates deposition of the exoskeletons. A million such symbionts may occupy a mere 2 cubic inches of coral reef. Were it not for the photosynthesis that the algae and dinoflagellates provide, the coral could not survive.

symbionts organisms living in close association with another organism

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



An aerial view of the Great Barrier Reef, between Cairns and Townsville, Australia.

Extent and Diversity

Corals cover 242,000 square kilometers (232,000 square miles) of ocean. Most reefs lie between 25 degrees north and south latitude, with more isolated growths in cooler waters farther from the equator. Most species require clear, warm water of about 20 degrees Celsius (68 degrees Fahrenheit). Less massive corals are found in colder waters that hug continents, including the fjords in Norway and along vertical banks of the coasts of England, New Zealand, Japan, and the western United States.

Biologists distinguish types of coral reefs by shape and organization. An atoll is a ring-shaped coral colony that encloses a lagoon, whereas a fringing reef forms next to shores where there isn't much rain, such as on one side of a tropical island. Barrier reefs surround islands or run alongside shorelines, enclosing lagoons. The Australian Great Barrier Reef is 1,303 square kilometers (1,250 square miles) long.

Threats to Coral Reefs

Many coral reefs are threatened, either by nature, human activity, or both. Winds destroy the delicate substructure of reefs, which have been damaged

both by the large-scale, long-lasting winds of El Niño and more localized but dramatic hurricanes. When stressed by climatic extremes, polyps disgorge their dinoflagellate symbionts, bleaching the coral. In addition, many corals in recent years have fallen victim to bacterial and viral infections. A dozen different viruses, for example, have decimated populations of elkhorn and staghorn corals in the Caribbean.

Building near shores threatens corals. Nitrogen and phosphorus fertilizer and soil in runoff from construction upsets the species balance of photosynthesizing symbionts.

Snorkelers are warned not to sample the coral, which many people erroneously think are plants or nonliving. In some areas, people catch fish by infiltrating living coral with explosives or cyanide, which often kills the coral and humans along with the fish. With all of these insults, ecologists estimate that by the middle of the twenty-first century, up to two-thirds of coral reefs may be gone. SEE ALSO ALGAE; BIOME; BONY FISH; CNIDARIAN; OCEAN ECOSYSTEMS: SOFT BOTTOMS; PORIFERA; SYMBIOSIS

Ricki Lewis

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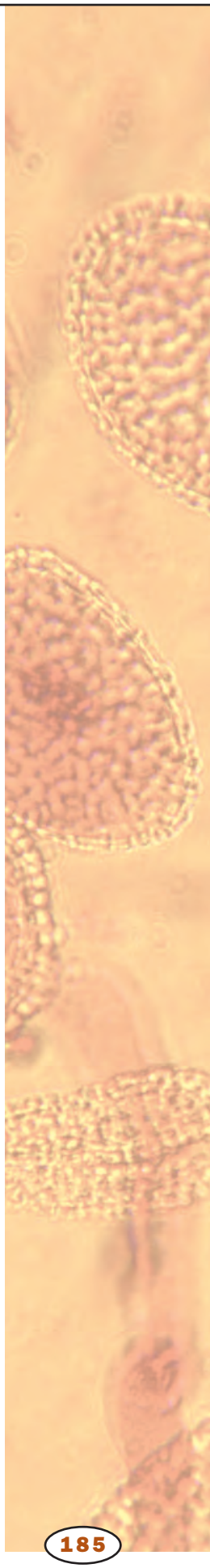
Creationism

In the broad sense, creationism is the belief that the universe and life were created by God. Within this definition are a broad range of beliefs. At one extreme are biblical literalists who believe that all life was created in its present form, including Adam and Eve as the first humans, as described in Genesis and with little or no evolutionary change since then (special creation). At the other end are creationists who have no quarrel with evolution and believe it is God's method of creating life (theistic evolution), the view accepted today by most Christian denominations.

In the United States, the creationism controversy began in earnest with the birth of Protestant fundamentalism in the 1910s. Fundamentalists, as they began calling themselves, argued for the literal truth of every word in the Bible, and thus rejected evolution and other philosophies of "modernism." They waged a campaign to outlaw the teaching of evolution and succeeded in getting five states to pass such laws from 1923 to 1929.

In Tennessee, this resulted in the famous Scopes trial of 1925, in which teacher John T. Scopes was convicted of teaching evolution. His fine was overturned on a technicality, but the Tennessee statute remained in effect until the legislature repealed it in 1967, both to improve the image of the state and to head off a threatened lawsuit. A similar law that had passed in 1928 in Arkansas was challenged by biology teacher Susan Epperson in 1965.



The U.S. Supreme Court ruled in her favor in 1968, stating that these anti-evolution statutes violated the First Amendment of the U.S. Constitution, which prohibits an entanglement of church and state. The last anti-evolution statute was repealed in 1969.

Creationists therefore changed their strategy. Briefly, they campaigned for laws to require "equal time for Genesis" if evolution was to be taught. Tennessee was the only state to pass such a law, in 1973, but it was overturned in court in 1975.

Failing at this tactic, creationists tried to have their views recognized as an alternative scientific theory and thus taught in the science curriculum. Many called their doctrine "scientific creationism," and founded such organizations as the Creation Research Society and Institute for Creation Research to promote their views. "Scientific creationists," as they called themselves, attacked the evidence for evolution, arguing over gaps in the fossil record, questioning the validity of radiometric dating, disputing the significance of human fossil remains, arguing that statistical probability or the laws of thermodynamics make evolution impossible, and claiming that geological features such as the Grand Canyon were evidence of Noah's flood, among many other lines of attack.

The scientific community never took the claims of creationists seriously but did publish numerous books to educate the public on why the claims were fallacious and why creationism was not a science. They founded organizations such as the National Center for Science Education and state Committees of Correspondence to counter the strategies of creationists in legislatures, school boards, and the media.

Despite their failure to convince many scientists of their views, creationists were more successful at the political level. Arkansas and Louisiana passed laws requiring the teaching of "creation science" in 1981. The Arkansas law was quickly struck down in a federal district court in 1982, whereas the Louisiana case dragged out until 1987, when the law was finally struck down by the U.S. Supreme Court. Both courts ruled that creationism had no reason to be part of a science curriculum; they recognized that these laws represented merely fundamentalist religion in disguise and were therefore in violation of the First Amendment. Creationists continue to press their case with some success, however, in local school boards, state boards of education, and textbook adoption committees. The result is often a watering down of the curriculum to include less (often much less) about evolution.

The eminent geneticist Theodosius Dobzhansky declared, "Nothing in biology makes sense except in the light of evolution." Because of the political efforts of creationists, evolution remains widely censored in biology courses today, and countless students are being kept in the dark about the facts of evolution. SEE ALSO DARWIN, CHARLES; EVOLUTION; EVOLUTION, EVIDENCE FOR; NATURAL SELECTION

Kenneth S. Saladin

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Crick, Francis

British biophysicist
1916–

Francis Crick.

Francis Harry Compton Crick, a British biophysicist, was co-winner of the Nobel Prize in physiology and medicine in 1962, for his work in genetics. This award was shared with American biologist James D. Watson and British biophysicist Maurice Wilkins.

Francis Crick, the son of a local shoe factory owner, was born on June 8, 1916, in Northampton England. He did his undergraduate work at University College, London, where he studied physics. Crick's science education was interrupted by World War II. After the war, in 1946, Crick's interest in chemical research was awakened after he attended a lecture given by American chemist Linus Pauling. Crick remained fascinated with **organic** molecules, and with quantum mechanics and the chemistry of genetics.

organic composed of carbon, or derived from living organisms

Crick went on to conduct research at the Cambridge Medical Research Council Unit at the famous Cavendish physics laboratory. He received his doctorate in 1953 from Cambridge University during the beginning of his collaboration with American biologist James Watson.

In 1952, at Cambridge, Crick and James Watson began to investigate the molecular structure, and significance to genetics, of nucleic acids. They began by looking specifically at earlier X-ray diffraction analyses of deoxyribonucleic acid (DNA), by Maurice Wilkins. DNA was already then considered to be the substance of which genes were made.

Watson and Crick used Wilkins's data, part of which came from coworker Rosalind Franklin, to create a three-dimensional model of the DNA molecule. The model included known facts, such as the chemical constituents (nitrogen bases, sugar, and phosphate), and took into account data from Wilkins's X-ray diffraction experiments.

Watson and Crick tried out various ways of arranging model molecules in space, finally settling on the aptly named double helix. Their model, afterwards referred to as the Watson-Crick model, showed DNA as a two-stranded twisted "helix." The two strands contain **complementary** nitrogen bases. This model both matched chemical facts previously known about DNA, and provided a viable explanation for how DNA could replicate, and thus for how genetic information could pass from one generation to the next generation of living organisms.

complementary matching opposite

Crick's discoveries revolutionized biology. After the acceptance of the Watson-Crick model, biologists could begin to understand living things at the molecular level. Living organisms could be related to one another according to their genetic similarities and dissimilarities.

Following the elucidation of the structure of DNA, Crick turned his attention to how genetic information is stored and used in a cell, and formulated the "central dogma" of molecular biology: that DNA dictates the

amino acid a building block of protein

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

sequence of ribonucleic acid (RNA), which dictates the sequence of **amino acids** in **proteins**, without the possibility of a reverse flow of information. He continued to make important theoretical contributions to genetics with a particular interest in development, until he turned his attention to neuroscience in the late 1970s. Crick's focus since then has been on the biology of consciousness and the nature of visual processing in the brain.

Among Crick's well-known publications are *Of Molecules and Men* (1996) and *Life Itself* (1982). SEE ALSO DNA; GENE; HISTORY OF BIOLOGY: INHERITANCE; NUCLEOTIDES; WATSON, JAMES

Hanna Rose Shell

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Crocodilians

ventricle fluid-filled chamber

The class Crocodylia consists of twenty-two species of alligators, caimans, gharials, and crocodiles worldwide, and is most closely related to birds (class Aves). Like birds (and mammals), crocodilians have the **ventricle** of their heart divided into left and right compartments (unlike amphibians, turtles, and reptiles, whose ventricles have but a single, undivided compartment). In addition, like mammals and birds, crocodilians demonstrate much parental care of their young, a behavior not found in amphibians, turtles, reptiles, and tuataras.

cloacal of, relating to the common exit cavity for intestinal, genital, and urinary tracts

transverse situated or lying across

lineage ancestral line

Crocodilians are covered with scales, a trait they share with reptiles (and to some extent with turtles, but not with amphibians, whose skin is scaleless and permeable), and their **cloacal** opening is a longitudinal slit (not **transverse** as in the classes Reptilia and Rhynchocephalia). Crocodilians are no longer classified as reptiles, but are considered a distinct and unique evolutionary **lineage**, the class Crocodylia. Crocodilians are tropical and subtropical in distribution. Some species, such as the saltwater crocodile, can attain lengths of up to 7 meters (23 feet). Crocodilians are carnivorous in diet, and females build nests in which to lay eggs.

During their 215-million-year evolutionary history, beginning in the middle Triassic, these magnificent beasts invaded diverse habitats, from ocean to swamp, from wet tropical forest to cascading mountain rivers. Today's comparatively small remnant of this once diverse group still live in these areas, but their numbers grow smaller with poaching and the continuing, unstoppable destruction of their habitat by world overpopulation. SEE ALSO AMPHIBIAN; CIRCULATORY SYSTEMS; REPTILE; TUATARA; TURTLE

Joseph T. Collins

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Crustacean

The Crustacea are a subphylum of the animal **phylum** Arthropoda. This is a large and diverse group with more than forty thousand species, including crabs, shrimp, lobsters, crayfish, barnacles, and many near-microscopic members of the zooplankton community. The subphylum is characterized especially by having mandibles and compound eyes and living in mostly aquatic habitats, although the "pillbugs" found under rocks and boards are also crustaceans, and many crabs spend much of their time on land.

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

The Crustacea are named for their hard, crusty **exoskeletons**, well known to anyone who has dined on lobster or crab. The hardness of the exoskeleton comes partly from **chitin**, but moreover from a heavy deposit of

exoskeleton external skeleton

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

A horseshoe crab on Fire Island National Seashore, New York. The Crustacea are a large and diverse group with more than forty thousand species.

calcium carbonate. The edible blue crab, for example, has as much calcium carbonate in its exoskeleton as four sticks of chalk. The rigid exoskeleton requires crustaceans to molt, or shed it periodically, in order to grow. Some crustaceans can mate only during the brief time just after they have molted and the new exoskeleton is still soft. This is also a time of great vulnerability to predators, so crustaceans often seek a place to hide before molting.

Some crustaceans resemble miniature adults from the moment they hatch, but many species have larval forms with little or no resemblance to the adult. These larvae, and some adult crustaceans, such as krill and copepods, are very important members of the freshwater and oceanic **plankton** community and are a major source of food for corals, fish, baleen whales, and other animals. A few crustaceans turn the tables on these predators by parasitizing the skin of fishes. These parasitic crustaceans are often wormlike and scarcely recognizable as relatives of shrimp and crabs. SEE ALSO ANIMALIA; ARTHROPOD; LAKES AND PONDS; OCEAN ECOSYSTEMS; PLANKTON

plankton microscopic floating organisms

Kenneth S. Saladin

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Cyanobacteria

Cyanobacteria (blue-green algae) are microorganisms that structurally resemble bacteria (they lack a **nucleus** and **organelles**). However, unlike other bacteria, cyanobacteria contain chlorophyll *a* and conduct oxygenic photosynthesis. Cyanobacteria are approximately 2.5 billion years old and thus are the oldest oxygenic phototrophs on Earth. The early evolution of Earth's oxygen-rich atmosphere is most likely due to cyanobacterial photosynthesis.

nucleus membrane-bound portion of cell containing the chromosomes

organelle membrane-bound cell compartment

Cyanobacteria are morphologically and physiologically diverse and broadly distributed in terrestrial and aquatic environments. Morphological groups include coccoid, filamentous nonheterocystous, and heterocystous genera. Heterocysts are specialized cells harboring nitrogen fixation, a process by which atmospheric nitrogen (N_2) is converted to a biologically useful form (NH_3). All heterocystous and some coccoid/filamentous cyanobacteria fix nitrogen. This enables cyanobacteria to exploit **ecosystems** devoid of nitrogen compounds, including those located in polar, open ocean, and desert regions. Cyanobacterial nitrogen fixation can be a significant source of biologically available nitrogen in these ecosystems.

ecosystem an ecological community and its environment

Cyanobacteria move by gliding, using mucilaginous excretions as propellant, or, in the case of **planktonic** genera, by altering buoyancy through gas **vesicle** formation and collapse. Cyanobacteria exhibit remarkable ecophysiological adaptations to global change. They tolerate **desiccation**, **hypersalinity**, hyperthermal, and high ultraviolet light conditions, often for many years. Over their long evolutionary history, they have formed numerous endosymbiotic and mutualistic associations with microorganisms, higher plants, and animals, including lichens (fungi), ferns, cycads, diatoms, seagrasses, sponges, and even polar bears. Cyanobacteria have also exploited

plankton microscopic floating organisms

vesicle membrane-bound sac

desiccation drying out

hypersalinity very high level of salt

man-made pollution of aquatic environments, especially nutrient-stimulated primary productivity or **eutrophication**.

Cyanobacterial blooms are highly visible, widespread indicators of eutrophication. Because of the toxicity of some bloom taxa, blooms can pose serious water quality and animal and human health problems. Foul odors and tastes, oxygen depletion, fish kills, and drinking/recreational impairment are symptoms of bloom-infested waters. Finally, the large contribution of cyanobacterial blooms to **phytoplankton** biomass and ecosystem nutrient fluxes can alter biogeochemical cycling and **food web** dynamics. SEE ALSO EUBACTERIA; PHOTOSYNTHESIS; WETLANDS

Hans Paerl

eutrophication process by which waters become enriched in dissolved nutrients that promote plant growth, which results in depletion of dissolved oxygen

phytoplankton microscopic floating creatures that photosynthesize

food web set of feeding relations in an ecosystem

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Cytokinesis

Cytokinesis is the process by which a cell divides its **cytoplasm** to produce two daughter cells. As the final step in cell division after **mitosis**, cytokinesis is a carefully orchestrated process that signals the start of a new cellular generation. The separation of one cell into two is accomplished by a structure called the contractile ring. The contractile ring is a structure believed to operate in a way similar to muscle. A molecular motor, myosin, contracts the actin filaments that form the contractile ring tighter and tighter until the cell is pinched in two. The contraction of the contractile ring has been likened to tightening a purse string to close the top of a pouch. The furrow created by this pinching process is also called the "cleavage furrow," as it is the site at which cleavage of one cell into two cells occurs.

cytoplasm material in a cell, excluding the nucleus

mitosis separation of replicated chromosomes

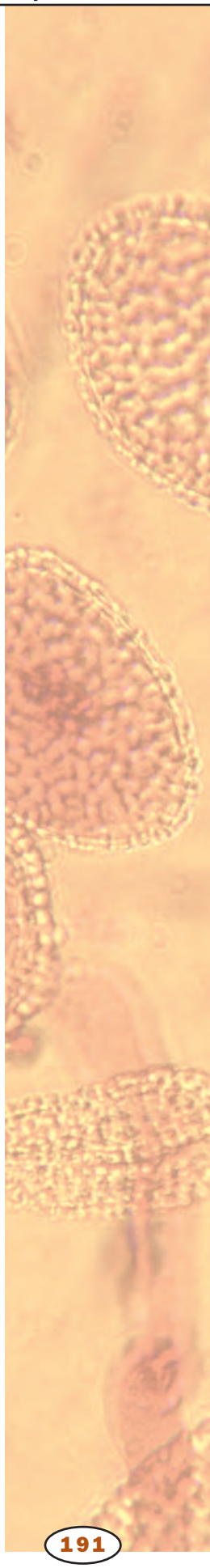
Cytokinesis consists of four major steps. The first step is to define the position at which the contractile ring will form. The spindle, the structure responsible for segregating the **chromosomes** into what will become the daughter cells, also appears to be responsible for defining where the contractile ring forms. The contractile ring forms perpendicular to the long axis of the spindle at its midpoint. Components of the spindle that come in contact with the plasma membrane, called astral microtubules, are believed to transmit a signal to the cell periphery that tells actin and other components of the contractile ring to assemble at that location. Actin and microtubules are both part of the **cytoskeleton**.

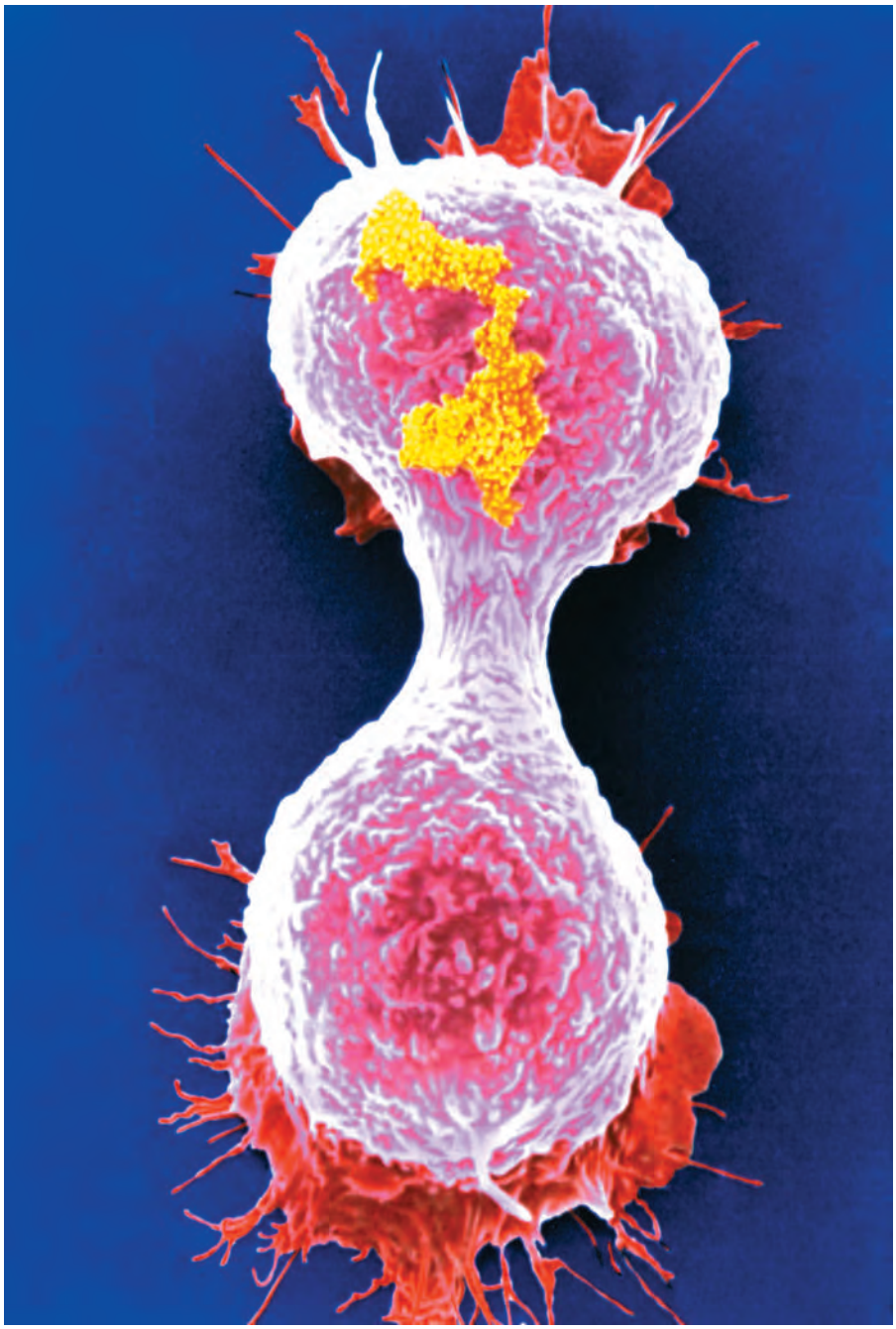
chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

cytoskeleton internal scaffolding in a cell, composed of protein

The second step in cytokinesis is to assemble the actin filaments that form the contractile ring. Additional **proteins**, including the molecular motor myosin, which powers contraction, also assemble in this same domain. The third step is the actual contraction of the contractile ring. In this step, the myosin motor, powered by adenosine triphosphate, moves the actin filaments past each other, much in the same way as myosin interacts with actin to power the contraction of muscle. This step also requires the removal of actin subunits to allow the ring to decrease in size. The final step, breaking and refusion of the plasma membrane, occurs once the ring has contracted

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





A colored scanning electron micrograph of a breast cancer cell dividing.

to its minimum size. This breaking and fusion finally separates the two daughter cells from each other.

As with each of the steps in mitosis, cytokinesis is highly regulated. If the cell were to divide its cytoplasm prior to the completion of duplication and segregation of the chromosomes, it is unlikely that each of the **progeny** cells would receive the proper genetic information. Thus the cell employs several regulatory mechanisms to assure that cytokinesis occurs only after all of the chromosomes have been properly segregated. There is, for example, a "spindle checkpoint" that assures that each and every chromosome has attached to the spindle. The entire process of cell division waits at the checkpoint until the conditions of the checkpoint have been satisfied.

progeny offspring

Once they have been, the process continues and concludes with cytokinesis. SEE ALSO CELL CYCLE; CYTOSKELETON; MITOSIS; MUSCLE

Rex L. Chisholm

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Cytoskeleton

The cytoskeleton is responsible for cell shape, motility (movement) of the cell as a whole, and motility of **organelles** within a cell. There are three types of filaments in the **cytoplasm** of most vertebrate cells: microfilaments, microtubules, and intermediate filaments. All of these filament systems share a critical feature: They are composed of proteins that have the unique property of being able to self-assemble into a filamentous network. Imagine a pile of bricks that could assemble by themselves into a wall; the proteins that make up the fibers of the cytoskeleton are able to do just this. The proteins that make each of the three different filament systems assemble into only the structure characteristic of that filament.

organelle membrane-bound cell compartment

cytoplasm material in a cell, excluding the nucleus

Unlike the human skeleton, the cytoskeleton is extremely dynamic, meaning the filament systems are able to lengthen or shorten very rapidly. This dynamic nature of the cytoskeleton is necessary for cells to be able to change shape, complete cell division, or migrate, and represents one of the cytoskeleton's most important features. Each of the self-assembling proteins has a characteristic concentration, called the "critical concentration," below which the **monomer** state is favored and above which the **polymer** state is favored. Increasingly, the subunit concentration favors filament building, and decreasing it favors filament deconstruction. This property allows the cell to rapidly control cytoskeleton structure.

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

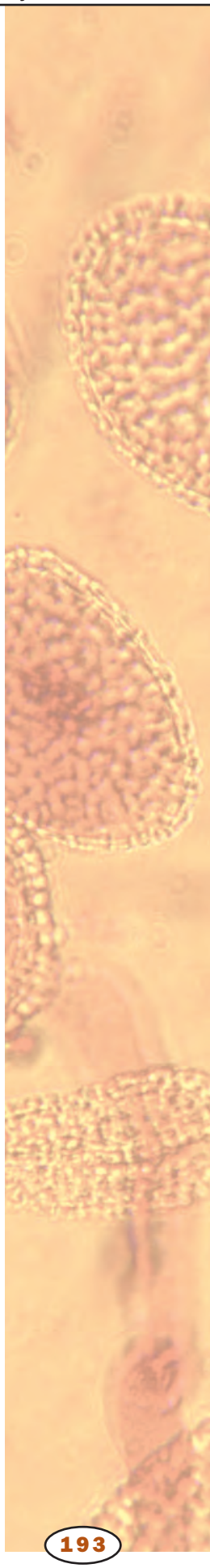
polymer molecule composed of many similar parts

Microfilaments

The microfilament system is a network of filaments 6 **nanometers** (nm) in diameter that are important for anchoring plasma membrane proteins, for producing cell movement, and for cell division. The base filament is composed of a protein called actin that is 42 kilodaltons (kd) in weight. Actin is also the protein that forms the thin filaments found in muscle. When purified actin is incubated in a test tube, 6 **nm** filamentous structures are formed. These threads consist of side-by-side actin monomers that twist around each other in a helix. Inside cells, actin exists in two states, the monomeric protein, called G-actin (for globular actin) and the 6 nm filament, called F-actin (for filamentous actin). The factor that determines the relative proportions of F-actin and G-actin is the concentration of actin protein. Each microfilament has a fast-growing, or "plus," end, and a slow-growing, or "minus," end. In most cells the plus ends of the filaments are oriented toward the edge of the cell. In this way rapid polymerization of actin monomers onto the plus ends of microfilaments can produce protrusions on the cell surface

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

nm nanometer; one-billionth of a meter



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

progeny offspring

enzyme protein that controls a reaction in a cell

vesicle membrane-bound sac

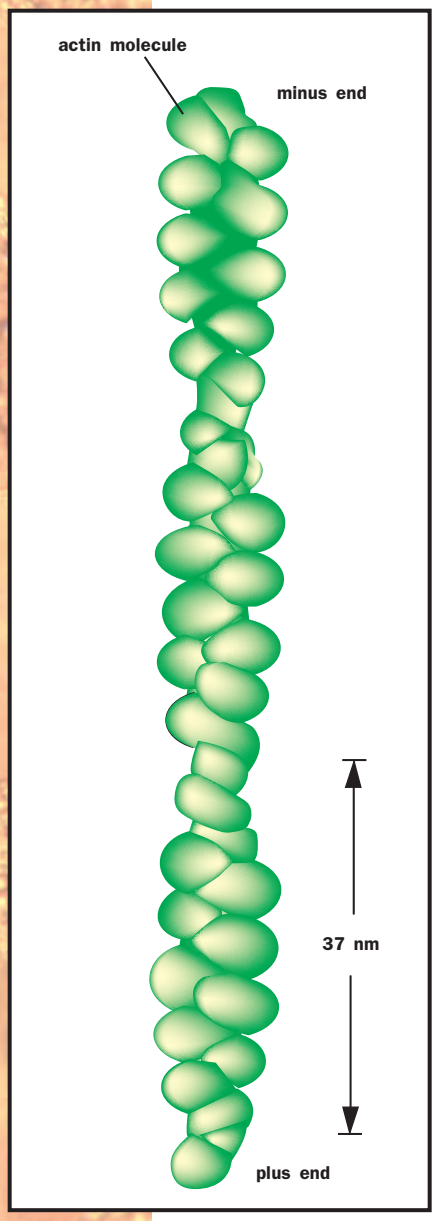
called **pseudopods**. These extensions are critical for the ability of cells to migrate in a directional fashion.

Microfilaments exist in their highest concentration in association with the cell periphery, where they are believed to play an important role in anchoring membrane proteins. Microfilaments can also be organized into bundles, called stress fibers, which serve as contractile elements, somewhat like little muscles, within cells. These structures are important for maintaining connections between the cell and the surface on which it grows. In addition, these structures may be important for producing contractility to generate directional force during cell motility. A third microfilament-based structure, the contractile ring, is critical for the separation of a cell into its two **progeny** during cytokinesis.

In most cells the concentration of actin exceeds the critical concentration for microfilament assembly, yet the actin is not entirely assembled into filaments. This occurs because cells make a variety of "actin-associated" or "actin-binding" proteins. One example of an actin binding protein is the G-actin-binding protein profilin. When bound to profilin, actin monomers cannot assemble into filaments. Binding of actin by profilin can effectively reduce the concentration of free actin monomer to below the critical concentration. The actin-binding activity of profilin is regulated in cells. Certain stimuli will cause profilin molecules to release their bound actin monomers, effectively increasing the concentration of actin and thereby stimulating actin assembly. Thus cells can control the relative proportions of G-actin and F-actin.

In general, the functions of actin-associated proteins are to modify the properties of the microfilament network in cells. Some filament-associated proteins, for example the protein tropomyosin, bind along the length of the filament to stiffen it. There are also proteins such as villin or filamin that bind microfilaments together side by side to produce bundles of actin filaments. Other actin-binding proteins cross-link actin filaments to form mesh-like structures such as those found in association with the cell membrane. Cells can also control the length of filaments through the action of proteins that can cut filaments to produce two shorter filaments. To keep the filaments a certain length, cells produce "capping" proteins that bind to the ends and prevent the addition of new actin subunits. By modulating the state of the microfilament network the cell can control the physical properties of the cytoplasm such as rigidity and viscosity.

One of the most interesting types of actin-associated proteins is a family of **enzymes**, called myosins, which have the ability to convert chemical energy into movement. The characteristic property of these so-called myosin molecular motors is their ability to bind actin in an adenosine triphosphate–sensitive fashion and to produce movement of actin filaments. Over fifteen different types of myosin motors have been identified. Some of them, such as those involved in cytokinesis and cell motility, are two headed, meaning they have two actin-binding motor domains, while others have only one head. Some of these myosins are involved in the movement of membrane-bound **vesicles** along actin tracks. The best characterized of these molecular motors, myosin II, slides actin filaments past each other either to power contraction of the contractile ring or to produce cell migration. A different version of this myosin motor forms the thick filaments that are responsible for the contraction of muscle.



Helical structure of actin molecules.

Microtubules

Microtubules are the largest of the cytoskeletal filaments with a diameter of 25 nm. There are many parallels between the microfilament cytoskeletal system and the microtubule system. Like microfilaments, microtubules are produced by the self-assembly of a subunit, which in the case of microtubules is a **heterodimer** composed of one alpha tubulin and one beta tubulin bound together. Alpha and beta subunits alternate to form a protofilament. Thirteen protofilaments line up side by side, forming the hollow tube of the microtubule.

heterodimer complex molecule composed of two different parts

Microtubules also have a fast-growing, or plus, end and a slow-growing, or minus, end. In most cells microtubules are organized in a radial array extending from a single site termed the microtubule organizing center (MTOC), generally positioned near the **nucleus**. This organization produces a network of microtubule tracks where the plus ends of the microtubules are near the cell surface and the minus ends are associated with the MTOC. This structure is well suited for the primary function of microtubules, which is to serve as tracks along which membrane-bound vesicles are moved. Vesicles transported include organelles such as **mitochondria**, as well as secretory vesicles destined for exocytosis.

nucleus membrane-bound portion of cell containing the chromosomes

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

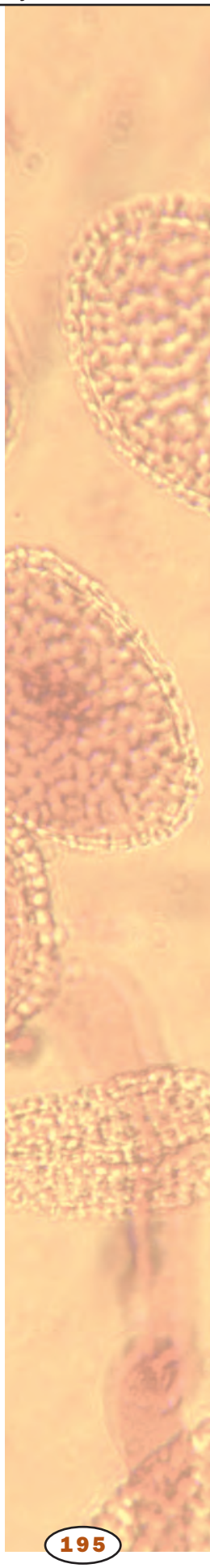
Another parallel with microfilaments is the highly dynamic nature of microtubules. Microtubules exhibit a phenomenon called "dynamic instability." Individual microtubules constantly grow and shorten, often shortening dramatically in a process called "catastrophe." This rapid turnover of microtubules allows cells to change shape quickly and facilitates reorganization of the tracks important for delivery of vesicles to sites throughout the cell. Like the microfilament cytoskeleton, the dynamics of microtubules can be modified by microtubule associated proteins, called MAPs. Some MAPs stabilize microtubules, while others cross-link microtubules, both with other microtubules as well as with microfilaments and the third cytoskeletal system, intermediate filaments (see below).

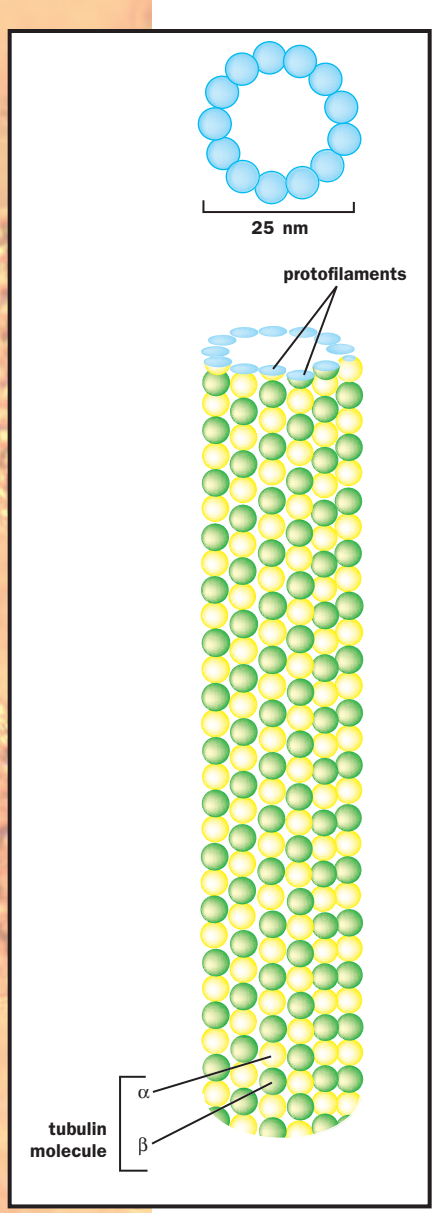
The dynamics of microtubules are also important for **mitosis**. Each time the cell goes through division the microtubule network is completely disassembled and the tubulin subunits are reassembled into a new structure called the spindle. The spindle is responsible for the segregation of **chromosomes** into each daughter cell and also plays an important role in specifying the position of the cleavage plane that will separate the two daughter cells (during cytokinesis).

mitosis separation of replicated chromosomes

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

The functions of microtubules in vesicle transport and chromosome segregation are dependent on molecular motors that bind to and move along microtubule tracks. These motors are divided into two families, kinesin and cytoplasmic dynein. Kinesin was the first microtubule motor to be identified. It is responsible for moving vesicles (the cargo of the motor) toward the plus ends of microtubules, that is, from the center of the cell toward the plasma membrane. Since discovery of the first kinesin, the family has been shown to consist of many members, some of which are important for spindle function during mitosis. Some of these kinesins move toward the minus ends of microtubules. In contrast, the other type of microtubule motor, cytoplasmic dynein, appears to move cargo exclusively toward the minus ends of microtubules, that is, from the cell periphery back towards the center.





Top: Illustration of the ring of 13 distinct subunits in a microtubule, each of which corresponds to a tubulin molecule. Bottom: A side view of a section of a microtubule, with the tubulin molecules in long, parallel rows called protofilaments.

hormone molecule released by one cell to influence another

secretion material released from the cell

keratin a major structural protein

The ability of these motors to move organelles around inside of cells is critical for processes such as **hormone secretion**, transmission of nerve impulses and recycling of membrane.

Intermediate Filaments

The third cytoskeletal system is called the intermediate filament system because the filaments, which are 10 nm in diameter, are intermediate in size between microfilaments and microtubules. There are many other features that set the intermediate filaments system apart from the other cytoskeletal systems. Unlike the other systems, which are composed of one or two different proteins, intermediate filaments can be formed by a relatively large number of different proteins. For example, the primary intermediate filaments found in epithelial cells (such as skin) are formed from pairs of **keratins**, one **basic** and one **acidic**. There are a large number of different keratin pairs, found in different tissues, that produce 10-nm filaments. Wool, hair, and nails are examples of structures formed from intermediate filaments. The different filament-forming keratins are developmentally regulated, and the keratins expressed early in embryos differ from those expressed later in development.

In contrast, a different cell type, **fibroblasts**, have intermediate filaments that are formed from a single protein, vimentin. In heart tissue, the intermediate filaments can be formed from a different single protein, desmin. In nervous tissue the intermediate filaments are formed from yet another family of **intermediate filament proteins** called neurofilament proteins. There are even structures in the nucleus formed from intermediate filament protein family members called nuclear lamins.

Although intermediate filaments can also self-assemble from their constituent subunits, the filaments differ from microtubules and microfilaments in that they do not have an obvious polarity. Structurally, intermediate filaments are formed from a bundle of subunit proteins which themselves are extended in structure, as compared to the more globular-shaped protein subunits that form microfilaments and microtubules. Intermediate filaments are generally more stable structures than the other cytoskeletal systems, although recently it has been shown that subunits are capable of exchanging in and out of the filament all across their length. Like other filament systems, intermediate filaments have associated proteins, but interestingly no molecular motors that use intermediate filaments as their track have been identified.

Intermediate filaments are organized within cells so that they link the cell surface and the nucleus. Intermediate filaments are believed to play an important role in cells by stabilizing structural integrity. Of all the cytoskeletal systems, intermediate filaments are best suited to play this structural role since they have the highest tensile strength (resistance to stretch). At the cell surface, intermediate filaments attach to specific junctions called desmosomes and hemidesmosomes. These junctions attach cells to neighboring cells or the extracellular **matrix**.

Mutations in intermediate filament subunit proteins have been shown to cause human diseases. For example, mutations in keratins cause blistering diseases that result from a loss of cellular integrity, causing cells to lit-

erally split in half. Similarly, mutations in the neurofilament proteins produce neurological diseases called neuropathies.

Cytoskeleton-Based Cellular Structures

Several cellular structures are built around a core of cytoskeletal proteins. Perhaps the best known examples are **cilia** and flagella. Flagella provide the motive force for sperm motility through their waving motion. Cilia line the surfaces of cells in the respiratory tract where their motion constantly moves mucus along the airway surface. The core of both flagella and cilia is composed of a highly organized bundle of specialized microtubules. Around a "central pair" of microtubules, there are nine pairs of modified microtubules called "doublet microtubules." The central pair and the outer doublet microtubules are connected by a number of different specialized proteins. The characteristic waving motion of cilia and flagella is generated by the action of a microtubule-based motor called axonemal dynein that moves the microtubules in the flagellum relative to each other. Axonemal dynein is related to the minus end directed motor cytoplasmic dynein that moves vesicles along microtubules. Dynein mutation causes cilia dysfunction, leading to respiratory illness and sperm immotility. Curiously, about half of the people with these mutations also have "situs inversus," in which the internal organs are reversed left for right.

Another microtubule-based cellular structure is the centriole. The centriole is a somewhat mysterious cylindrical structure containing vanes formed from microtubules that run the length of the cylinder. Centrioles together with the associated pericentriolar material form a somewhat larger structure called a centrosome. Centrosomes function as microtubule organizing centers during interphase of the **cell cycle**, and become the center of the spindle poles during mitosis.

Finally, several cell types such as intestinal epithelial cells have protrusions from their surface called microvilli. At the core of the mirovilli are bundles of actin filaments. These protrusions are believed to increase the surface area of the intestinal cells to maximize their ability to absorb nutrients. SEE ALSO CELL JUNCTIONS; CELL MOTILITY; CYTOKINESIS; ENDOCYTOSIS; MEMBRANE PROTEINS; MITOSIS; MUSCLE; NUCLEUS; PLASMA MEMBRANE; SLIME MOLDS

Rex L. Chisholm

basic having an excess of OH^- ions, and a high pH

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

fibroblast undifferentiated cell normally giving rise to connective tissue cells

intermediate filament protein one type of cytoskeleton protein

matrix a network, usually of threadlike fibers

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

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

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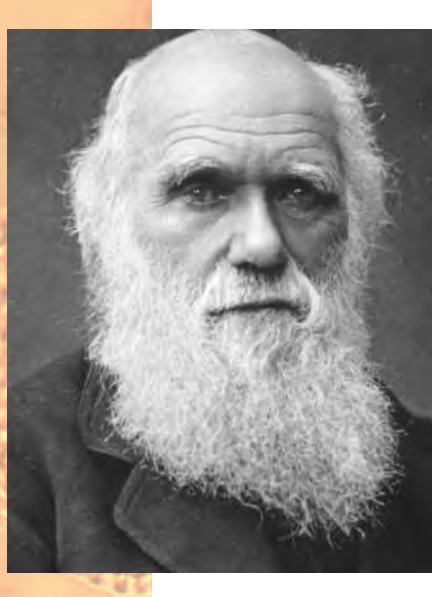
Darwin, Charles

English naturalist
1809–1882

Charles Darwin was the founder of modern evolutionary thought, and the developer, along with Alfred Russel Wallace, of the theory that natural se-



Charles Darwin.

lection is a principle driving force in evolution. Darwin is generally recognized as the single greatest thinker in the history of biology, whose contributions provided the basis for understanding the immense diversity that characterizes the natural world.

Darwin was born February 12, 1809, into a wealthy English family. A lifelong interest in natural history led him to embark, at age twenty-two, on a five-year voyage to South America aboard the HMS *Beagle* as the ship's naturalist. Darwin collected a wealth of specimens and made observations of both living species and fossils he encountered. Darwin was particularly struck by similarities he observed between the species found on the Galapagos Islands off the western coast of South America, and species of the mainland. He also noted differences and similarities among species found on the numerous islands of the Galapagos. The evidence suggested each species had not been independently formed by the Creator, but rather had diverged from a smaller group of common ancestors.

Upon returning home, Darwin pondered these ideas in conjunction with two other streams of thought. The first was the theory of uniformatarianism of geologist Charles Lyell. Uniformatarianism held that major geologic features, such as mountains and canyons, were formed not by rapid and short-lived catastrophic events such as floods, but rather by the slow, steady action of forces such as erosion. This mechanism suggested that Earth was much older than previously believed, a fact which Darwin saw provided the requisite time for the steady accumulation of change that would turn one species into another. The second idea was from *An Essay on the Principle of Population*, in which economist Thomas Malthus contrasted the potential for exponential increase in human population with the much slower increase in food supply. Malthus suggested that competition, disease, war, and famine kept the human population in check. Darwin saw that this principle provided the selective force needed to bring about change in a species.

Natural Selection

Between 1837 and 1838, Darwin developed his ideas into the principle of natural selection, which combines struggle, heritable variation, and differential reproduction. He proposed that in all species, limited resources leads to a struggle for existence, either against other members of the species, or against the environment. Members of a species differ from one another, and some of those variations influence the success of an organism's struggle. Organisms with more useful variations will leave more offspring, who inherit those variations and so are better able to cope with the environment. As this process continues over time, with successive rounds of struggle, variation, and differential reproduction, the population will become increasingly well adapted to the environment. Organisms of one species who become separated into different environments, such as the birds of the Galapagos, could develop over time into separate species through the accumulation of differences best adapted for their separate environments.

For the next decade, Darwin collected evidence to support his theory, and discussed his ideas only with a small circle of colleagues. But in 1858, he learned that naturalist Alfred Russel Wallace had developed a similar theory. Urged on by friends, Darwin agreed in 1858 to jointly submit papers

with Wallace to the *Journal of the Linnaean Society*, and this was how the world first learned of the principle of natural selection. A year later, Darwin published *On the Origin of Species, or the Preservation of Favored Races in the Struggle for Life*. It is no exaggeration to call this the most important book ever published in biology. In it, Darwin provided so convincing an argument for natural selection that it became widely accepted by scientists shortly after publication. With natural selection, Darwin had provided a mechanism for evolution and an explanation for the diversity of life.

Despite the power of the arguments Darwin provided, numerous problems remained with the theory, especially with the mechanism of inheritance. Critics argued that blending of traits (for instance, tall with short to give medium height) would ultimately dilute out any variations. It was not until the particulate nature of inheritance was discovered, from the work of Gregor Mendel, that this problem was resolved.

Darwin continued to explore the ramifications of natural selection in a series of books published over the next twenty years. In 1871, he published *The Descent of Man, and Selection in Relation to Sex*, in which he applied the theory of natural selection to argue that humans evolved from earlier ape-like creatures, and suggested sexual selection as an important adjunct to natural selection.

On his death in 1882, in recognition of his scientific achievements, Darwin was buried in Westminster Abbey, along with Isaac Newton, Michael Faraday, and other great English scientists. SEE ALSO Adaptation; Buffon, Count (Georges-Louis Leclerc); Creationism; Evolution, Evidence for; Lamarck, Jean-Baptiste; Mendel, Gregor; Natural Selection; Sexual Selection; Species

Richard Robinson

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HUXLEY, THOMAS HENRY (1825–1895)

English biologist and paleontologist famous for his enthusiastic public debates in support of English naturalist Charles Darwin's theory of evolution. Huxley never finished college, but went to work as an assistant surgeon aboard a British frigate. When he returned to England four years later, he had sent home so many specimens and scientific papers that he was immediately elected to the Royal Society. He never returned to college.

De Saussure, Nicolas-Théodore

Swiss botanist
1767–1845

Nicolas de Saussure was an early pioneer in plant physiology. He was born and lived in Geneva, Switzerland, and later became professor of mineralogy and geology at the Geneva Academy. De Saussure's most famous book was *Recherches chimiques sur la végétation*, or "Chemical Research on Plant Matter," published in 1804.

De Saussure studied gas and nutrient uptake in plants, using the scientific method of controlled experimentation. By enclosing plants in glass containers and weighing the plants and enclosed carbon dioxide before and after, de Saussure demonstrated that plants absorb carbon dioxide during photosynthesis. This showed that carbon in plants comes from the atmosphere (not the soil, as some believed). Extending the work of Jan Ingenhousz, who showed oxygen was released during photosynthesis, de Saussure proved that

the volume of carbon dioxide absorbed is approximately equal to the volume of oxygen consumed. Because the weight of carbon absorbed was less than the total weight increase of the plant, de Saussure reasoned that water is absorbed, and in so doing correctly outlined the major chemical transformations in photosynthesis.

De Saussure also studied oxygen consumption in germinating seeds and plants grown in the dark, and argued (correctly) that the use of oxygen by plants was similar to that of animals. Later in life, he analyzed plant ashes to show that the mineral composition differed from that of the soil, thereby demonstrating that plants absorb nutrients selectively. SEE ALSO VAN HELMONT, JAN; HISTORY OF PLANT PHYSIOLOGY; INGENHOUSZ, JAN; PHOTOSYNTHESIS

Richard Robinson

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Dentist

A dentist is a medical professional who cares for the oral health of his patients. Dentists administer both prophylactic (preventative) care and corrective treatments for teeth and gums. Dentists in a general practice perform procedures such as cavity filling, root canals, gingivitis (gum disease) correction, and much more. Specialties in dentistry include orthodontics (structural correction), oral surgery, pediatric dentistry, endodontics (complex root canals and dental implants), oral surgery, periodontics (advanced gum care), and prosthodontics (reconstructive dentistry).

The most familiar work setting for a dentist is private practice. Traditionally, dentists in private practice provide oral health services for families. However, dentists are also employed in a variety of other situations. For example, many hospitals (especially those that specialize in long-term care, such as geriatric and psychiatric hospitals) employ dentists to attend to the oral health of their patients. Additionally, public health agencies that organize relief efforts for inner cities, the rural poor, or developing nations employ dentists to provide dental care to people groups that cannot normally afford it. Many insurance companies also employ dentists as consultants that help review and process dental claims.

In order to become a dentist, one must attend four years of dental school after obtaining a bachelor's degree from an undergraduate college. To gain admittance into dental school, a strong high school and college background in biology, chemistry, math, and physics is required. SEE ALSO DOCTOR, FAMILY PRACTICE; MEDICAL ASSISTANT

Susan T. Rouse

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Desert

Deserts are environments shaped by aridity, or dryness. Aridity reflects the balance between precipitation and potential evapotranspiration (PET), or the air's ability to absorb water (determined by temperature and water content). In arid zones, precipitation may be 5 to 20 percent of PET; semi-arid regions receive more precipitation, and hyper-arid regions less, in relation to PET.

Features of a Desert

Roughly one-third of Earth's land surface is arid or semi-arid. The major desert regions are: Australia, western North America, western South America (Atacama), southern Africa (Namib), and Asia-northern Africa. There are so-called polar deserts; however, most arid lands are in the warm subtropics.

There are two primary causes of aridity. One is the subtropical high-pressure belts, where high altitude air masses move away from the tropics. Tropical heat causes air to rise and cool, and therefore drop moisture as it moves away from the equator. The air then becomes more cool and dense. This air then sinks, warms as it nears the surface, and regains the ability to absorb water, thus creating zones of aridity. A second cause is the rainshadow effect caused by mountain ranges. Continental interiors are dry because most air masses have moved long distances or over mountains and in doing so have lost water.

Desert conditions may be quite harsh. Intense solar radiation and lack of shade cause surface temperatures as high as 50 degrees Celsius (130 degrees Fahrenheit). Limited precipitation and rapid evaporation greatly limit plant growth, and water is rarely available for animal consumption. Precipitation is predictable in some systems (such as winter rains in California's Mojave) but nonseasonal in others. Many sites experience long rain-free periods; in portions of the Atacama, rainfall has never been recorded.

Variability is another characteristic of deserts. Precipitation is episodic; rainstorms may be quite intense, with much of the annual total falling in just minutes. Similarly, resources may be spatially patchy. Arroyos or erosion channels and low spots may collect runoff from surrounding areas; rockiness and soil surface crusts contribute to runoff. Seeds and litter accumulate and support plant growth in low, relatively moist locations. Permanent water sources (desert springs or oases) are rare but important.

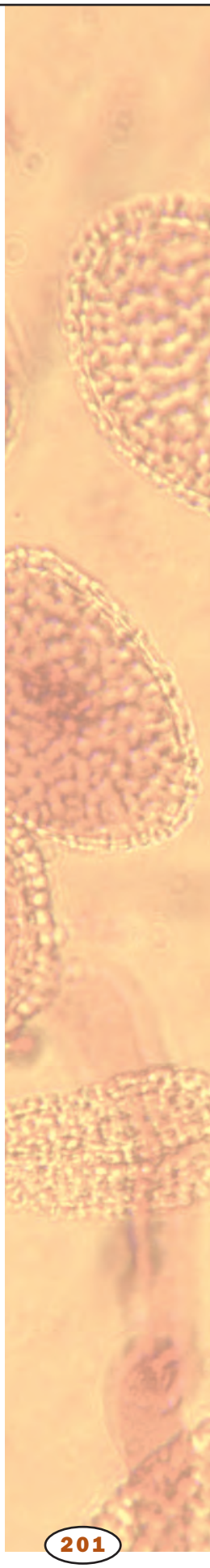
Evaporation draws water from the surface, leaving dissolved **minerals** as a salty crust. Sparse plant growth adds little **organic** material to the soil; thus the soil has limited capacity to retain water and minerals. Sparse vegetation also increases the erosional influences of high wind, runoff, and extreme temperatures. Sand dunes are accumulations of eroded materials; their instability makes them harsh environments for most organisms.

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

organic composed of carbon, or derived from living organisms

Desert Life

Desert organisms adapt to arid environments either by tolerating extreme conditions or by escaping them. Toleration is survival under stress. Many adaptations are related to water acquisition. Plants may have shallow, extensive root systems to absorb rainfall from the largest area possible. Animals obtain moisture from live food. Tenebrionid beetles of the Namib



Shadows form on the El Oued dunes in the Sahara Desert in Algeria.

oxidation reaction characterized by loss of electrons, or reaction with oxygen

extract water from coastal fogs: The beetles do "headstands" on dune ridges, and moisture condensing on the beetle's textured carapace trickles down to the mouth. Kangaroo rats obtain virtually all of their water by **oxidation** of fats in dry seeds (metabolic water). Other adaptations involve water retention: storage of water in succulent tissues; specialized photosynthetic processes minimizing water loss; leaflessness, small leaves, or leaf loss during drought, also reducing plant water use; and animal use of burrows or shade. Finally, some organisms simply tolerate tissue dehydration.

Escape or avoidance results in activity only during favorable periods. Annual plants, completing their life cycle in a single year, are abundant in many deserts. They may spend years as dormant seeds; only after sufficient rainfall do they germinate and grow, reproducing quickly before the soil redries. Some invertebrates and amphibians remain dormant up to several years, the invertebrates as eggs or in the "suspended animation" of **cryptobiosis**, the amphibians as **aestivating,** or dormant adults, beneath the surface. When temporary ponds form after rain, these organisms hatch or awaken; feeding, reproduction, and growth of juveniles are all a race against time so that at least some mature before the ponds dry. Some organisms are

cryptobiosis when a plant or animal becomes so inactive that its life processes nearly come to a stop

aestivating remaining dormant for the summer

A high desert oasis in Sedona, Arizona.

nomadic or migratory, finding temporary patches created by local rainfall: These include large mammals such as antelope, birds, and even insects (for example, desert locusts or grasshoppers).

Arid and semiarid regions have been important for livestock grazing throughout history. As energy sources have made irrigation feasible, some regions have been converted to cultivation. Urban populations are increasing rapidly where groundwater or river water is available and affordable; the southwestern United States, for example, contains several rapidly growing metropolitan areas in desert, such as Phoenix, Arizona. Depletion of underlying groundwater is a major environmental consequence in such areas.

SEE ALSO BIOME; GRASSLAND; WATER CYCLE

Laura F. Huenneke

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Desertification

savanna open grassland with sparse trees

Desertification is the degradation of grasslands, **savannas**, and woodlands to a more desert-like condition, with resulting decrease in plant production and the land's ability to support livestock grazing or other human uses. Vegetation becomes sparse; exposed soil becomes more vulnerable to erosion; and yields from cropland or grazing are reduced. The margins of most semi-arid regions (in North and South America, much of central Asia, the African Sahel, South Africa, and Australia) are at high risk of desertification. Estimates of land degradation rates range from 50,000 to 120,000 square kilometers per year, affecting up to 60 percent of semi-arid rangeland and cropland.

ecosystem an ecological community and its environment

Multiple causes may trigger desertification. Climatic shifts, especially long-lasting drought cycles, can drive **ecosystems** to more desert-like conditions. Over the past 40,000 years many regions have experienced repeated shifts in vegetation from semiarid to desert and back again in response to natural environmental variation. Semiarid ecosystems contain organisms well adapted to tolerate drought under natural conditions. Human activities such as woodland clearance, severe soil disturbance, or inappropriate cultivation practices have clearly contributed to desertification in many regions, and human disturbance makes semi-arid systems vulnerable to further degradation.

Frequently, desertification is marked by the decline of grasses and the replacement of continuous grasslands by scattered shrubs and thorny vegetation, leaving much bare soil. One result is that soil resources become more concentrated around the large plants, and conditions grow increasingly difficult for most organisms in the bare areas. These exposed surfaces are then vulnerable to further degradation through erosion, evaporation, and high temperatures. Desertification can also result when cultivated areas are abandoned and soil conditions have been so altered as to impede recovery of natural ecosystems. Such alterations include erosion, increased salt from irrigation, and loss of soil organisms.

Desertification is a challenge to developed as well as developing nations. Because semi-arid ecosystems have historically been important as livestock-producing areas, desertification has negative consequences for human populations. Desertification may also trigger further aspects of global environmental change. The increased proportion of bare soil relative to green vegetation can change Earth's radiation balance (the balance between absorbed and reflected solar energy) and thus temperatures. Dust eroded from exposed soil can be transported long distances, affecting other ecosystems and altering air quality.

Minor changes in average climate may have potentially large effects on semi-arid vegetation; hence "global warming" could exacerbate desertification. Because air temperature, carbon dioxide (CO^2) concentrations, and relative humidity affect plant growth and water use in complex, interacting ways, it is difficult to predict the net effect of atmospheric and climatic changes on dryland vegetation. Even if warming climate were to result in greater moisture and hence more precipitation in some areas, some areas, such as continental interiors, would likely experience warming without significant additions of precipitation; hence concerns about desertification may

be well founded. However, intensified land use, higher numbers of grazing livestock, and other pressures resulting from growing human populations are likely to be far more significant drivers of desertification in the near future than any climatic shifts. SEE ALSO DESERT; GLOBAL CLIMATE CHANGE; GRASSLAND

Laura F. Huenneke

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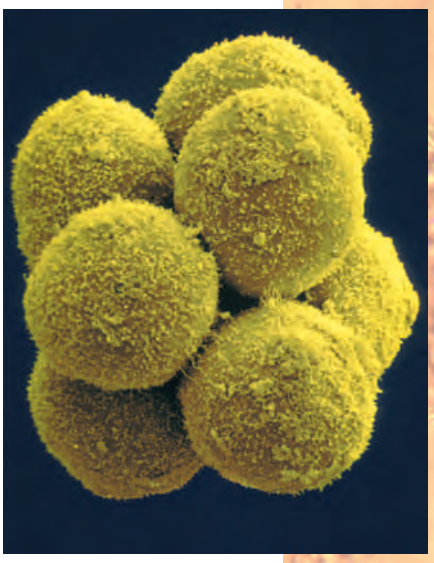
Development

Reproduction and development are integral factors of life. Multicellular organisms arise through a process that begins with the fertilized egg and ends with a new individual. The fertilized egg undergoes cell divisions to increase the number of cells; simultaneously, the cells produced differentiate into the organs and organs systems of the fully formed organism. The scientific study of these developmental processes is called embryology. Aristotle (384–322 B.C.E.), considered the first embryologist, described the growth of a chick embryo from a small dot of tissue to a fully formed bird.



A scanning electron micrograph of a human embryo at the eight-cell stage (day three).

Early Ideas in Embryology

Prior to the mid-1800s, scientists believed that development was the result of preformation. Preformation means that animals develop from an already existing miniature animal that merely required the right conditions to unfold and grow into a new organism. Scientific debates over whether the miniature animal was contained in the egg (ovum) or the sperm raged for decades. Scientists who believed that the miniature animal was in the egg were called ovists; those who believed that the miniature animal was in the sperm were called spermists.

In 1675, Marcello Malpighi (1628–1694), an ovist, reported seeing a miniature chick in the chicken egg. Anton Leeuwenhoek (1632–1723), a spermist, reported seeing a miniature human (homunculus) in each sperm (see Figure 1). In 1775, Lazzaro Spallanzani (1729–1799) demonstrated that both egg and seminal fluid were needed to produce a new individual. He conducted a series of experiments using amphibian eggs and seminal fluid. When the eggs were exposed to seminal fluid, they began to develop. However, if the eggs were exposed to filtered seminal fluid, fewer eggs developed. The more highly the seminal fluid was filtered, the fewer eggs developed. If the eggs were combined with the material left on the filter paper, they began to develop. Although Spallanzani correctly concluded that both egg and seminal fluid were necessary for development, he believed that the sperm seen in the seminal fluid were **parasites**. He postulated that the fertilizing agent was composed of the **proteins** and fats in the fluid.

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

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

William Harvey (1578–1657) viewed embryological development as a continuing process of remodeling and growth from unspecialized tissues to specialized structures. This theory, which is termed epigenesis, was largely ignored until 1759 when Kaspar Friedrich Wolff (1733–1794) offered empirical evidence of epigenesis from his detailed studies of chick development. In 1828, Karl von Baer (1792–1876) described four fundamental concepts of development. These four concepts, referred to as von Baer's law, are: (1) general features such as **appendages** appear earlier in the embryo than specialized features such as fingers; (2) development proceeds from general to specific characteristics; (3) as an embryo develops, it becomes increasingly different from other species; and (4) the early embryo of a higher animal is never like an adult of a lower animal, but only similar to the lower animal's embryo. Because they delineated the basic concepts of development, Wolff and von Baer are considered founders of modern embryology.

appendage attached organ or structure

Fertilization

The process of development begins with the fusion of **gametes**: egg (ovum) and sperm. The **motile** sperm swims to the egg, pierces its cell membrane and enters the cell. **Fertilization** is the fusion of the nuclei of the egg and sperm, and the single cell that results from this fusion is called the fertilized egg or **zygote** (see Figure 2). During fertilization, the genetic material of the sperm and egg are combined. Each gamete is **haploid**, that is, it contains one-half of the normal number of **chromosomes** for the species. At fertilization, the gametes combine to produce a zygote with the full number of chromosomes for that particular species. Another way to say this is that fertilization restores the **diploid** number. For example, haploid human gametes have twenty-three chromosomes; when the egg and sperm fuse, the diploid state of forty-six chromosomes is restored to the zygote. Thus, each parent contributes one-half of the chromosomal complement of the new individual, resulting in a new organism with genetic characteristics of both parents. This single cell, the fertilized egg, gives rise to all the organs of the individual—muscles, brain, liver, eyes—through highly regulated and timed processes.

gamete reproductive cell, such as sperm or egg

motile able to move

fertilization union of sperm and egg

zygote fertilized egg

haploid having single, non-paired chromosomes in the nucleus

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

diploid having pairs of chromosomes in the nucleus

The stages from fertilization to the birth or hatching of an individual organism are identical to those of all individuals of the same species. Developmental stages include rapid cell division or cleavage; formation of the germ layers through the process of gastrulation; and differentiation and growth of the organs and organ systems. These stages are categorized as the periods of embryogenesis (cleavage and gastrulation) and organogenesis (formation of organs and organ systems).

Cleavage

As soon as the sperm enters the egg, the cell membrane of the egg undergoes changes that prevent the entrance of additional sperm. Meanwhile, the chromosomes from each parent come together and, within a few hours, the first cell division begins. The egg degrades the **cytoplasm** and **organelles** of the sperm; only the chromosomes of the sperm contribute to the fertilized egg.

The early cell divisions of the fertilized egg are called cleavage. The fertilized egg divides into two daughter cells called blastomeres. These two

cytoplasm material in a cell, excluding the nucleus

organelle membrane-bound cell compartment

blastomeres divide into four blastomeres, the four blastomeres divide into eight, and so on. During cleavage, the total number of cells increases, but the size of each cell decreases. The reason for this strange situation is that cell division occurs so rapidly that there is not enough time for the individual cells to grow bigger. The constant doubling of cells during cleavage results in a multicellular embryo very quickly.

In a short period, the embryo has over one hundred cells arranged as a solid ball of blastomeres called a morula. The cells of the morula rearrange themselves into a single layer of cells surrounding a fluid-filled central cavity; the embryo at this stage is called a blastula (see Figure 2).

Gastrulation

The next step in development is the formation of the gastrula by invagination, the folding in of the cells of the blastula at a point called the blastopore. The resulting gastrula is a double-layer cup of cells. The outer layer of cells is termed the ectoderm and the inner layer of cells is termed the endoderm. The inner endodermal layer surrounds a new cavity, the primitive gut. A third layer of cells, the mesoderm, develops between the ectoderm and endoderm in most animals. Ectoderm, mesoderm and endoderm are the three germ layers from which all cells, tissues and organs develop (see Figure 2).

Cells of the ectoderm differentiate into the epidermis, hair, nails, claws, sweat glands, tooth enamel, brain, and spinal cord. Mesoderm differentiates into muscles, blood, blood vessels, heart, spleen, reproductive organs, and kidneys. Endoderm differentiates into the cells lining the digestive and respiratory systems, the liver, gallbladder, and pancreas.

Induction

One of the more fascinating aspects of development is the determination of body form, pattern, and differentiation. Put simply, how does a cell know what it is supposed to grow up to be? How do cells of the endoderm know they are supposed to form the digestive and respiratory systems? Induction is the process during which individual cells are "told" what they are supposed to become. A modern understanding of molecular events in development is discussed in the article *Genetic Control of Development* in volume 2 of this reference work. This essay outlines some pioneering work by Hans Spemann and Hilde Mangold.

Hans Spemann (1869–1941) received the Nobel Prize in 1935 for over twenty years of research on development in amphibians. In a series of elegant and delicate "baby hair loop" experiments, he demonstrated that when cells invaginate during gastrulation, they are induced to form specific cells and organs and that the primary inducer is a specific region of the blastopore. Spemann tied a strand of baby's hair around a fertilized newt egg so that the **nucleus** and some cytoplasm were on one side of the ligature while the other side contained only cytoplasm. After several cell divisions, Spemann loosened the ligature and allowed a nucleus to pass over into the other side. When cell divisions began on the side with the transported nucleus, the ligature was again tightened to separate the two masses of cells. The result was the production of two newt larvae, one a bit older than the other.

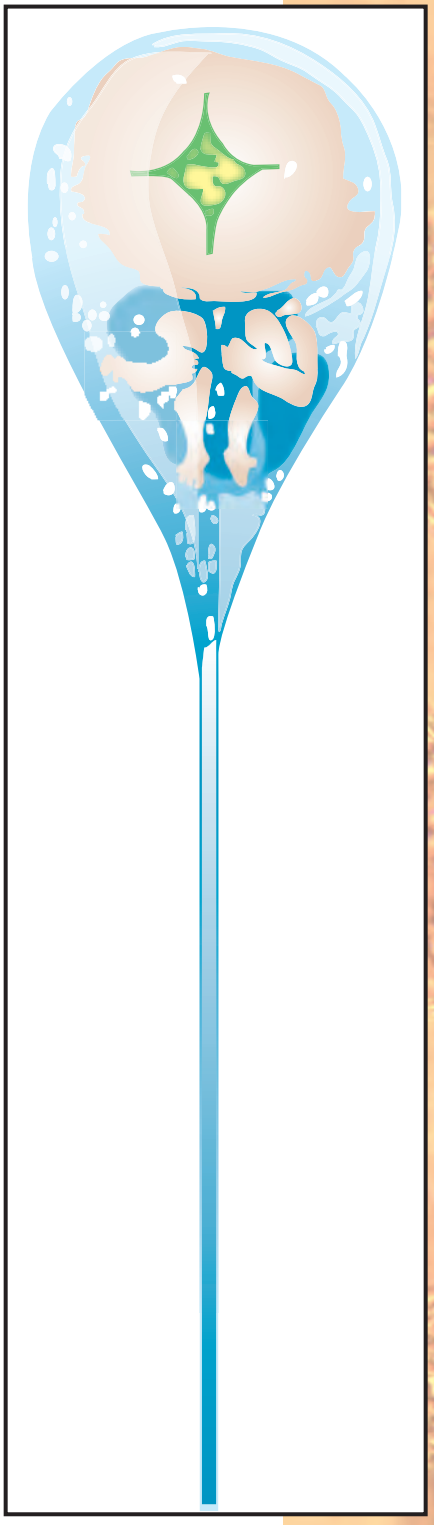


Figure 1. The human infant preformed in the sperm as depicted by Nicholas Haartsoecker (1694).

nucleus membrane-bound portion of cell containing the chromosomes

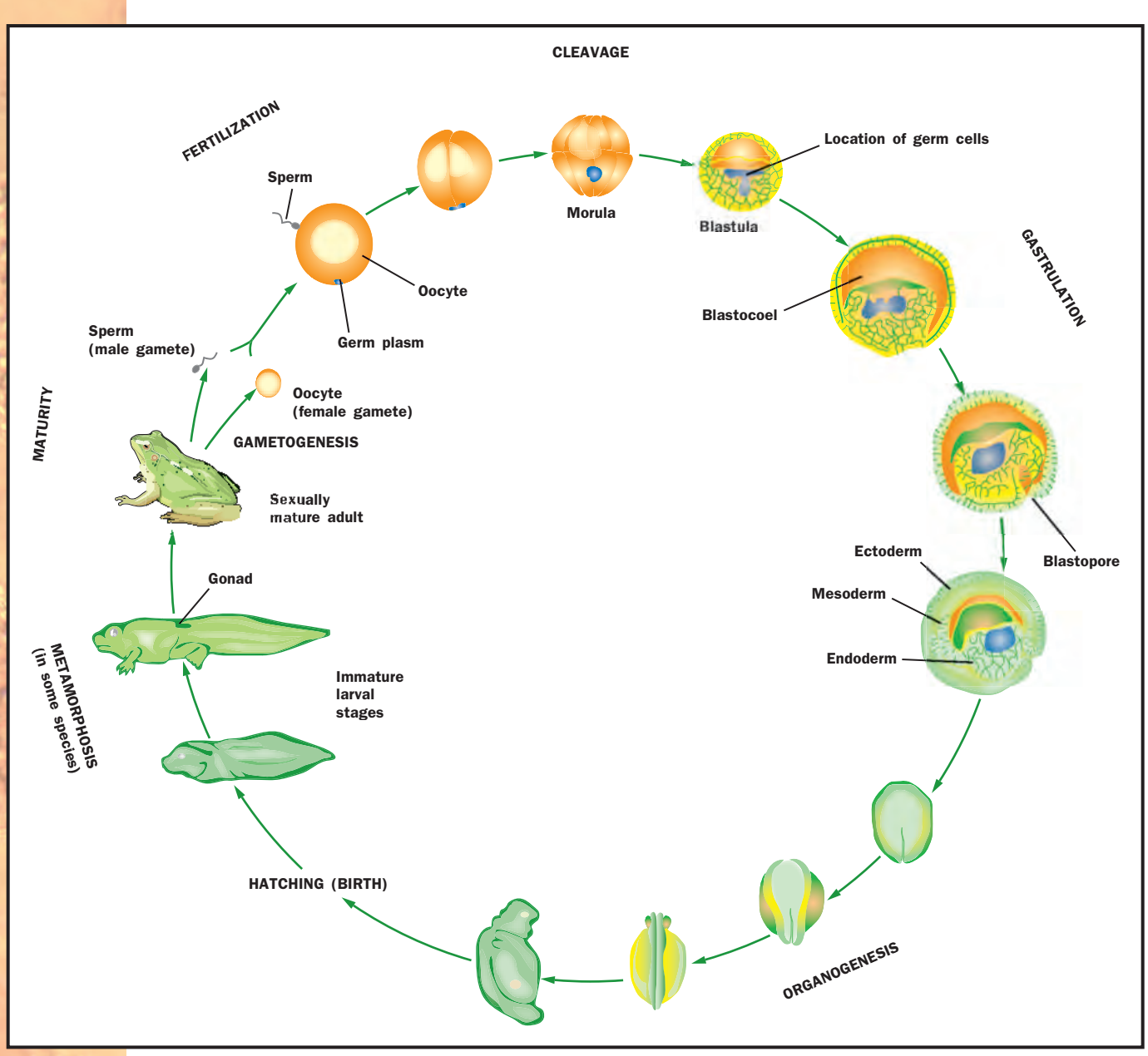
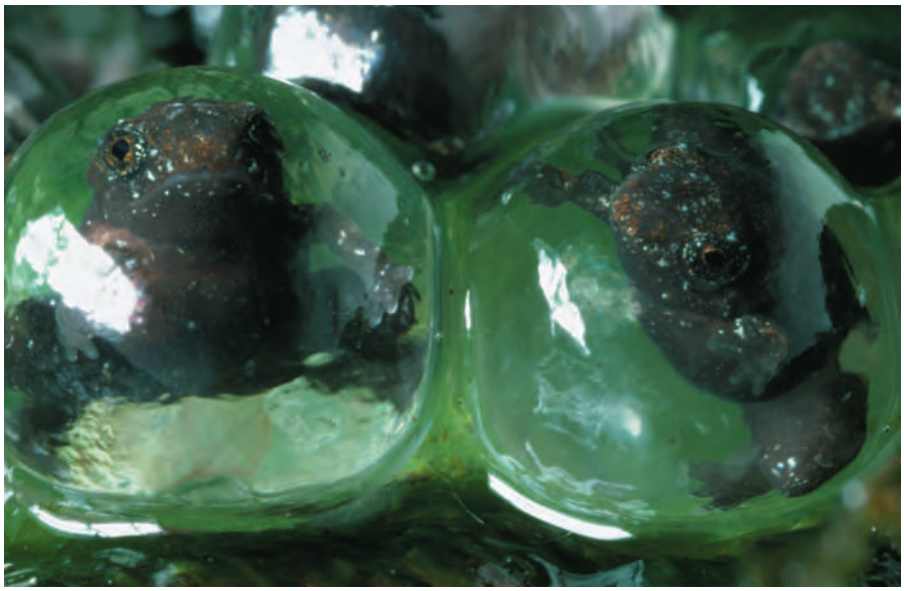


Figure 2. Developmental history of the frog. The stages from fertilization through hatching are known collectively as embryogenesis.

These experiments demonstrated that all the nuclei of an early embryo are capable of producing embryos. This ability is the basis for much current practice of cloning agriculture or lab animals.

In later experiments, Spemann found that the location of the ligature was important. If the ligature were placed so that each half of the fertilized egg contained the certain cells (called the gray crescent because of their color) from the region destined to become the blastopore, two newts would develop. However, if the ligature were placed so that the gray crescent was only on one half of the cell, that part would form a newt, but the half without the gray crescent would remain a formless mass of cells he called the belly piece. Further experimentation demonstrated that during gastrulation cells became committed to their developmental fates.

Spemann and his graduate student Hilde Mangold (1898–1924) demonstrated that specific cells of the blastopore are the only determining region



Frog embryos begin their development inside eggs.

in the gastrula. When these cells were transplanted to other embryos, the embryos were induced to undergo gastrulation and form a second embryo. These experiments that Mangold performed for her doctoral dissertation formed the foundation for much of Spemann's later work. Mangold died at age twenty-six when the heater in her apartment exploded. She could not share the Nobel Prize awarded to Spemann eleven years later because the prize is not awarded posthumously.

Protostomes and Deuterostomes

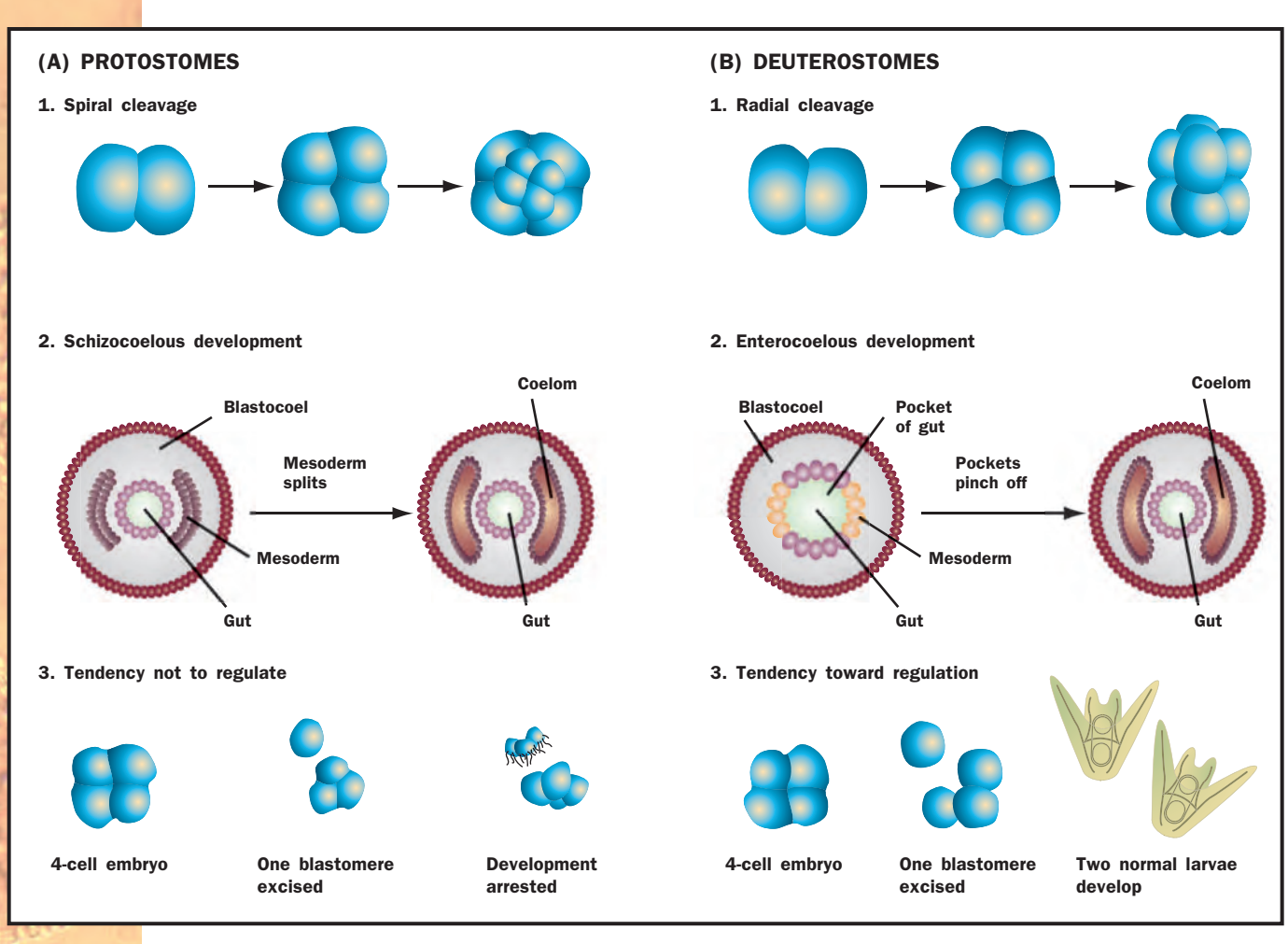
The fate of the blastopore is used to classify animals that have three germ layers into two large categories, **protostomes** and **deuterostomes**. Most adult animals have two external openings, the mouth and the anus, into the digestive tract. During gastrulation, the blastopore is the opening into the primitive gut. During further development, the blastopore becomes the mouth in animals classified as protostomes; the blastopore becomes the anus in deuterostomes. Organisms belonging to the phyla Mollusca (clams and snails), Arthropoda (insects and crustaceans) and Annelida (earthworms) are protostomes; members of the phyla Echinodermata (starfish) and Chordata (fish and humans) are deuterostomes. The type of cleavage and the development of the body cavity are other important differences between the protostomes and deuterostomes.

protostome "mouth first"; referring to the early development of the oral pore during gut tube formation

deuterostome "mouth second"; referring to the early development of the anal pore during gut tube formation

Protostomes exhibit spiral cleavage in which the blastomeres divide at acute angles to one another and are not aligned over one another. If one of these blastomeres is removed from the embryo, neither the removed blastomere nor the remaining cells develop into an individual. This type of determinate cleavage indicates that the fate of the daughter cells is determined early in development. A final characteristic of protostomes is that the body cavity, or coelom, develops as a split within the middle of the mesodermal layer. This type of coelom formation is termed schizocoelous development.

Deuterostomes, on the other hand, exhibit radial cleavage in which the blastomeres divide perpendicular or parallel to one another and are



Development in protostomes and deuterostomes.

aligned over one another. If one of these blastomeres is removed from the embryo, both the removed blastomere and the remaining cells can develop into individual organisms. This type of indeterminate cleavage indicates that the fate of the daughter cells is determined later in development. Identical twins are possible because of indeterminate cleavage. Genetic testing of human embryos is possible because of indeterminate cleavage: One blastomere can be removed from an eight-celled embryo and tested without interfering with the normal development of the remaining seven cells. In deuterostomes the coelom develops as buds from the primitive gut. This type of coelom formation is termed enterocoelous development.

Biogenetic Law

Ernst Haeckel (1834–1919), a physician, was so influenced by Charles Darwin's *The Origin of Species* that he gave up medicine and devoted himself to comparative anatomy. He disagreed with Darwin's theory of natural selection, and suggested that the environment acted directly on organisms, producing new species. In 1868, he proposed the biogenetic law, which sought to explain evolution as a series of stages in which the new characteristics of the next animal to evolve are simply added on to the lower animal. Briefly put, his biogenetic law stated that ontogeny recapitulates phylogeny (the

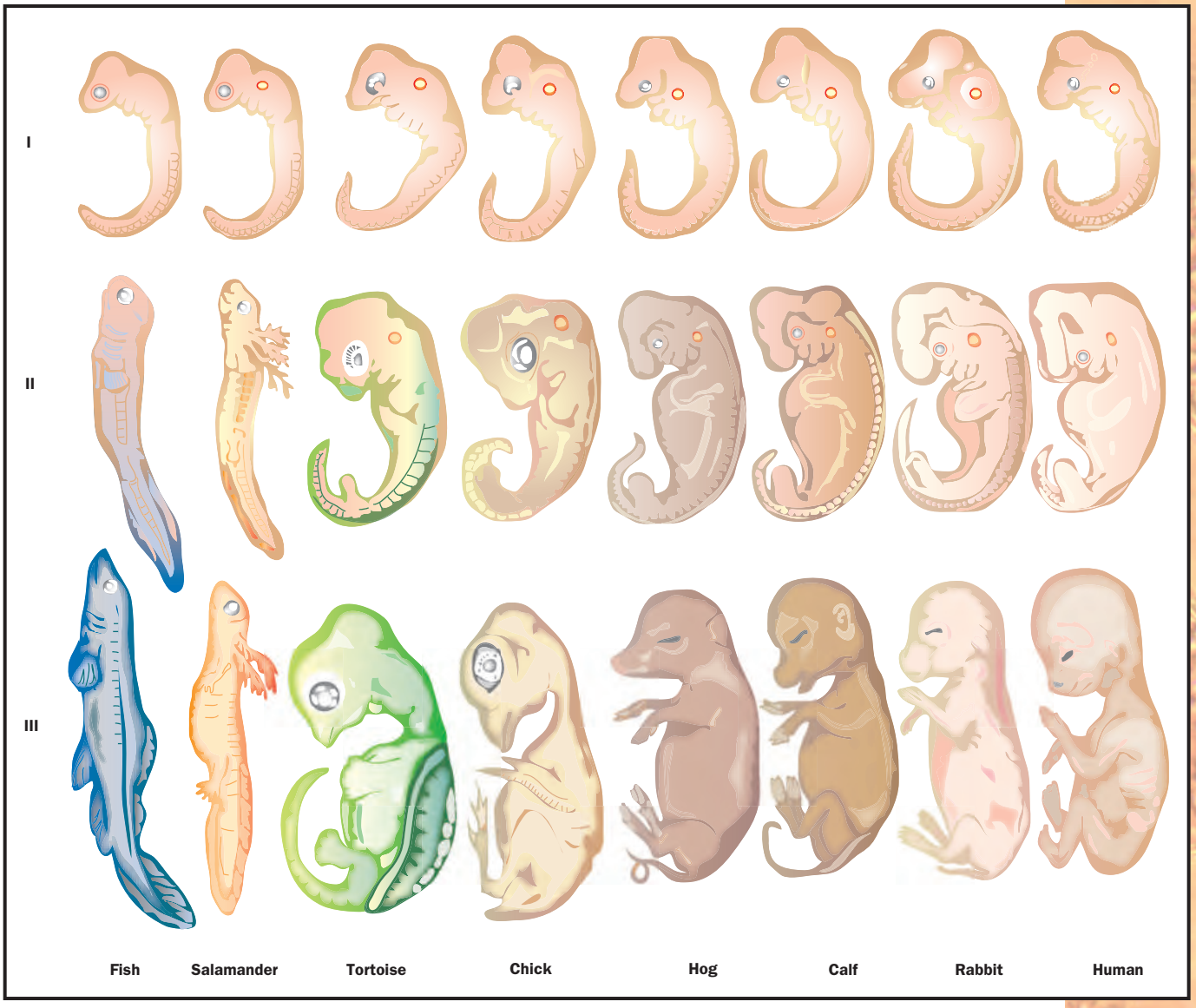


Figure 3. Illustration of von Baer's law.

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

embryological development of a particular species repeats the evolutionary history of that species). Although Haeckel is best remembered for his "ontogeny recapitulates phylogeny" statement, he also coined the terms **phylum**, ecology, and phylogeny.

Modern scientists do not subscribe to the biogenetic law as postulated by Haeckel. However, there are elements of recapitulation that are important in comparative embryology. In 1828, Karl von Baer pointed out that vertebrates share common characteristics during development (see Fig. 3). Examination of vertebrate embryos reveals that during corresponding stages of early development, the embryos appear to be very similar. For example, all vertebrate embryos pass through stages in which they have gill pouches. The pouches eventually develop into the gill apparatus in fish; in later-evolving vertebrates that do not have gills, the gill pouches undergo further refinement and develop into structures associated with the head and neck. Similarly, all early vertebrate embryos have

tails, which persist in some animals but regress during the later stages of development of humans. Thus, the individual development of an animal occurs through a series of stages that paint a broad picture of the evolutionary stages (phylogeny) of the species to which it belongs. SEE ALSO ANNELID; ARTHROPOD; CLONE; ECHINODERM; FETAL DEVELOPMENT, HUMAN; GENETIC CONTROL OF DEVELOPMENT; GROWTH; MEIOSIS; MOLLUSK; REPRODUCTIVE TECHNOLOGY

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Dicot

See Eudicot

Differentiation in Plants

Differentiation in plants refers to the processes by which distinct cell types arise from precursor cells and become different from each other. Plants have about a dozen basic cell types that are required for everyday functioning and survival. Additional cell types are required for sexual reproduction. While the basic diversity of plant cell types is low compared to animals, these cells are strikingly different. For example, some cells such as parenchyma cells retain the potential to respond to environmental and/or hormonal signals throughout their life and, under the right conditions, can be transformed into another cell type (transdifferentiation). Other cells such as the water-conducting vessel elements undergo cell death as part of their differentiation pathway and thus can never transdifferentiate to another cell type.

Meristem Origins

apical meristem growing tip from which all plant tissues arise

nucleus membrane-bound portion of cell containing the chromosomes

cytoplasm material in a cell, excluding the nucleus

ribosome protein-RNA complex in cells that synthesizes protein

Despite the differences among mature cells, all are ultimately derived from the **apical meristems**, populations of embryonic cells at the tips of the shoots and roots. Meristem cells are uniform in appearance: they are small and cuboidal in shape, and have a thin, flexible cell wall, a high **nucleus** to **cytoplasm** ratio, and dense cytoplasm with numerous **ribosomes**. The first step in the differentiation pathway is the formation of the precursors of the three tissue systems: protoderm (dermal tissue system), ground meristem (ground tissue system), and procambium (vascular tissue system).

Plant Tissue Systems

Each of the three tissue systems is found in a predictable location and consists of one or more multicellular tissues that carry out a unique function. For instance, the dermal tissue system is found at the surface of the plant and consists of a single tissue type, the epidermis. The epidermis functions

to protect the plant from water loss, to permit gas exchange, and to provide a barrier to the invasion of harmful fungi and other microorganisms. The ground tissue system occurs internally to dermal tissue and may consist of three tissue types: parenchyma tissue, collenchyma tissue, and sclerenchyma tissue.

Parenchyma tissue is a multipurpose tissue that functions in photosynthesis and storage, while both collenchyma and sclerenchyma function to support the aboveground parts of the plant against the pull of gravity. The vascular tissue system occurs at the center of roots, stems, and leaves and functions in the long-distance transport of water and **solutes**. It consists of two tissues: **xylem** tissue and **phloem** tissue. Xylem provides a conduit for the movement of water and dissolved mineral elements from the roots to the shoot system. In contrast, phloem transports an **aqueous** solution of the products of photosynthesis from the green photosynthetic shoots to the roots and other parts of the plant that are using or storing food energy.

solute dissolved substance

xylem water-transporting system in plants

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

aqueous watery or water-based

Overview of Plant Cell Types

Epidermal Cell Types. Epidermal cells are the most common cell type in the epidermis. These cells are often called "pavement cells" because they are flat polygonal cells that form a continuous layer, with no spaces between individual cells. Epidermal cells secrete the waxy **hydrophobic** substance cutin that polymerizes on the surface, forming a barrier to water evaporation. Epidermal cells are transparent because their plastids remain small and undifferentiated; hence light readily penetrates through to the photosynthetic tissues beneath the epidermis.

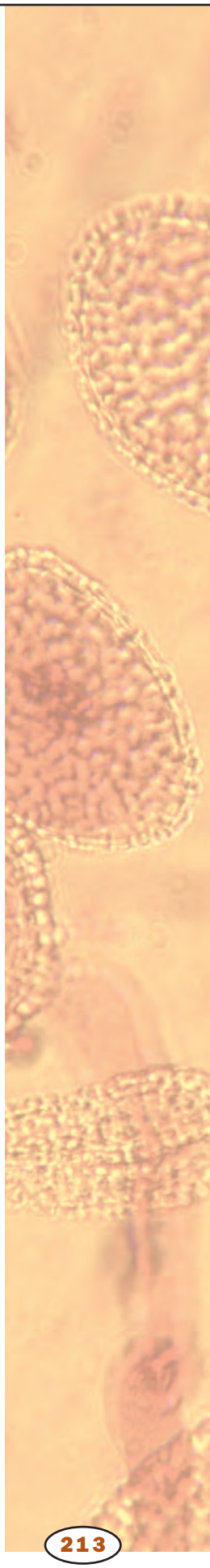
hydrophobic "water hating," such as oils

Two more specialized cell types are also found in the epidermis: **guard cells** and trichomes. Guard cells are kidney-shaped cells that are filled with chloroplasts. They always occur in pairs and form a small pore between them. The pair of guard cells and their pore is called a stomate and functions in gas exchange. Typically, the guard cells open the pore during daylight hours to allow CO_2 to diffuse into the photosynthetic tissues below. At night, however, the guard cells close the pore, preventing the diffusion of water vapor from internal tissues. The green chloroplasts of the guard cells function to provide the energy that fuels the opening and closing process.

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

Trichomes are long, narrow epidermal cells that grow perpendicular to the surface. Trichomes are either unicellular or multicellular and come in an amazing array of shapes. Some are branched and some are shield- or umbrella-shaped. Trichomes form a hairlike covering on the surface of leaves, stems, and roots and perform several important functions. The simple, unbranched trichomes of roots are called root hairs and function in the absorption of water from the soil. Trichomes on the surface of leaves and stems function primarily to retain water vapour and reduce the evaporative loss of water. Some trichomes secrete defense compounds that repel insect herbivores.

Ground Tissue Cell Types. Parenchyma cells are relatively unspecialized cells that make up the bulk of the soft internal tissues of leaves, stems, roots, and fruits. Parenchyma cells have thin, flexible cell walls and their cytoplasm typically contains a large, water-filled vacuole that fills 90 percent of the cell's volume. The vacuole may also contain compounds such as sugars (in



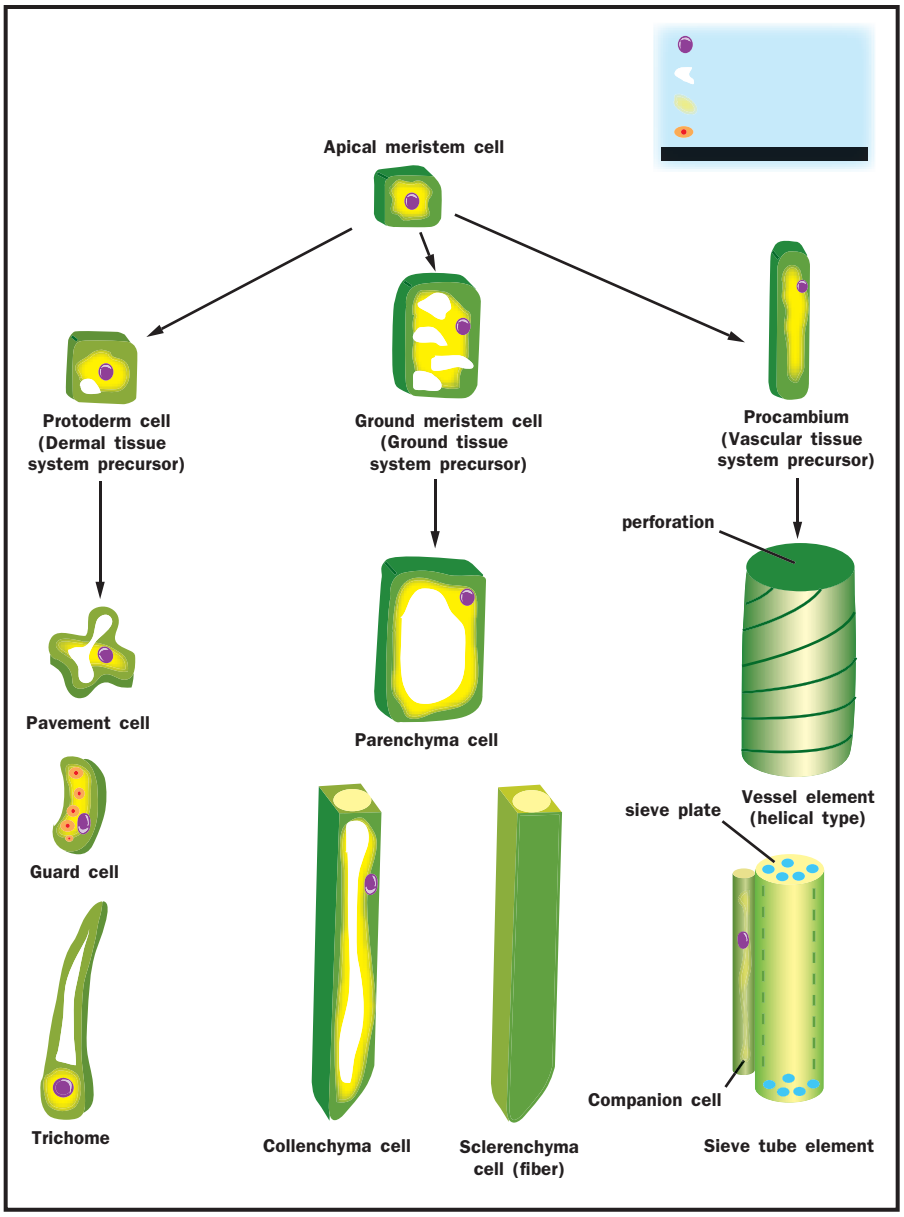


Figure 1. Distinct plant cell types are all ultimately derived from apical meristems.

organic composed of carbon, or derived from living organisms

sweet fruits such as apples), **organic** acids (as in oranges), or defense compounds such as the tannins found in tea leaves. Other specialized parenchyma cells may have starch-containing plastids such as those of potato tubers.

Collenchyma cells are long narrow cells with thick, strong, yet extensible, cell walls. Collenchyma cells are found in strands or sheets beneath the epidermis and function to provide support while a stem or leaf is still expanding. When growth is complete, sclerenchyma cells take over the role of providing mechanical support. Typical sclerenchyma cells are also long narrow cells (called fibers) with thick strong walls. Unlike collenchyma, the cell walls of sclerenchyma fibers are hard and rigid due to the deposition of **lignin** within the wall.

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

Fibers contribute more than half the volume of woody tissues and are found in all stems and leaves that are hard and tough. Other specialized sclerenchyma cells are shorter (sclereids) and have a protective function such as

those of seed coats, walnut shells, or peach pits. Since the supportive or protective functions of sclerenchyma are carried out by the **lignified** cell walls, there is no requirement for living cytoplasm and these cells typically die as part of the differentiation process.

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

Vascular Tissue Cell Types. The vascular tissues are complex tissues, each consisting of a number of distinct cell types. The xylem contains conducting cells called vessel elements, as well as sclerenchyma fibers and parenchyma cells.

Vessel elements are highly specialized cells. Like sclerenchyma fibers, they form a thick cell wall that is impregnated with lignin. This cell wall can take many forms, depending on the time and location of its formation within the plant. In tissues that are growing, the lignified part of the cell wall is formed in rings or a helix, allowing the vessel elements to extend as the plant grows. In nonexpanding parts of the plant the cell wall forms as a netlike or pitted structure; these patterns contribute to the mechanical support of the plant and prevent cell collapse. Vessel elements are aligned end to end within the xylem. The part of the cell wall between adjacent cells is degraded, so that the interior of all the vessel elements in a file becomes continuous, forming a vessel. Vessel elements are dead at maturity, leaving a hollow tube for the flow of water upward from the roots to the shoot system.

Phloem is also a complex tissue, containing two unique cell types, the sieve tube elements and companion cells, as well as parenchyma and sclerenchyma cells. Sieve tube elements are elongate cells with thick flexible cell walls. Adjacent cells are aligned end to end, forming the sieve tube. The end walls between adjacent cells have numerous pores; the sievelike appearance of these end walls led early microscopists to give these cells their name.

Sieve tubes transport the products of photosynthesis from the leaves to all parts of the plant where energy is needed or stored. The mechanism of transport requires that the sieve tube elements have a living cell membrane, but not other large components of the protoplast that might block the pores on the sieve plate. Thus mature sieve tube elements lack a vacuole, a nucleus, rough **endoplasmic reticulum**, and golgi. Sieve tube elements often live for years, but only because each is associated with a specialized parenchyma cell called a companion cell. The nucleus and cytoplasm of the companion cell must do the work for two cells, making and exporting the **proteins** required for sieve tube element function.

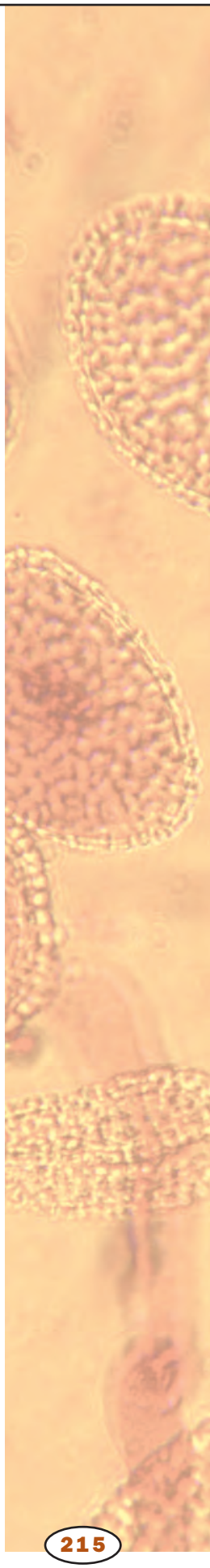
endoplasmic reticulum network of membranes within the cell

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

Examples of Cell Differentiation

Trichomes. The distinctive branched unicellular trichomes of plants such as *Arabidopsis* differentiate from undistinguished precursor cells in the protoderm. These precursor cells initiate the differentiation pathway by undergoing deoxyribonucleic acid (DNA) synthesis without accompanying cytokinesis, so that trichome precursors typically have eight or sixteen times the amount of DNA of adjacent pavement cells. Next, trichome precursors begin cell expansion in the plane perpendicular to the epidermis, forming a tubular extension. Once this stalk is formed, the nucleus migrates from the base of the stalk to its tip, using the cell's **cytoskeleton** to pull it to a new location. The trichome then undergoes an unusual pattern of cell wall growth, in which the cell wall balloons out at three locations, forming the

cytoskeleton internal scaffolding in a cell, composed of protein



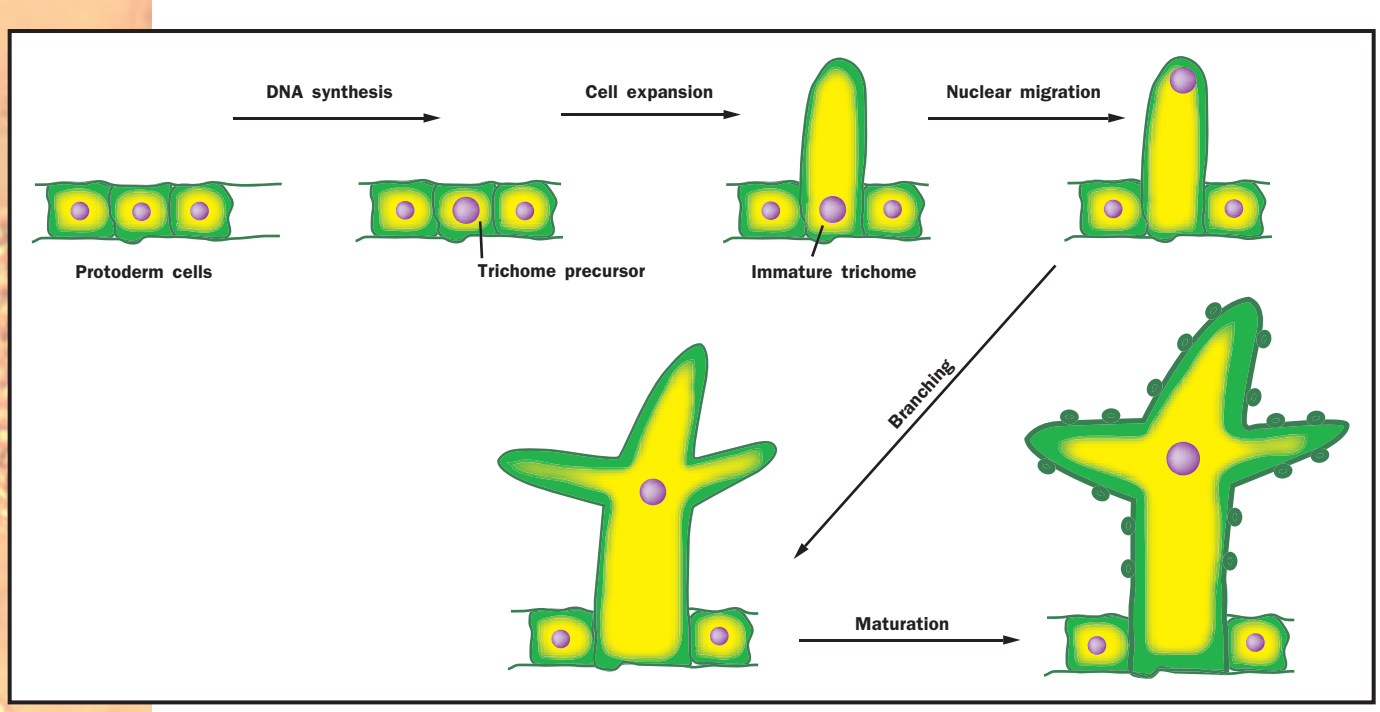


Figure 2. Trichrome differentiation.

three trichome branches. When the trichome cell has reached its full size and shape, it adds thickness to its cell wall and deposits sharp crystals of calcium oxalate on the surface of the trichome, adding to its effectiveness in defense against herbivores (see Figure 2).

Vessel Elements. Vessel elements differentiate from cells of the procambium. Vessel elements are first differentiated from other procambial cells because they expand more than their neighbors. Vessel element precursors next begin to deposit the thickened, lignified parts of their cell walls in either the ringlike, helical, netlike, or pitted pattern. The pattern can be predicted by the location of elements of the cytoskeleton within the cytoplasm that help guide wall precursor to the proper location. When cell wall synthesis is complete, special wall-degrading **enzymes** attack the end walls of the cell, forming the perforation between adjacent elements in a vessel. Finally, the vessel elements undergo programmed cell death. The cell makes protease enzymes and nuclease enzymes that reduce proteins and nucleic acids to their simple building blocks. Surrounding parenchyma cells absorb these small molecules, leaving an empty vessel (see Figure 3).

enzyme protein that controls a reaction in a cell

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

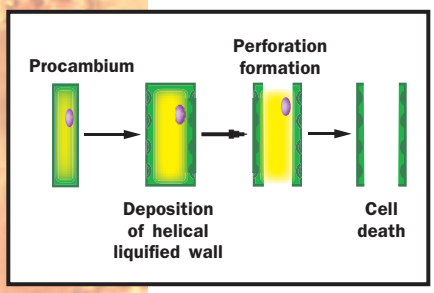


Figure 3. Vessel element differentiation.

Bundle Sheath Cells. In most plants, the cells of the photosynthetic ground tissue are uniform in size, shape, and chloroplast development. Two types of photosynthetic parenchyma cells are sharply differentiated in plants that have the C4 photosynthetic pathway, however. These two cell types, the mesophyll and bundle sheath cells, begin differentiation as similar-appearing ground meristem cells. During leaf expansion, the bundle sheath cells begin to enlarge first. The cell wall becomes thickened and impermeable to the diffusion of gases. Their plastids replicate, grow, and become asymmetrically placed within the cell. In contrast, the mesophyll cells undergo a minimal amount of enlargement and have thin, permeable cell walls. The number of plastids is low and the plastids remain small. During cell differentiation the **genes** encoding the enzymes of the C4 biochemical path-

way are expressed exclusively in the mesophyll cells, whereas the genes encoding the enzymes of the C3 pathway are expressed only in the bundle sheath cells (see Figure 4).

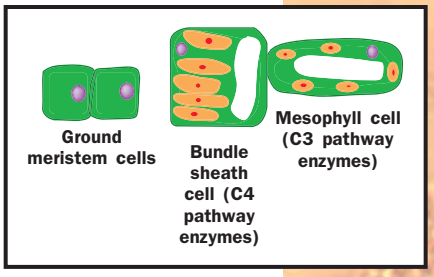


Figure 4. Bundle sheath cell differentiation.

Cell Differentiation and Development

Cell differentiation is only part of the larger picture of plant development. As plant organs develop (the process of organogenesis), the precursors of the tissue systems form in response to positional signals. Then, within each tissue system precursor, cell types must be specified in the proper spatial pattern. For instance, the spacing of trichomes and stomates within the protoderm must be specified before their precursor cells begin differentiation. Exchange of signals among neighboring cells is an important aspect of the processes of spatial patterning and cell differentiation. In addition, long distance signals are required so that the strands of xylem and phloem cells within the leaf vascular bundles connect perfectly with those in the stem.

Hormonal Influences

Many aspects of differentiation are controlled by **hormones**. The hormone auxin, for example, plays an important role in the differentiation of vessel elements, both in intact and wounded plants. This role was first demonstrated in experiments where small incisions were made in stem internodes that cut though the phloem and xylem of a single vascular bundle. Auxin produced by the apical meristem and young leaves above the wound induces parenchyma cells to regenerate the damaged vascular tissue. Parenchyma cells undergo transdifferentiation.

hormone molecule released by one cell to influence another

Although they already had differentiated as parenchyma cells from ground meristem precursors, they now repeat the steps that procambial cells take when they differentiate as vessel elements. Cells are induced to do this in a chainlike pattern, so that a new continuous strand of vascular tissue is formed as a detour around the original incision. Scientists know that auxin is involved, since transdifferentiation is blocked when the sources of natural auxin (young leaves and buds) are removed or when auxin transport inhibitors are applied. If natural sources of auxin are removed, and artificial sources added, transdifferentiation of parenchyma cells will occur, regenerating the vascular bundle. SEE ALSO C4 AND CAM PLANTS; CELL WALL; FRUITS; HORMONES, PLANT; LEAVES; MERISTEMS; ROOTS; SECONDARY METABOLITES IN PLANTS; SHOOTS; VACUOLE; WATER MOVEMENT IN PLANTS

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Digestion

Digestion breaks down foods into nutrient molecules that are small enough to be absorbed into an animal's circulatory system. Following digestion, nu-

trients are delivered to cells, where energy is extracted from their chemical bonds. Digestion often begins with a mechanical tearing apart of food into smaller pieces, which are then chemically dismantled in a stepwise fashion.

Because digestive chemicals are harsh, food processing in an animal's body takes place in compartments. Some single-celled organisms, such as protista, sequester food particles in food vacuoles, where **enzymes** break them down. Simple multicellular organisms, such as hydra and flatworms, have one-opening digestive systems. They must digest the nutrients and expel the waste before eating anew. Digestive systems of more complex animals have two openings, allowing simultaneous ingestion, digestion, and excretion. Roundworms have the simplest two-opening digestive system, which is little more than a tube. Enzymes in the tube break down the food, and nutrients are absorbed from there into the body fluids. More complex animals, such as vertebrates, have a gastrointestinal tract that is specialized into compartments where digestive enzymes and other substances process the food. Waves of muscular contraction called peristalsis help to move the food along.

enzyme protein that controls a reaction in a cell

Digestive system specializations reflect the lifestyles of their owners. Birds eat and digest nearly all the time. They can store food in an enlarged sac called a crop, and have a muscular organ called a gizzard that uses small pebbles to grind food. In some migratory species, the intestines actually enlarge before a long flight, enabling the animal to obtain energy throughout the journey. Ruminants such as cows have several stomachs, which contain **cellulose**-digesting bacteria, enabling them to digest grasses.

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

In humans, digestion begins at the mouth, where teeth tear food into small pieces, and the enzyme salivary amylase begins the breakdown of starch. During swallowing, food travels quickly through the **esophagus**, landing in the stomach. Here, the food is churned and further mechanically broken down as it mixes with gastric juice into a slurry called chyme. Each day, 40 million cells that line the stomach's interior release up to three quarts of gastric juice, which consists of water, mucus, salts, hydrochloric acid, and the enzyme pepsin, which breaks down **protein** into peptides. Hydrochloric acid unwinds proteins and kills many microorganisms.

esophagus tube connecting throat to stomach

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

After a length of time that reflects the components of the meal, a drawstringlike muscular structure called the pyloric **sphincter** at the stomach's exit opens, and chyme squirts into the duodenum, the first ten inches of the small intestine. The next two segments are the jejunum and the ileum. In addition to peristalsis, the small intestine undergoes localized muscle contractions that slosh the chyme back and forth, exposing it to several types of digestive enzymes. Trypsin and chymotrypsin continue the breakdown of peptides, and then peptidases break these down further into **amino acids**. Carbohydrases and pancreatic amylase continue the carbohydrate digestion that began in the mouth, and nucleases break down deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). Bile, which is produced in the liver and stored in the gallbladder, emulsifies fats, which are then chemically digested by lipases into fatty acids and monoglycerides. The pancreas secretes trypsin, chymotrypsin, amylase, lipase, and nucleases.

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

amino acid a building block of protein

Absorption of most of the products of digestion occurs in the small intestine. Water, **electrolytes**, and **minerals** are absorbed in the large in-

electrolytes ions in body fluids

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

testine. The remaining material, which consists mostly of bacteria, bile, cellulose and shed intestinal lining cells, is compacted into feces in the rectum, and exits the body through the anus. SEE ALSO DIGESTIVE SYSTEM

Ricki Lewis

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Digestive System

The human digestive system is responsible for food ingestion and digestion as well as the absorption of digested food molecules and the elimination of undigested molecules. It consists of a long tube called the gastrointestinal tract or GI tract (alimentary canal) and several accessory organs. The major components of the GI tract are the mouth, **pharynx**, **esophagus**, stomach, small intestine, and large intestine. The major accessory organs are the teeth, salivary glands, liver, gallbladder, and pancreas.

pharynx throat

esophagus tube connecting throat to stomach

Mastication and Swallowing

Ingestion (the intake of food) occurs in the mouth where food is chewed and mixed with saliva. The teeth have different shapes to perform different tasks; the incisors (chisel-shaped **anterior** teeth) are used to cut into food, the canines (pointed teeth located lateral to the incisors) are used to tear or pierce food, and the premolars and molars (having broad surfaces) are used for crushing and grinding food. Chewing (mastication) of food is accompanied by mixing of the food with saliva. The mouth is normally kept moist by the continual production of small quantities of saliva by numerous tiny intrinsic salivary glands located in the inner lining of the mouth.

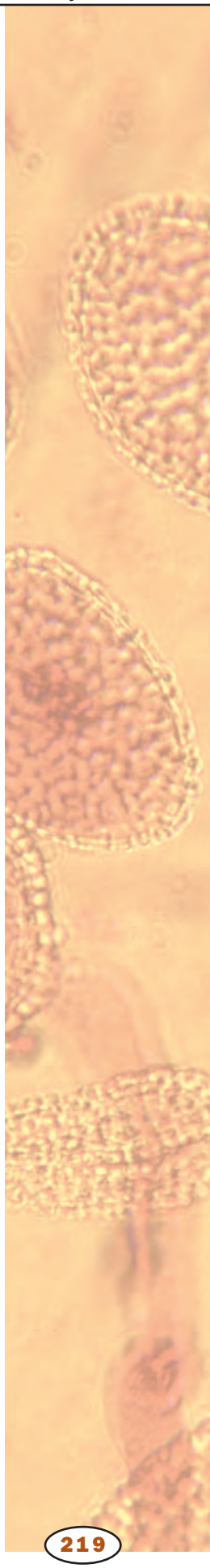
anterior toward the front

During chewing, much greater quantities of saliva are secreted by three pairs of extrinsic salivary glands, namely the parotid glands (located under the skin anterior to each earlobe), the submandibular glands (located under the base of the tongue), and the sublingual glands (located in the floor of the mouth). Saliva is a watery fluid containing several components including lysozyme, an **enzyme** that kills bacteria, and salivary amylase, an enzyme that begins the digestion of starch.

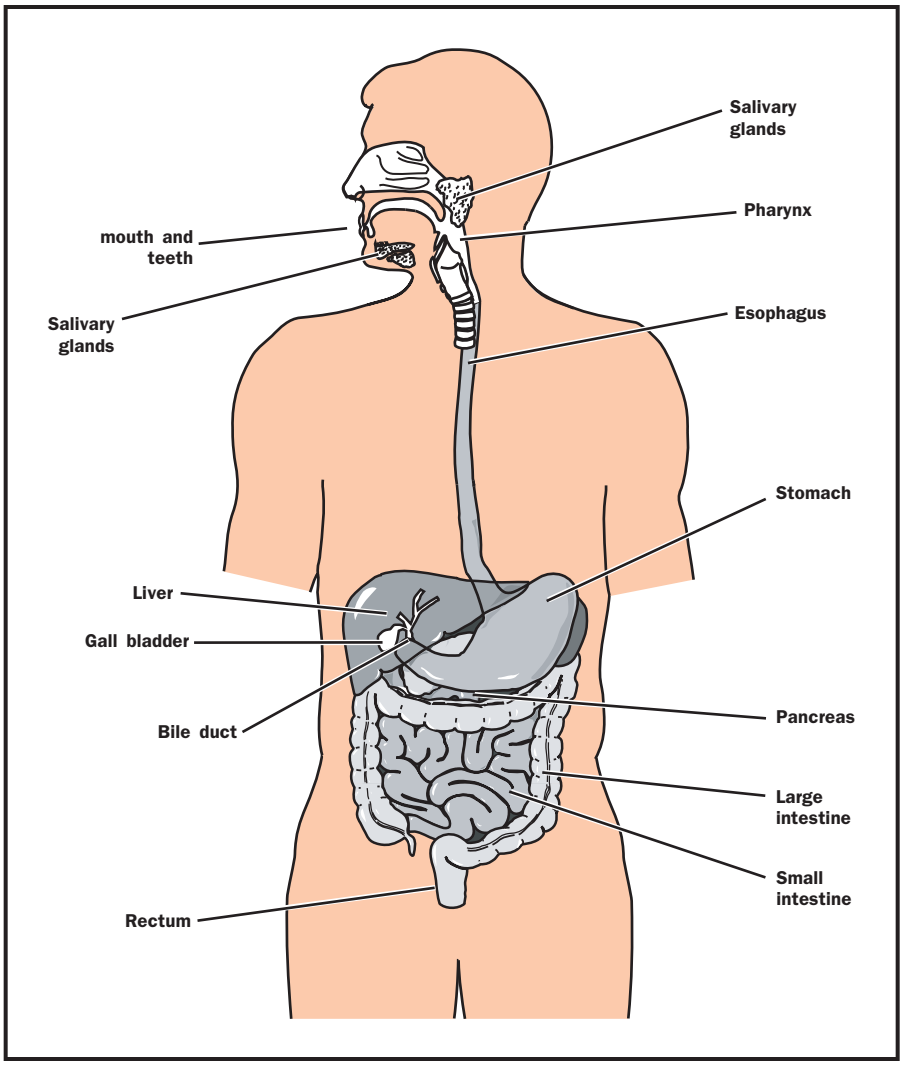
enzyme protein that controls a reaction in a cell

Once the food has been chewed into a soft, flexible mass called a bolus, it is swallowed for delivery to the stomach. On its journey, the bolus passes through the pharynx and then through the esophagus, a straight muscular tube that descends through the thoracic (chest) cavity, anterior to the spine. Each bolus of food is propelled through the esophagus by gravity, and by the process of peristalsis, a wave of muscular contraction that pushes the bolus downward. The lower end of the esophagus, which passes through a hole in the diaphragm to meet the stomach within the abdominal cavity, has a lower esophageal (or gastroesophageal or cardiac) **sphincter** which briefly relaxes to allow the bolus of food to enter the stomach.

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



Parts of the digestive system.



Stomach and Intestines

The stomach is a muscular sac that is located in the upper left portion of the abdominal cavity. The inner lining of the stomach wall contains millions of tiny gastric glands that secrete gastric juice, which dissolves the food to form a thick liquid called chyme. Gastric juice contains several substances including hydrochloric acid, intrinsic factor (which is essential for the intestinal absorption of vitamin B_{12}) and pepsinogen (an inactive **protein**-digesting enzyme). The hydrochloric acid has several functions including destroying ingested bacteria, and converting pepsinogen into its active form, pepsin, in order to initiate the digestion of protein.

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

At the lower end of the stomach is the pyloric sphincter, a valve through which chyme must flow to enter the small intestine. Most meals are gradually emptied into the small intestine after two to six hours due to peristaltic contractions that travel toward the lower end of the stomach. Most digestion and absorption occur within the small intestine. The small intestine consists of three segments named the duodenum, jejunum and ileum. The duodenum receives chyme from the stomach as well as pancreatic juice from the pancreas and bile from the liver (and stored in the gallbladder).

Pancreatic juice contains digestive enzymes capable of digesting proteins, **carbohydrates**, and **lipids**. Bile emulsifies lipids to increase the efficiency of lipid digestion and absorption. Once digestion has been completed, the digested nutrients are absorbed into blood vessels and lymphatic vessels within the wall of the small intestine.

Peristaltic contractions move chyme through the small intestine and into the large intestine. The large intestine consists of three major segments, the cecum (which receives chyme from the small intestine), the colon, and the rectum. As peristalsis moves chyme through the colon, water is absorbed to gradually convert the chyme into semisolid material called feces. The feces contain indigestible food molecules (primary **cellulose**) and intestinal bacteria that live in the colon (primarily *Escherichia coli*). Peristalsis delivers the feces into the rectum where they are stored until they are expelled through the anus by the process of defecation. SEE ALSO DIGESTION; LIVER; PANCREAS

Izak Paul

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

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

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Disease

Disease (or "lack of ease") is any damage or injury that impairs an organism's function. Diseases (sometimes called deviations from the norm) can be classified in numerous ways. Generally, an acute disease comes on quickly and lasts for only a relatively short time. A chronic disease usually begins slowly and lasts for a longer time.

Diseases can also be classified according to type. Common disease types or categories include: infectious, genetic (hereditary), psychiatric, deficiency, degenerative, **congenital** (whether genetic or not), neurological, cardiovascular, metabolic, chemical, and occupational.

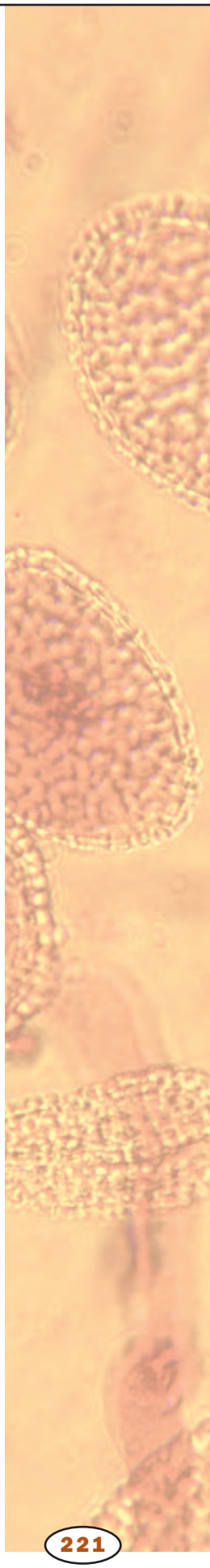
congenital present at birth; inherited

Infectious or microbial diseases (the pathogenic diseases) are often classified by their causative agents: bacteria, fungi, protozoans, viruses, or prions. Progressive diseases, particularly those caused by microbes, have several clinical stages: infection, incubation, acute, decline, and convalescent. "Prodromal" refers to the initial stages when perhaps only one or two early characteristics of the disease can be observed. **Communicable** diseases are transmitted either directly or indirectly (via carriers or **vectors**) from one organism to another. Contagious diseases are rapidly transmitted infectious diseases. Malignant diseases usually progress quite rapidly and are potentially life threatening.

communicable transmissible from person to person

vector carrier

In contrast to disease (the deviation itself), "illness" is feeling of being sick, or suffering some effect of the disease. Many people have hypertension (the disease), for example, without feeling any illness until it is so far advanced that is causes a stroke or kidney failure. This is why hypertension is sometimes called "the silent killer." SEE ALSO AUTOIMMUNE DISEASE; BACTERIAL DISEASES; CARDIOVASCULAR DISEASES; GENETIC DISEASES; HISTORY OF MEDICINE;



Homeostasis; Neurologic Diseases; Parasitic Diseases; Psychiatric Disorders, Biology of; Sexually Transmitted Diseases; Viral Diseases

Roberta M. Meehan

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DNA

DNA (deoxyribonucleic acid) is the molecule that stores genetic information in living systems. Like other **organic** molecules, DNA mostly consists of carbon, along with hydrogen, oxygen, nitrogen, and phosphorus. The fundamental structural unit of DNA is the **nucleotide**, which has two parts: an unvarying portion composed of sugar and phosphate, attached to one of four nitrogen-containing bases named adenine, cytosine, guanine, or thymine (abbreviated A, C, G, T).

organic composed of carbon, or derived from living organisms

nucleotide the building block of RNA or DNA

The Double Helix

The structure of DNA, deduced in 1953 by James Watson, Francis Crick, and Rosalind Franklin, resembles that of a twisted ladder or spinal staircase composed of two long chains of nucleotides that are coiled around each other to form a double helix. The DNA ladder's two sidepieces (its double-stranded backbone) are made of alternating units of sugar and phosphate. The sugar is deoxyribose, which contains a ring of four carbons and one oxygen. A phosphate is an atom of phosphorus bonded to four oxygens. Bases attached to opposing sugars project inward toward each other to form rungs or steps, called **base pairs**. In contrast to the strong covalent (electron-sharing) bonds between nucleotides in a strand, the two bases in a base pair are held together only by much weaker **hydrogen bonds**. However, the cumulative attractive force of the hydrogen bonds in a chain of base pairs maintains DNA as a double-stranded molecule under physiological conditions. In the cell **nucleus**, DNA is bound to **proteins** to form **chromosomes**, and is coated with a layer of water molecules.

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

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

nucleus membrane-bound portion of cell containing the chromosomes

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

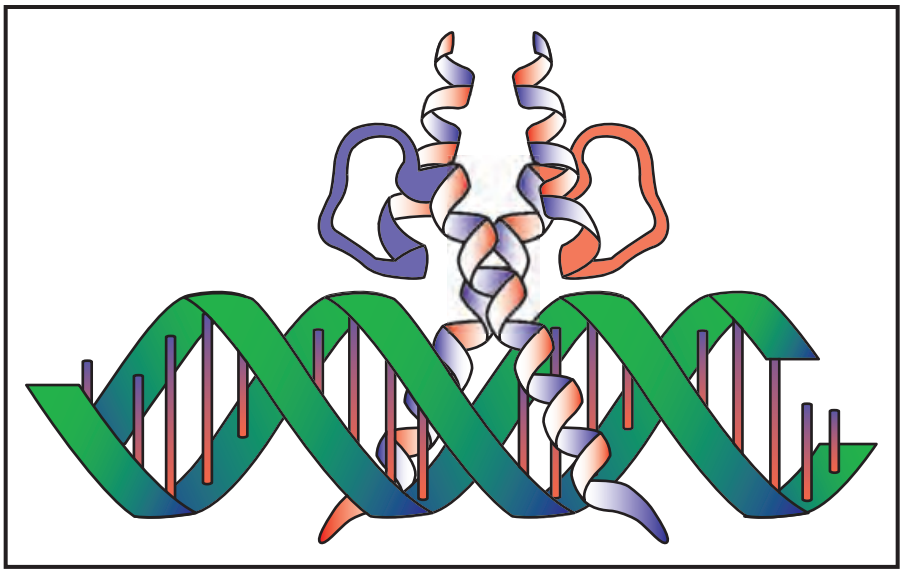
chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

To make a sturdy rung, the two bases in a base pair have to interlock like pieces of a jigsaw puzzle, which only happens if their shapes and hydrogen-bonding characteristics are compatible. Only two combinations fulfill these requirements in DNA: G–C and A–T. This rule makes the two strands of a DNA molecule **complementary**, so that if the bases of one strand are ordered GGTACAT, the bases of the opposite strand must be ordered CCATGTA. The order of the bases on a strand (mirrored in the complementary strand) is called the sequence of the DNA, and embodies coded instructions for making new biomolecules: proteins, ribonucleic acid (RNA), and DNA itself.

complementary matching opposite

Complementarity and Replication

Each strand of DNA has a direction in which it can be read by the cellular machinery, arising from the arrangement of phosphates and sugars in the



A helix-loop-helix dimer bound to DNA.

backbone. The two strands of DNA are oriented antiparallel to each other, that is, they lie parallel to each other but are decoded in opposite directions. Because of the numbering convention for the combinations in sugar, the directions along the backbone are called 5′ → → → 3′ ("five-prime to three-prime") or 3′ → 5′. The complementary nature of the two strands means that instructions for making new DNA can be read from both strands.

When DNA replicates, the weak hydrogen bonds of base pairs are broken and the two strands separate. Each strand acts as a **template** for the synthesis of a new complementary strand. Since the resulting new double-stranded molecule always contains one "old" (template) strand and one newly made strand, DNA replication is said to be semiconservative; it would be termed conservative if the two original template strands rejoined. By a similar mechanism (transcription), a DNA strand can be a template for the synthesis of RNA, which is a single-stranded nucleic acid that carries coded information from the DNA to the protein synthesizing machinery of the cell. During protein synthesis, the **genetic code** is used to translate the order of bases originally found in the DNA sequence into the order of **amino acid** building blocks in a protein.

Genes, Noncoding Sequences, and Methylation

DNA exists in nature as a macromolecule millions of base pairs long. In multicelled organisms, the complete set of genetic information—the **genome**—is divided among several DNA **macromolecules** (called chromosomes) in the cell nucleus. In contrast, the genomes of many one-celled organisms consist of a single, often circular, chromosome. The human genome contains 3.2 billion base pairs distributed among twenty-three chromosomes. Laid end to end, these would make a macromolecule 1.7 meters (5.5 feet) long; printed out, they would fill one thousand one-thousand-page telephone books. Furthermore, two copies of the genome are in almost every cell of humans and other **diploid** organisms. This vast amount of DNA packs into a cell nucleus, whose volume is only a few millionths of a cubic meter, by first spooling around globular proteins called **histones**. The DNA/histone complex then coils and curls up into even denser configura-

template master copy

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

amino acid a building block of protein

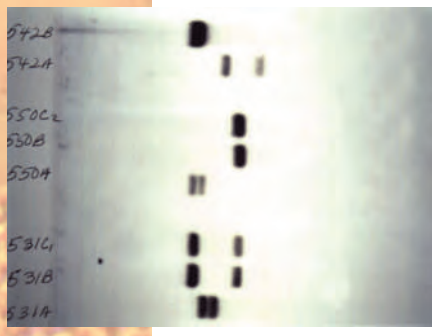
genome total genetic material in a cell or organism

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

diploid having pairs of chromosomes in the nucleus

histone protein around which DNA wraps to form chromosomes

A defect in the gene for a methylating enzyme causes Rett syndrome, a disorder responsible for mental retardation and movement disorders in young girls.



A human DNA fingerprint taken from blood to match donor and patient in an organ transplantation.

tions, like a rubber band does when one holds one end and rolls the other end between one's fingers. Yet the human genome isn't nearly nature's biggest: the genome of a lily is just over ten times larger than a human's, although its nuclei are not significantly larger.

The information storage capacity of DNA is vast; a microgram (one-millionth of a gram) of DNA theoretically could store as much information as 1 million compact discs. The "useful" information contained in genomes consists of the coded instructions for making proteins and RNA. These information-containing regions of a genome are called genes. However, genes comprise less than 5 percent of the human genome. Most genomes consist largely of repetitive, noncoding DNA (sometimes called junk DNA) that is interspersed with genes and whose only apparent function is to replicate itself. Perhaps it helps to hold the chromosome together. The tenfold greater size of the lily genome compared to humans' is due to the presence of enormous amounts of repetitive DNA of unknown function.

neuron nerve cell

methylation addition of the methyl group CH_3

While most cells of higher organisms contain all the genes in the genome, specialized cells such as **neurons** or muscle require expression from only some of the genes. One strategy for silencing unneeded genes is **methylation**. A methyl group ($-CH_3$) is added to cytosine nucleotides, but only if they are followed by a guanine in the sequence, that is, CG. Adding methyl groups to a region of DNA attracts repressive DNA-binding proteins to it and may also cause the region to compact even further, making it inaccessible to proteins that make RNA from DNA (the first step of protein synthesis). During DNA replication the pattern of methylation is preserved by specific proteins that add methyl groups to the new strand based on the location of CG methyl groups in the template strand. The most extreme case of repression by methylation is X-inactivation, in which one of the two X chromosomes in cells of a female mammal is entirely shut down, presumably because expression from one X provides enough protein in females, as it does in males (who have only one X chromosome). SEE ALSO CHROMOSOME, EUKARYOTIC; CONTROL OF GENE EXPRESSION; CRICK, FRANCIS; GENE; MUTATION; NUCLEOTIDES; REPLICATION; RNA; WATSON, JAMES

Steven A. Sullivan

WILKINS, MAURICE (1916–)

New Zealand–born British biologist who helped James Watson and Francis Crick deduce the structure of deoxyribonucleic acid (DNA), for which the three men received a 1962 Nobel Prize. Wilkins secretly showed Watson an x-ray diffraction photo of DNA taken by researcher Rosalind Franklin. Watson and Crick later used Franklin's extensive unpublished data to build a model of DNA.

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DNA Sequencing

genome total genetic material in a cell or organism

The **genome** of an organism is the sum total of its genetic information. The genome is not only a blueprint for the organism it also contains historical notes on the evolution of the organism. The ability to determine the sequence of deoxyribonucleic acid (DNA) and thus read the messages in the genome is of immense biological importance because it not only describes the organism in detail but also indicates its evolutionary history.

DNA is a linear chain of four **nucleotides**: adenosine (A), thymidine (T), cytidine (C), and guanosine (G). The genetic information in DNA is encoded in the sequence of these nucleotides much like the information in a word is encoded in a sequence of letters. The technique for determining the sequence of nucleotides in DNA is based on the same mechanism by which DNA is replicated in the cell. DNA is composed of two **complementary** strands in which the As of one strand are paired with the Ts of the complementary strand and the Cs of one strand are paired with the Gs of the complementary strand. When DNA is replicated, a new DNA strand (primer strand) is extended by using the information in the complementary (template) strand. The DNA has a direction (polarity); the growing end of a DNA strand is the end that is 3′ and the other end is the 5′. An **enzyme**, DNA polymerase, replicates DNA by adding nucleotides to the 3′ end of the **primer** strand, which complement the **template** strand. (Figure 2.)

nucleotide the building block of RNA or DNA

complementary matching opposite

enzyme protein that controls a reaction in a cell

primer short nucleotide sequence that helps begin DNA replication

template master copy

hydroxyl chemical group consisting of -OH

DNA polymerase has an absolute requirement for a **hydroxyl** group (OH) on the 3′ end of the template strand. If the 3′ hydroxyl group is missing no further nucleotides can be added to the template strand. This termination of the elongation of the template strand is the basis for determining the DNA sequence. If the DNA polymerase is presented with a mixture of nucleotides, some of which have 3′ OH groups and others of which have no 3′ OH group (and are bound to a colored dye), both types of nucleotides are added to the growing template strand. When a nucleotide with no OH group is added to the primer strand, elongation is terminated with the colored dye at the 3′ end of the strand.

All essential elements for determining the sequence of nucleotides in the primer DNA strand are in place. A DNA synthesis reaction is set up in a test tube (in vitro), including DNA polymerase, a template DNA strand, a short uniform primer DNA strand, and a mixture of the four nucleotides (A, T, C, and G). The short primer DNA strands are synthesized chemically and are identical so they pair with a specific sequence in the template DNA strand. Each of the nucleotides is present in two forms, the normal form with a 3′ hydroxyl group and the terminating form with a colored dye and no 3′ hydroxyl group. Each different terminating nucleotide (A, T, C, and G) has a different colored dye attached.

The amount of normal nucleotides present in the reaction is much larger than the terminating nucleotides so that DNA synthesis proceeds almost normally, and only occasionally is the elongation of the primer strand terminated by the incorporation of a dye labeled nucleotide lacking a 3′ hydroxyl group. However, eventually all of the primer strands do incorporate a dye labeled nucleotide and their elongation is terminated. Thus, at the end of the reaction there is a vast collection of primer strands of varying lengths each terminated with a nucleotide that has a colored dye specific to the terminal nucleotide.

All of the primer strands start at the same point, specified by the sequence of the short uniform primer DNA. Thus, the *length* of the primer strand corresponds to the position of the terminal nucleotide in the DNA sequence relative to the starting position of the primer DNA strand. The *color* of the dye on the primer strand identifies the terminal nucleotide as an A, T, C, or G. Once the primer strands are arranged according to length, the DNA sequence will be indicated by the series of colors on progressively longer primer strands.

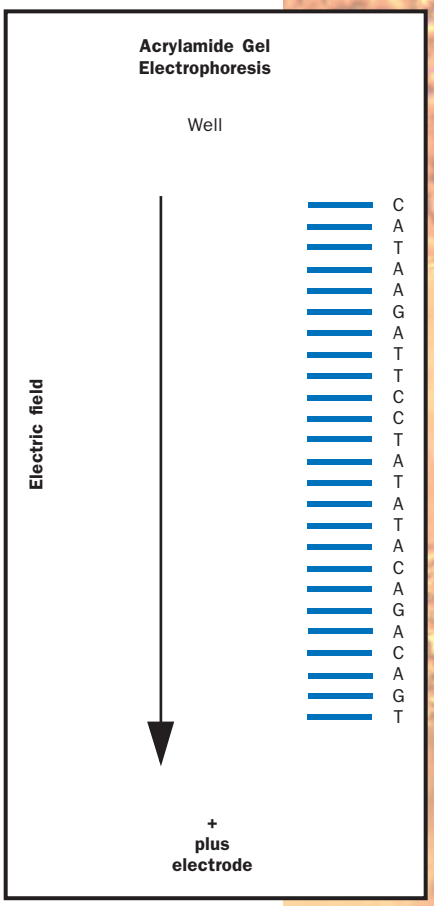


Figure 1. DNA strands can be separated according to length by acrylamide gel electrophoresis.

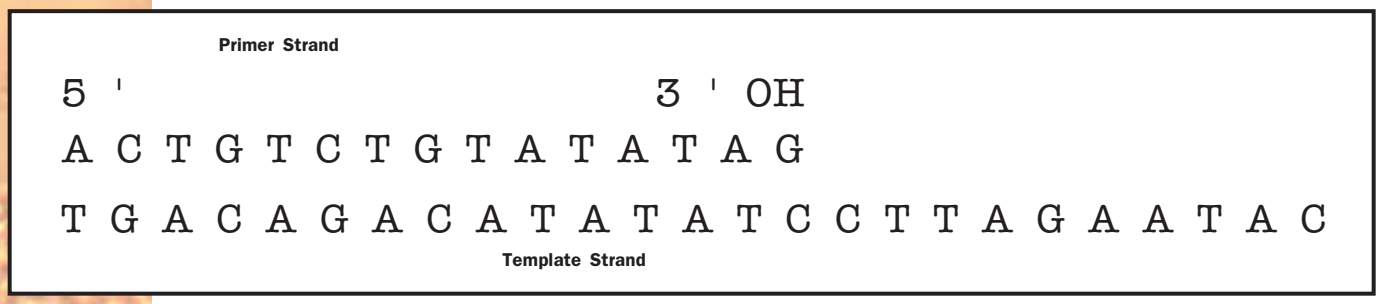


Figure 2. DNA polymerase replicates DNA by adding nucleotides that complement the template strand to the 3' end of the primer strand.

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

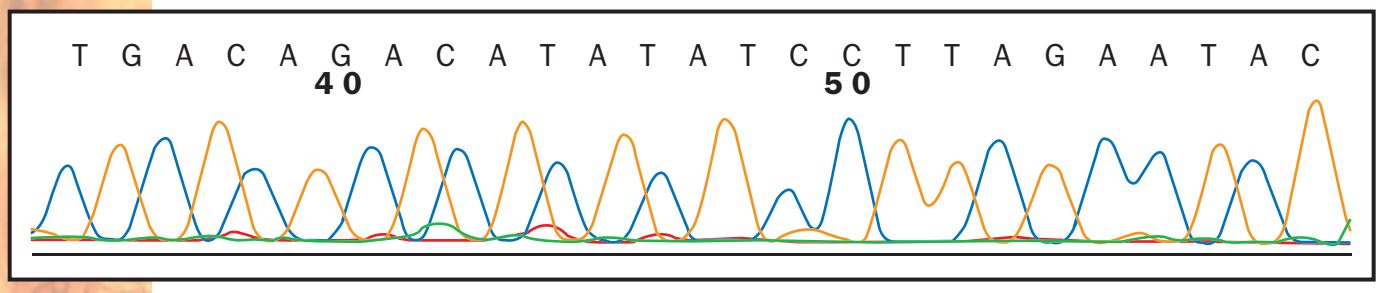
matrix a network, usually of threadlike fibers

The DNA strands can be readily separated according to length by acrylamide gel **electrophoresis** (see Figure 1). The acrylamide gel is a loose **matrix** of fibers through which the DNA can migrate. The DNA molecules have a large negative charge and thus are pulled toward the plus electrode in an electric field. The whole collection of primer strand DNA molecules is placed in a well at the top of an acrylamide gel with the plus electrode at the bottom of the gel. When the electric field is applied the DNA molecules are drawn toward the plus electrode, with shorter molecules passing through the gel matrix more easily than longer molecules. Thus the smaller DNA molecules move the fastest.

After a fixed period of time, the DNA molecules are separated according to length with the shortest molecules moving furthest down the gel. All of the molecules of a given length will form a band and will have the same terminal nucleotide and thus the same color. The DNA sequence can be read from the colors of the bands. One reads the sequence of the DNA from the 5′ end starting at the bottom of the gel to the 3′ end at the top of the gel.

In practice the whole process is automated; the bands are scanned with a laser as they pass a specific point in the gel. These scans produce profiles for each nucleotide, as shown in the lower portion of Figure 3. A computer program then determines the DNA sequence from these colored profiles, as shown in the upper portion of Figure 3. A single automated DNA sequencing instrument can determine more than 100,000 nucleotides of DNA sequence per day and a large sequencing facility can often produce over 10 million nucleotides of sequence per day. This high sequencing capacity has made it feasible to determine the complete DNA sequence of large genomes including the human genome. SEE ALSO DNA; ELECTROPHORESIS; HUMAN GENOME PROJECT; SEPARATION AND PURIFICATION OF BIOMOLECULES

Figure 3. Laser scans produce profiles for nucleotides, as shown in the lower portion of the figure. A computer program then determines the DNA sequence, as shown in the upper portion of the figure.



Clifford Brunk

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DNA Viruses

Viruses can be classified based on **proteins** encoded within the viral genetic material or **genome**. Viruses with deoxyribonucleic acid (DNA) genomes are called DNA viruses. Like all viruses, DNA viruses are small when compared to the cells they infect and as such are obligate intracellular parasites (parasites that can only replicate within cells). In the appropriate cell, DNA viruses are able to program the cell to replicate the virus using the genes contained within the viral DNA genome.

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

genome total genetic material in a cell or organism

The extracellular form of a virus is known as a virion. For a DNA virus, the virion is composed of a set of DNA genes protected by a protein-containing coat called a capsid. The coat is often characterized by regularity and symmetry in its structure and is capable of binding to and invading cells. In the case of some DNA viruses, the capsid can be surrounded by a membrane that is formed from cellular membranes. On invasion of a susceptible cell the virion is disassembled to release the viral genome into the cell, at which time the genes within the viral DNA are transcribed, producing viral messenger ribonucleic acid (mRNA).

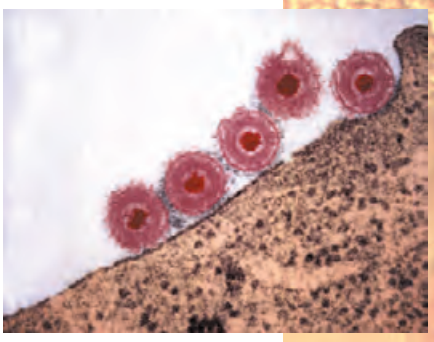
The viral mRNA is translated into protein. These "early" proteins are responsible for altering normal cellular functions which in some cases allow the infected cell to evade the immune system. These "early" proteins are also important for promoting "late" viral gene synthesis and preparing the cell for the production of **progeny** virus. Following late gene synthesis, which includes proteins that are important for replicating and encasing the virus, progeny virions are then released by the infected cell to invade other cells so that the process can be repeated.

progeny offspring

kilobasepair one thousand DNA base pairs; a measure of size of a piece of DNA

gastroenteritis inflammation of the gastrointestinal tract, often from infection

There are six different DNA virus families that infect and may cause significant disease in humans. These can be further subdivided into those with "small" DNA genomes or "large" DNA genomes. DNA viruses with small DNA genomes have genome sizes of less than 10 **kilobasepairs**, whereas DNA viruses with large genomes are over 30 kilobasepairs. Small DNA viruses generally have less than ten genes encoded within the viral genome, whereas large DNA viruses can have anywhere from fifty genes to well over one hundred genes. Viruses with small DNA genomes include human papillomavirus (HPV). HPV infects epithelial cells of the skin. It causes common warts on hands and feet and in some cases is important for the development of cervical cancer in women. Hepatitis B is another small DNA virus that infects the liver, causes hepatitis, and is associated with liver cancer. Adenovirus, herpesvirus, and poxvirus are all examples of large DNA viruses that infect humans. Adenoviruses, of which there are many types, cause **gastroenteritis** and respiratory disease in humans.



A scanning electronic micrograph of herpes simplex virus (HSV6).

Herpesviruses are a very diverse family of viruses. There are a total of eight herpesviruses that infect humans and establish latent infection. Her-

pes simplex viruses I (HSV-1 and HSV-2) typically cause lesions in the oral or genital **epithelium**. Following productive infection at an epithelial site, HSV-1 and HSV-2 then establish a latent ("resting") infection in sensory **neurons**, which may erupt in times of stress.

epithelium one of four tissue types found in the body, characterized by thin sheets and usually serving a protective or secretory function

neuron nerve cell

Other herpes viruses that infect humans include Epstein-Barr virus, which causes mononucleosis and is important in a variety of human cancers, and varicella-zoster virus, which causes chickenpox in children and shingles in adults. The final large DNA virus that can infect humans is smallpox. Prior to vaccination and eradication of smallpox in 1970s, smallpox caused significant morbidity in human populations with anywhere from 1 to 25 percent of the cases resulting in death. SEE ALSO CANCER; DNA; VIRAL DISEASES; VIRUS

Richard Longnecker

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Doctor, Family Practice

A family practice doctor is the primary health care professional responsible for treating people for most conditions. Family physicians work in private offices, group practices, and hospitals, caring for every family member from before birth until the time of death. Under America's health insurance system, most people go first to their family practice doctor for all complaints, from infections to chronic illnesses to preventive medicine.

Family practice doctors approach the treatment of the family as a unit, focusing on health promotion, disease prevention, and psychological issues affecting health, as well as treatment of disease. Depending on the condition, treatment may include prescribing medicines, recommending lifestyle changes such as exercise and diet, or referral for other types of treatment, including surgery, physical therapy, or psychotherapy. The doctor works in partnership with other health care professionals, including nurse practitioners, nurses, and medical assistants.

To become a family practice doctor, one must first earn a bachelor's degree (either a bachelor of arts or bachelor of science) from a four-year college, and then earn a doctorate of medicine (M.D.) degree from a medical school. This usually takes four years, and combines classes and clinical experience. Following this, doctors undergo three years of postgraduate training, called internship and residency. During residency, they receive training in the full range of medical disciplines, including pediatrics, obstetrics/gynecology, internal medicine, preventive medicine, surgery, and psychiatry. Family practice doctors often choose this career because they enjoy participating in the comprehensive care of people of all ages, and they desire to help people attain and maintain good health. SEE ALSO DOCTOR, SPECIALIST; NURSE; NURSE PRACTITIONERS

Richard Robinson

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DELBRÜCK, MAX (1906–1981)

German-born U.S. biologist who received, with Salvador Luria and Alfred Hershey, the 1969 Nobel Prize in physiology for his work on bacteriophages, viruses that infect bacteria. In 1939, Delbrück invented an easy way to grow bacteriophages in the lab, and in 1949 he and Hershey showed that the genetic material of different viruses can combine to make entirely new viruses.

Doctor, Specialist

A medical specialist focuses on diagnosis and treatment of a particular organ or body system, a specific patient population, or a particular procedure. Medical care of humans is a complicated task due to the many different organ systems that comprise the human body. Each stage of life presents a variety of health issues that need to be addressed as well. Moreover, males and females also have very different medical needs through puberty and adulthood. This complexity of life necessitates a high degree of specialization in the physicians that care for people's medical needs. There are many types of medical specialties.

General Educational Requirements for Medical Specialists

All physicians, regardless of their ultimate specialization, must obtain a bachelor's degree from an undergraduate college and graduate from medical school (four years). During the last two years of medical school, students perform clinical rotations in which they are exposed to a wide variety of medical specialties. This provides broad training for all medical professionals, as well as gives the students an opportunity to choose a specialty.

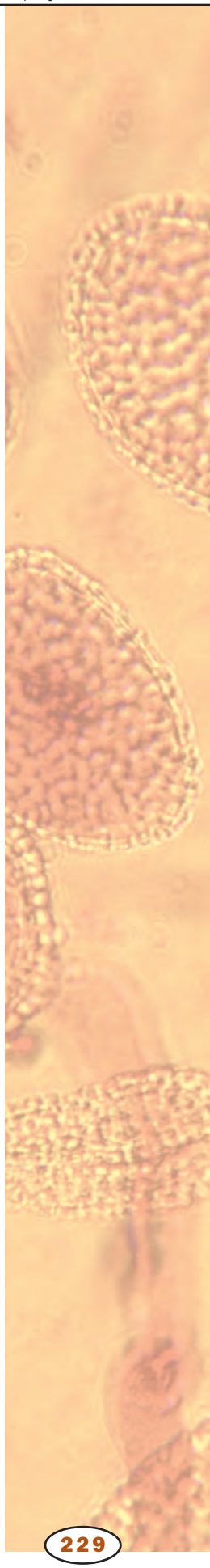
After medical school, all physicians are required to do a residency. The purpose of the residency is to provide specific, detailed training in the chosen specialty. The length of the residency is determined by the specialty. The tables on page 231 include the average residency length for each of the specialties listed. Oftentimes, physicians will have a particular expertise within their specialized area. For example, most surgeons are subspecialized in the organ system on which they operate (neurosurgeons, cardiac surgeons, and orthopedic surgeons are examples). These subspecialties are obtained during a fellowship period that lasts one to two years after the residency is completed. It is not uncommon for a highly specialized doctor (such as a pediatric neurosurgeon) to invest ten years or more in his or her medical education after graduating from college.

Job Duties and Educational Requirements for Sample Specialties

Cardiologist. A cardiologist is a physician who cares for people with heart disease. Cardiologists treat conditions such as myocardial infarction (heart attack) and angina (chest pain). They use diagnostic tools such as an electrocardiogram (EKG) and ultrasound to visualize the electrical and structural functioning of the heart. Cardiologists are employed by hospitals but also work in private practice. Since cardiology is considered a subspecialty of internal medicine, cardiologists must first complete a residency in internal medicine that lasts about three years after medical school. Cardiologists then complete a subspecialty residency in cardiology (another three years).

Neurologist. A neurologist is a physician who treats patients with neurological disorders (involving the brain, spinal cord, and **peripheral** nervous system). Conditions that would necessitate treatment by a neurologist include, Parkinson's disease, multiple sclerosis, myasthenia gravis, Alzheimer's

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



A surgeon reviewing CAT scans.

disease, traumatic brain or spinal cord injury, epilepsy, or stroke. Diagnostic techniques used by neurologists to detect these disorders include (but are not limited to) sensory and motor skills assessments, memory tests, magnetic resonance imaging (MRI) scans, and positron emission tomography (PET). To treat these types of disorders, neurologists may prescribe medication, physical therapy, occupational therapy, or surgery. There are several new and very effective surgical treatments for diseases such as Parkinson's disease. Neurologists must complete at least four years of residency in an accredited neurology program before being eligible for certification by the American Board of Psychiatry and Neurology.

Obstetrician/Gynecologist (OB/GYN). An OB/GYN specializes in the care of women from puberty through pregnancy and menopause. An obstetrician focuses on the care of pregnant women and the delivery of babies. Although some doctors choose to specialize in either obstetrics or gynecology, it is very common for a physician to specialize in both since the two fields are so closely linked. In addition to delivering babies, OB/GYNs perform diagnostic tests such as pelvic exams (to look for ovarian cysts and other abnormalities), pap smears (to screen for cervical cancer), and obstetrical ultrasound (to assess the development of a fetus). After medical school, OB/GYNs must complete a four-year residency. Many OB/GYNs practice their specialty in private practices that are closely affiliated with hospitals in which they deliver babies. However, most hospitals employ OB/GYNs directly as well.

Oncologist. An oncologist cares for patients with cancer. Cancer is a very complex disease that demands very specialized attention and intensive treatment. It is common for an oncologist to specialize in a particular type of cancer, such as lung or colon cancer. Oncologists may work in private practices that are closely affiliated with a particular hospital or may be directly employed by a hospital. Like cardiology, oncology is considered a subspecialty of internal medicine. Oncologists must first complete a residency in internal medicine that lasts about three years after medical school. They then must complete a subspecialty residency in oncology (another three years).

Doctors who have expertise in a particular disease/condition

Specialist	Oncologist	Emergency physician	Allergist
Area of expertise	Cancer	Urgent and crisis medical needs	Allergies
Sample disease/ disorders treated	AIDS-related lymphoma, leukemia, Hodgkin's disease, lung cancer, breast cancer, skin cancer, colon cancer, etc.	Traumatic brain injury, emergency births, cardiac arrest, gunshot wounds, poisoning, etc.	Asthma, hay fever, contact eczema, etc.
Average # of years of residency	6 years (3 years-internal medicine; 3-years oncology)	3 years	5-6 years (3 years in internal medicine or pediatrics and 2-3 years in allergy, asthma, and immunology)

Pediatrician. Infants and children have very specialized medical needs due to their rapidly changing and maturing bodies. Pediatricians are experts in the developmental stages of children and medical treatments of childhood diseases. In addition to treating childhood illnesses such as ear infections, jaundice, and respiratory infections, pediatricians also perform periodic exams of healthy children to ensure their proper development, administer immunizations to prevent disease, and advise parents on the proper care for each developmental stage. Pediatricians commonly work in private practice, but many are employed by children's hospitals as well. They are required to complete three years of residency before they are eligible for certification by the American Board of Pediatrics.

Radiologist. The ability to visualize internal organs revolutionized twentieth-century medicine. A radiologist is a doctor who has expertise in a variety of diagnostic imaging technologies. These technologies include

Doctors who have expertise in a particular organ system

Specialist	Cardiologist	Neurologist	Dermatologist	Ophthalmologist	Podiatrist	ENT	Orthopedist	Endocrinologist	Urologist	Gastroenterologist
Area of expertise	Heart	Brain (nervous system)	Skin	Eyes	Feet	Ear, nose, throat	Bones	Hormone imbalances	Urinary tract, kidneys	Digestive system
Sample disease/ disorders treated	Angina, atrial fibrillation, congestive heart failure, heart attack, high cholesterol, etc.	Stroke, epilepsy, Alzheimer disease Bell's palsy, epilepsy, fibromyalgia, migraine, Lou Gehrig's disease, Parkinson's disease, multiple sclerosis, vertigo, etc.	Acne, birthmarks, eczema, fungal infections, moles, psoriasis, skin cancer, etc.	Glaucoma, cataracts, etc.	Achilles tendonitis, athlete's foot, bunions, corns, gout, heel pain, rheumatoid arthritis, osteoarthritis, etc.	Middle ear infections, sinus infections, allergies, balance disorders, strep throat, etc.	Broken bones, bone malformations, joint problems	Thyroid disorders, infertility, diabetes, hypoglycemia	Bladder control problems, erectile disfunction, incontinence, kidney stones, Peyronie's disease, urinary tract infections, etc.	Peptic and duodenal ulcers, acid reflux, impacted bowels, colon cancer, etc.
Average # of years of residency	6 years (3 years-internal medicine; 3 years-cardiology)	4 years	4 years	3 years	2-4 years	5 years	5-6 years	5 years	4-6 years	5 years

x ray, ultrasound, and MRI. All of these procedures produce a picture of the internal organs. Radiologists often serve as consultants to other specialists who need to visualize a specific organ in a patient that they are treating. However, radiologists do participate in treatments such as unblocking arteries in the legs and trunk that eliminate the need for more invasive procedures like surgery. Although most radiologists work within hospitals, they are rarely employed by the hospital itself. Instead, they are employed by private practices and contract with the hospital to provide services. Radiologists must complete a residency of at least four years, and oftentimes they complete additional years of a fellowship to become an expert in a particular type of imaging technique. SEE ALSO CARDIOVASCULAR DISEASES; DOCTOR, FAMILY PRACTICE; IMAGING IN MEDICINE; NEUROLOGIC DISEASES; NURSE PRACTITIONERS; REPRODUCTIVE TECHNOLOGY; TRANSPLANT MEDICINE

Susan T. Rouse

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Drug Testing

Drug testing refers to the process of detecting "drugs" in human or animal specimens. Drug testing may be performed in the contexts of sports, workplace safety, therapeutic drug monitoring, **forensics**, toxicology, and drug abuse prevention.

forensic related to legal proceedings

Human drug testing is most commonly performed by analysis of urine or hair samples. Blood may provide a more appropriate source in certain circumstances, for example, monitoring doses of pharmaceuticals. In some cases, testing can be done on excised (removed) tissue samples.

Drug testing is complex because most foreign chemicals taken into the body and entering the blood system, either by injection or ingestion through the digestive system, undergo some form of **metabolism** or chemical transformation. This generally occurs in the liver. One or more **metabolites** (transformed chemicals) are produced that may be removed via filtration through the kidneys and ultimately **excreted**. Although the drug in its native chemical form may be rapidly broken down, its metabolites may persist for extended periods of time.

metabolism chemical reactions within a cell

metabolite molecule involved in a metabolic athway

excreted deposited outside of

Some metabolites accumulate in tissue. For example, if a metabolite or drug transported in the blood manages to penetrate the barrier surrounding the brain, it tends to accumulate, often resulting in some pharmacologic (desired) or toxic (undesired) response.

Technical approaches used in drug testing have undergone significant advancement. When a drug-testing laboratory performs such analyses, the specimen is fractionated, or divided, into its components. The compound of interest and its metabolites are characterized based on specific physical and/or chemical properties, which allow subsequent identification. For example, the charge and molecular weight of a compound often provides a specific "signature" of that chemical.

There are numerous separation techniques, with the simplest being liquid chromatographic (LC) procedures and the most complex being a com-

bination of two analytical methodologies such as gas chromatography (GC) with mass spectrometry (MS). Liquid chromatography can also be combined with mass spectrometry. For optimal sensitivity, GC-MS and LC-MS may be done as complementary procedures, providing the most convincing identification of a particular chemical. The sensitivity of MS is significantly greater than that of LC or GC procedures; consequently MS can identify trace amounts of material. Analytical chemists develop and test these procedures. The sophistication of these methods makes it extremely difficult to intentionally fool the test.

Home drug testing kits for a number of drugs of abuse are now available by online purchase but are not as sensitive as laboratory methods. They generally work by producing a color reaction demonstrating the presence of a specific drug of interest. The application of laboratory and home testing procedures provides safer workplaces and ultimately leads to a safer environment. SEE ALSO ANABOLIC STEROIDS; KIDNEY; LIVER; PSYCHOACTIVE DRUGS

David S. Lester

A technician performing a density test from urine samples at the Australian Sports Drug Testing Laboratory in Sydney.

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Dubos, René

American bacteriologist
1901–1982

In 1939 René Dubos launched the antibiotic era by reporting the discovery of gramicidin after the first systematic search for antimicrobial agents. Following this discovery he warned of microbial resistance to antibiotics, completed innovative studies of tuberculosis, expanded investigations into the nature of disease and, ultimately, examined the question of health.

Born near Paris in 1901, Dubos studied agronomy in France and, through a chance meeting with biochemist Selman Waksman, was invited to study soil science at Rutgers University. In his Ph.D. studies, Dubos discovered that local soil characteristics determine which microbes decompose **cellulose**.

By good fortune again, Dubos joined Oswald Avery of the Rockefeller Institute (now University) who was trying to decompose the **polysaccharide** capsule surrounding the deadly pneumococcus bacterium. Dubos succeeded by using a soil enrichment technique to find a specific microbial **enzyme**.

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

polysaccharide carbohydrate composed of many individual units of sugar

enzyme protein that controls a reaction in a cell

He further discovered this enzyme was produced only if the polysaccharide capsule was the microbe's sole food, a phenomenon now known as an induced enzyme. He described this as "his greatest hour in science . . . one of the most important biological laws I have ever been in contact with."

In 1939, using the same techniques, he found *Bacillus brevis*, a microbe that digests and destroys other microbes. From it he extracted an antibacterial agent he named tyrothricin that contains two **polypeptides** he called gramicidin and tyrocidine. Within a few months, he and organic chemist Rollin Hotchkiss described the bacterial, chemical, clinical, and pharmaceutical properties of these antibiotics. This work stimulated two English scientists, Howard Florey and Ernst Chain, to revive the stalled research on penicillin, found accidentally in 1929 by Scottish bacteriologist Alexander Fleming.

polypeptide chain of amino acids

In 1942 Dubos warned that bacterial resistance to antibiotics should be expected, saying, "In the analysis of . . . antibacterial agents . . . susceptible bacterial species often give rise with 'training' to variants endowed by great resistance to these agents."

Dubos turned his interest to tuberculosis in 1944. He began a renaissance in studying this disease by creating a culture **medium** to produce rapid, luxuriant, and well-dispersed growth of bacilli. He pioneered international standards for the BCG vaccination against tuberculosis and described social aspects of the disease in "The White Plague" (1952). Later he investigated how environmental effects of crowding, malnutrition, pesticides, toxins, and stress increase susceptibility to disease.

medium nutrient source

Dubos observed that people coexist with both good and bad microbes and that disease-producing microbes reside quiescently (dormant) in the body until stress alters resistance. He restated the germ theory, saying a microbe is necessary but not sufficient to cause disease. He concluded that in order to improve one's physical and spiritual well-being, one must first understand and then control one's impact on one's own surroundings.

When he won the Pulitzer prize in 1969 for *So Human an Animal*, Dubos was thrust into the swelling environmental debate. He became well known for balancing views between those who believe that humans can improve on nature and those who advocate wilderness preservation. Hundreds of lectures and two dozen books evolved from medical considerations of environment and health, to cultural and scientific aspects of medicine, to an ecological philosophy encompassing health of Earth. He coined many aphorisms such as "think globally, act locally" to explain complex issues. SEE ALSO BACTERIAL DISEASES; HISTORY OF MEDICINE; NATURAL SELECTION

Carol L. Moberg

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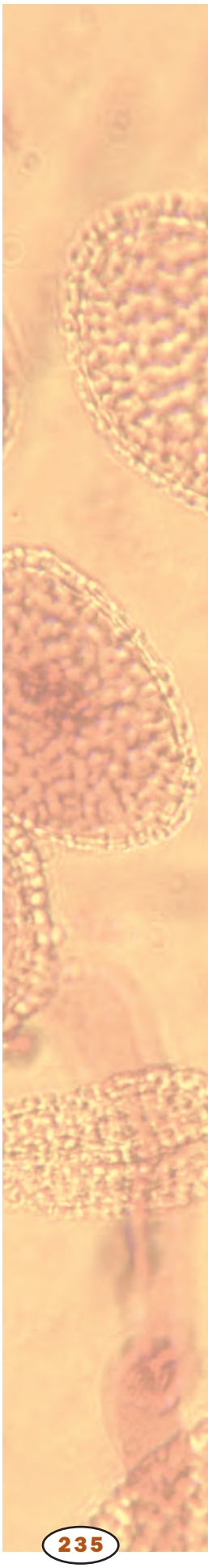

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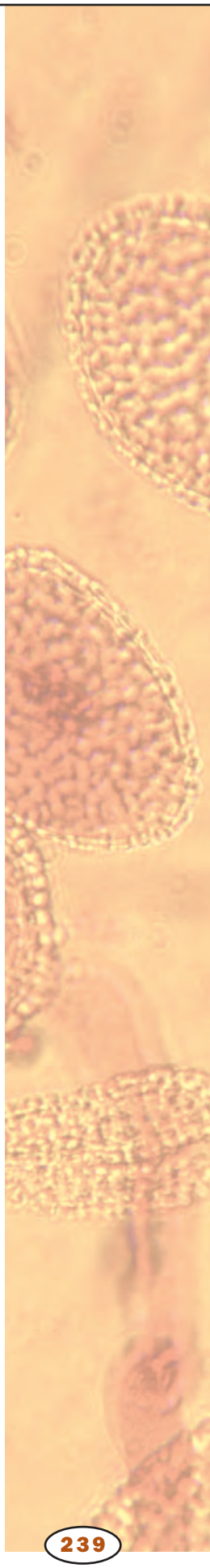

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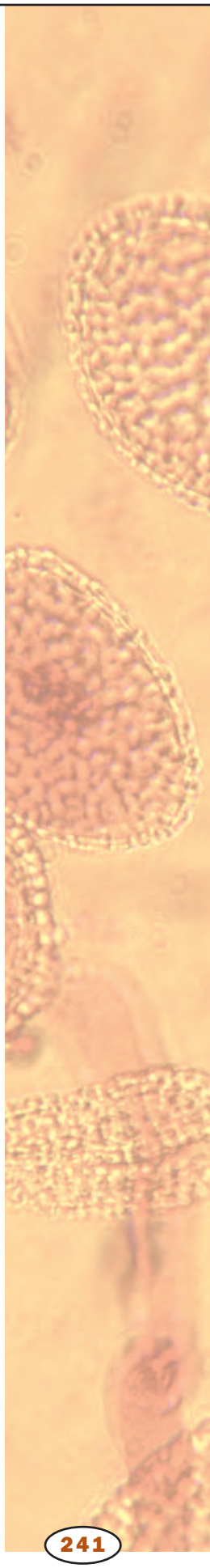


Glossary

abiotic nonliving

abscission shedding of leaves; falling off

acetylation addition of an acetyl group, CH_3-CHOO-

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

acinus one of the small divisions of a fruit such as a raspberry

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

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

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

adhesion attachment; sticking to the surface of

ADP adenosine diphosphate, the low-energy form of ATP

adventitious growing from a nonstandard location

aerobe organism that needs oxygen

aerobic with oxygen, or requiring it

aestivating remaining dormant for the summer

affinity attraction

aflatoxin toxic compound produced by a mold fungus

agar gel derived from algae

agnosia "not knowing"; loss of ability to recognize familiar objects

agroecosystem agricultural ecosystem

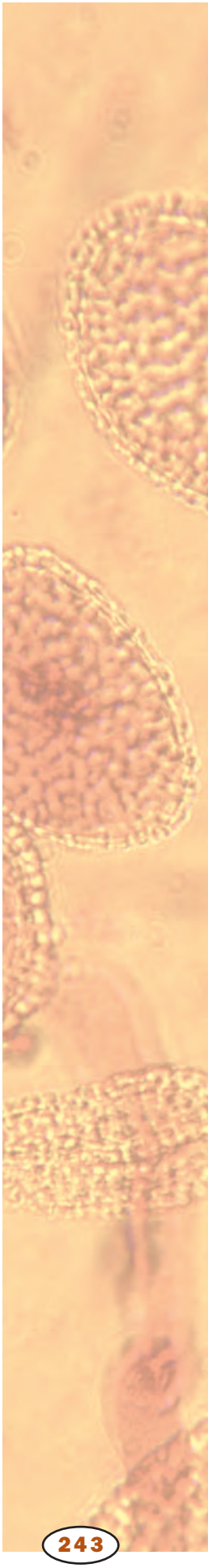
alkaline chemically basic, with an excess of OH- ions

allele a particular form of a gene

allelopathy inhibition of one plant's growth by another plant

amino acid a building block of protein

amoeba a single-celled protist that moves by crawling



amoeboid like an amoeba, especially in movement via extension of portions of the membrane

AMP adenosine monophosphate, form of ATP after removal of two phosphate groups

amphipathic having both polar and nonpolar regions

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

anadromous describes fish that return to the rivers where they were born in order to breed

anaerobe organism not needing oxygen

anaerobic without oxygen, or not requiring oxygen

anemia lack of oxygen-carrying capacity in the blood

aneurysm bulging of the wall of a blood vessel

antagonism working against

antagonist muscle muscle that works against the action undertaken

anterior toward the front

anterograde forward

anthocyanins colored compounds made by plants

anthropogenic of, or relating to, the influence of human beings or nature

antibody immune system protein that binds to foreign molecules

antigen foreign substance that provokes an immune response

antioxidant substance that prevents damage from oxidation

antitoxin molecule used to inactivate a toxin

aphasia loss of the ability to form ideas into words

apical at the tip

apical meristem growing tip from which all plant tissues arise

appendage attached organ or structure

aqueous watery or water-based

areolar related to a small space within a tissue

aromatic compound including a double-bonded carbon ring

arterioles any of the small, terminal twigs of an artery that ends in capillaries

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

asymptomatic without symptoms

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

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

attenuation lessening over time

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

autonomic independent; regulating involuntary actions

autonomic nervous system one of the branches of the motor system, controlling involuntary muscles and glands

autosomal dominant pattern of inheritance in which inheritance of a single allele from either parent results in expression of the trait

avian concerning birds

axon long extension of a nerve cell down which information flows

B lymphocyte white blood cell that makes antibodies

B.C.E. before the Common Era, equivalent to B.C.

basal lowest level

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

basic having an excess of OH^- ions and a high pH

bilaterally symmetric symmetric, or similar, across a central line

bilayer composed of two layers

bioaccumulate build up within organisms

bioluminescence production of light by biochemical reactions

biopharmaceuticals drugs produced by and harvested from living organisms

biosynthetic forming a complex molecule from simpler ones

biotic living

bolting sudden spurt of growth

boreal of, relating to, or located in northern regions

brood parasite organism of one species that lays its eggs in the nest of another species

C4 and CAM plants plants that employ accessory systems for trapping carbon for photosynthesis

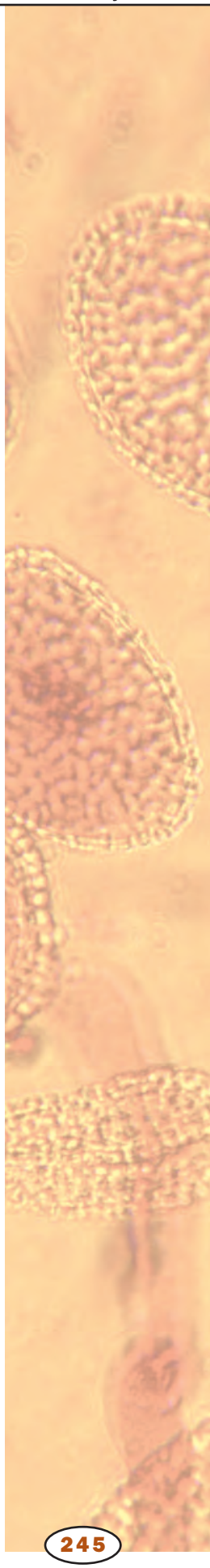
cadherins family of calcium-dependent adhesion proteins

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

cardiomyopathy heart muscle disease

catalysis aiding in the reaction of

catalyst substance that aids in a reaction without being used up



catalyze aid in the reaction of

caudate toward the tail

C.E. Common Era; equivalent to AD

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

cellulose carbohydrate made by plants and some other organisms; part of the cell wall

central nervous system brain and spinal cord

centromere region of the chromosome linking chromatids

cerebral cortex outermost wrinkled portion of the brain

chemiosmosis use of proton gradients to make ATP

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

chromatid a replicated chromosome before separation from its copy

chromatin complex of DNA, histones, and other proteins making up chromosomes

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

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

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

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

circadian related to a day or daylength

clavicle collar bone

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

codon sequence of three mRNA nucleotides coding for one amino acid

cognition mental processes of thought and awareness

cognitive related to thought or awareness

communicable transmissible from person to person

complementary matching opposite

complex carbohydrate molecules formed by linking simpler carbohydrates such as sugars

condensation compaction of chromosome strands into a tight structure

conformation three-dimensional shape

congenital present at birth; inherited

conjunctiva eye membrane that helps seal the eye socket

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

consanguineous descended from the same ancestor

constitutive at a constant rate or continually

contiguous adjacent to or touching

continental shelf submerged offshore area demarcated by land on one side and deep sea on the other

coralloid resembling coral

coronary artery artery supplying blood to the heart

cortical related to the cortex, or outer portion

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

cranial related to the cranium, or brain cavity

cryptobiosis when a plant or animal becomes so inactive that its life processes nearly come to a stop

cutaneous related to the skin

cutaneous respiration gas exchange through the skin

cytology study of cells

cytoplasm material in a cell, excluding the nucleus

cytoskeleton internal scaffolding in a cell, composed of protein

cytosol fluid portion of a cell, not including the organelles

Darwinian fitness capacity to survive and reproduce

deciduous trees that shed their leaves in the fall

deciliter one-tenth of a liter; a unit of volume

dementia neurological illness characterized by impaired thought or awareness

desiccation drying out

desynchronized not happening at the same time

deuterostome "mouth second"; referring to the early development of the anal pore during gut tube formation

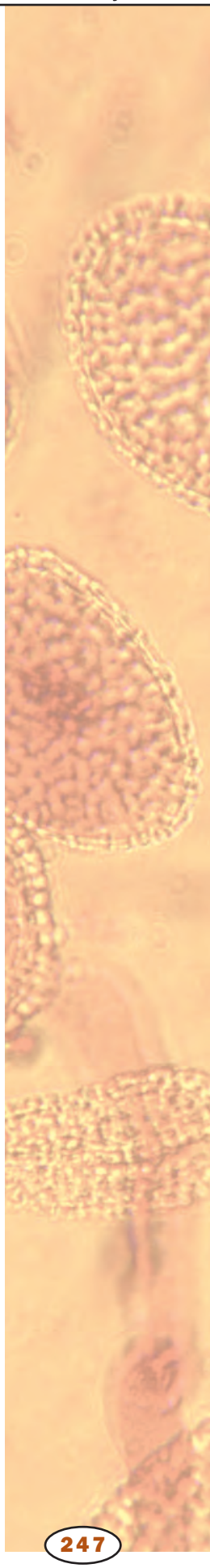
dialysis cleansing by partial filtration

dicot plant having two cotyledons, or seed leaves

dikaryotic cell cell with a pair of nuclei

dilation expansion or swelling

dimer polymer formed from two molecules of a simple compound



dimerizes forms a pair

diploid having pairs of chromosomes in the nucleus

dissociate break apart

distal away from

diurnal active during the daytime

dorsal to the back of

ecosystem an ecological community and its environment

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

efferent conducting outward or directing away from

electrolytes ions in body fluids

electromagnetic radiation light, X rays, and other forms of radiant energy

electron transport system membrane-bound system of proteins that extracts energy from high-energy electrons, found in mitochondria and chloroplasts

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

electrophoresis gel porous medium through which molecules can be separated using an electric current

embalming treating a dead body to protect it from decay

embryology development of the embryo

emulsify suspend in solution through interaction with soap or similar molecules

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

endogenous caused by factors inside the organism

endometriosis disorder of the endometrium, the lining of the uterus

endoplasmic reticulum network of membranes within the cell

endosperm nutritive tissue within a seed

endosymbiosis symbiosis in which one partner lives within the other

endothermic characterized by regulation of body temperature through metabolic activity

Enlightenment eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

enzymatic related to the function of an enzyme

enzyme protein that controls a reaction in a cell

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

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

epithelium one of four tissue types found in the body, characterized by thin sheets and usually serving a protective or secretory function

esophagus tube connecting the throat to the stomach

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

eukaryotic cell a cell with a nucleus

eutrophication process by which waters become enriched in dissolved nutrients that promote plant growth which results in depletion of dissolved oxygen

evapotranspiration loss of water from a plant by evaporation within the leaf

evidentiary DNA profile analyzed DNA from a sample used as evidence

excrete deposit outside of

exocrine gland gland that secretes substances to an external or internal surface rather than into the bloodstream

exoskeleton external skeleton

extensibility ability to expand or grow larger

fallopian tubes tubes through which eggs pass to the uterus

fecundity ability to reproduce

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

fertilization union of sperm and egg

fibroblast undifferentiated cell normally giving rise to connective tissue cells

filtrate material passing through a filter

focal at a point

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

food web set of feeding relations in an ecosystem

forb broad-leaved herbaceous plant

forensic related to legal proceedings

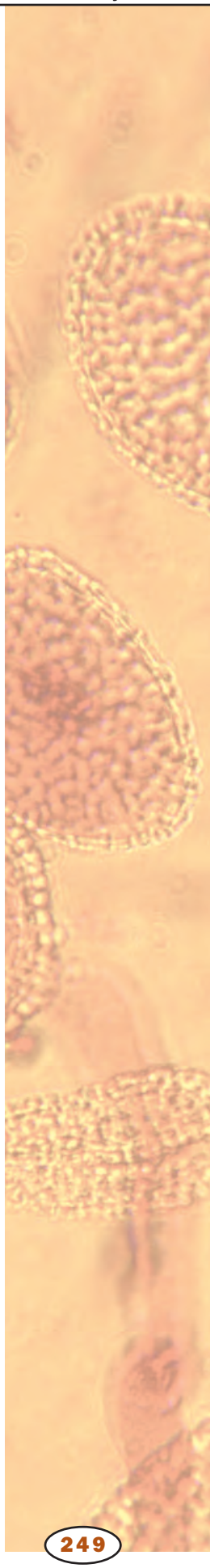
fulcrum pivot point of a lever

fungi major group of parasitic, lower plants that obtain their food from the products of organic decay (e.g. molds, smuts, etc.)

gamete reproductive cell, such as sperm or egg

gametophyte a haploid plant that makes gametes by mitosis

ganglia cluster of nerve cell bodies



gastroenteritis inflammation of the gastrointestinal tract, often from infection

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

gene expression use of a gene to create the corresponding protein

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

genitalia reproductive organs

genome total genetic material in a cell or organism

germ line cells creating eggs or sperm

gestation period of fetal development within the mother

glial supporting tissue of the elements of nervous tissue, including the brain, spinal cord, and ganglia

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

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

glycolysis initial stages of sugar breakdown in a cell

gradient difference in concentration between two places

grafting attachment and fusing of parts from different plants

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

gymnosperms "naked seed" plants, including conifers

hallucination altered sensory experience resulting in the perception of objects that are not real

haploid having single, nonpaired chromosomes in the nucleus

hectare 10,000 square meters (2.47 acres)

heme the deep red, iron containing, nonprotein portion of hemoglobin and myglobin

hemicellulose complex carbohydrate related to cellulose and found in cell walls of plants and some other organisms

hemoglobin oxygen-carrying protein complex in red blood cells

herbarium a collection of dried plant specimens systematically arranged for reference

hermaphrodite organism possessing both male and female reproductive structures

heterodimer complex molecule composed of two different parts

heterogeneous composed of, or containing, different parts or types

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

hexamer a structure composed of six parts

histogenesis origin or production of tissues

histology study of tissues

histone protein around which DNA wraps to form chromosomes

homologous similar in structure

homologous chromosomes chromosomes carrying similar genetic information

homologous recombination exchange of DNA segments between chromosomes

homozygous containing two identical copies of a particular gene

hormone molecule released by one cell to influence another

hybrid combination of two different types

hydrocarbon molecule or group composed only of C and H

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

hydrolyze to split apart using water

hydrophilic "water loving"

hydrophobic "water hating," such as oils

hydroponics growing of plants without soil

hydroxyl chemical group consisting of -OH

hypersalinity very high level of salt

hypersecretion excess secretion

hypersensitivity reaction immune reaction characterized by rapid and severe response, often with swelling of airways

hyphae threadlike part of the vegetative portion of the fungus

hyposecretion lack of secretion

hypothermia subnormal temperature of the body

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

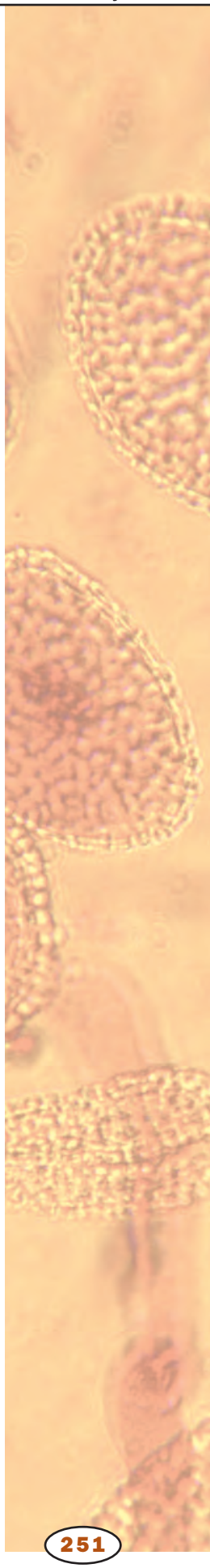
immunoglobulin an immune protein, also called an antibody

immunosuppressant inhibition of the immune response

in utero inside the uterus

in vitro "in glass"; in lab apparatus, rather than within a living organism

inbred repeatedly bred with close relatives, creating organisms with very little genetic variation



inducible able to be switched on

inflorescence characteristic arrangement of flowers on a stalk

infrastructure roads, phone lines, and other utilities that allow commerce

inorganic not bonded to carbon

insectivorous insect-eating

integrins a family of transmembrane linking proteins

interferons signaling molecules of the immune system

intermediate filament protein one type of cytoskeleton protein

interspecific between different species

interstitial space space between cells in a tissue

intracellular within a cell

intraocular within the eyeball

intrinsic to intimate part of; within

intron untranslated portion of a gene that interrupts coding regions

ion an electrically charged particle

ionic based on or functioning by means of ions

ionizing radiation high-energy radiation that destroys chemical bonds

isometric relating to contraction without movement

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

keratin a major structural protein

kilobase one thousand DNA bases; a measure of size of a piece of DNA

kilobasepair one thousand DNA base pairs; a measure of size of a piece of DNA

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

Krebs cycle central metabolic pathway in mitochondria

lactation production of milk by the mammary glands

laparoscopic surgery surgery in which an instrument is inserted through a very small incision, usually guided by some type of imaging technique

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

lateral side-to-side

lethargy lack of excitability; torpor

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

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

lineage ancestral line

lipid fat or waxlike molecule, insoluble in water

lipoprotein combination of protein and lipid, or fatlike molecule

locus site on a chromosome (plural, loci)

lotic of, relating to, or living in actively moving water

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

lymphatic system network of tubes that permeates the body for transport of lymph and combat of infection

lymphocyte white blood cell found in lymph nodes

lyse break apart

lysine an amino acid

lysing disintegration or dissolution of cells

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

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

materialism the belief that life is due entirely to biochemical interactions, without the intervention of supernatural forces

matrix a network, usually of threadlike fibers

medium nutrient source

meiosis cell division that forms eggs or sperm

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

metabolism chemical reactions within a cell

metabolite molecule involved in a metabolic pathway

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

metaphase intermediate stage in cell division, in which chromosomes line up before separating

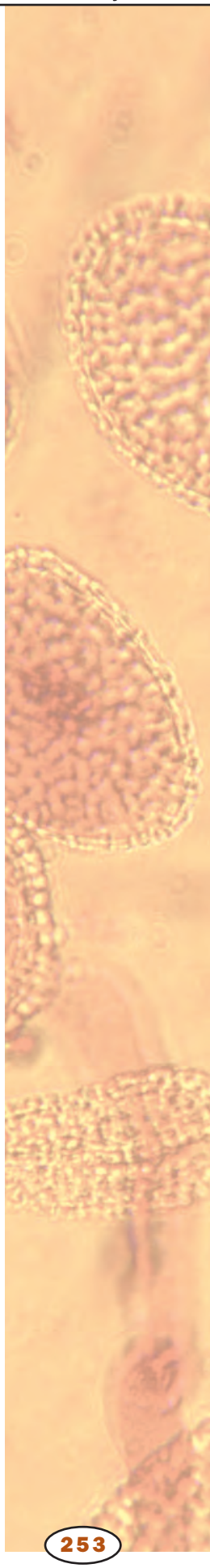
metastasis breaking away of cancer cells from a solid tumor to travel elsewhere in the body

metazoans animals other than sponges

methylation addition of the methyl group CH_3

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

mid-dorsal middle of the back



middle lamella layer of material between two plant cells that holds them together

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

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

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

mitogen substance that stimulates mitosis

mitosis separation of replicated chromosomes

molecular hybridization base-pairing among DNAs or RNAs of different origins

monocot any of various flowering plants, such as grasses and orchids, that have a single cotyledon in the seed

monoculture cultivation of a single type of crop in a large area

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

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

montane mountainous region

morphology related to shape and form

motile able to move

motor neuron nerve cell that controls a muscle or gland

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

multimer composed of many similar parts

multinucleate having many nuclei within a single cell membrane

muscle tone low level, constant muscle contraction

mutualism symbiosis between two organisms in which both benefit

mycorrhizae symbiosis between soil fungus and plant root to maximize absorption

myxedema thyroid disorder characterized by dry skin, swelling in the face, and mental deterioration

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

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

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

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

neritic zone near the shore

neural related to nerve cells or the nervous system

neurologist doctor who treats brain disorders

neuron nerve cell

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

niche the habitat supplying the right environment for a particular species

nm nanometer; one-billionth of a meter

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

nondisjunction failure of separation of homologous chromosomes during meiosis

nuclear envelope double membrane surrounding the cell nucleus

nucleated having a nucleus

nucleotide the building block of RNA or DNA

nucleus membrane-bound portion of cell containing the chromosomes

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

octomer composed of eight parts

oligosaccharide chain of several sugar molecules

oncogene gene that causes cancer

oocyte unfertilized egg

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

organelle membrane-bound cell compartment

organic composed of carbon, or derived from living organisms; also, a type of agriculture stressing soil fertility and avoidance of synthetic pesticides and fertilizers

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

osseous related to bone

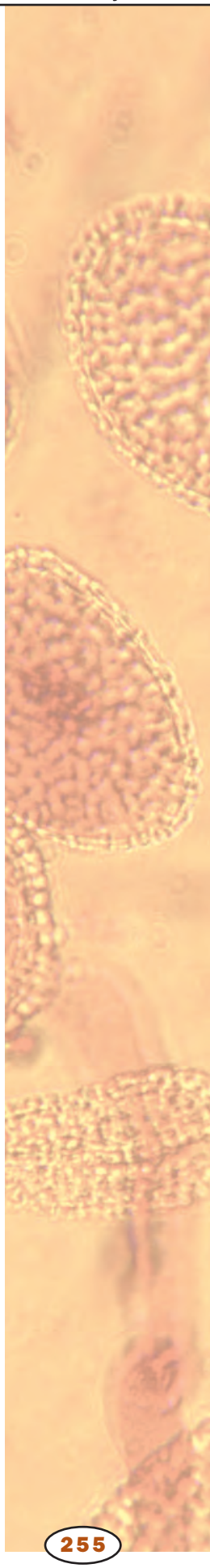
outcross fertilization between two different plants

ovipary production of eggs that hatch outside the body

ovovivipary production of eggs that hatch within the female's body

ovule multicellular structure that develops into a seed after fertilization

oxidation reaction characterized by loss of electrons, or reaction with oxygen



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

oxidative characterized by oxidation, or loss of electrons

oxidative phosphorylation use of oxygen to make ATP

oxidize to react or make react with oxygen

palatine bone bone of the hard palate at the roof of the mouth

paleoanthropology study of ancient humans

palindromic reading the same forward and backward

pandemic disease spread throughout an entire population

papillate small, nipplelike projection

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

parasitology study of parasites

parasympathetic nervous system branch of the nervous system promoting nutrient absorption and other maintenance activities

pathogen disease-causing organism

pathogenesis pathway leading to disease

pathologic related to disease

pectin carbohydrate in plants that forms crosslinks to stabilize cell walls

peptide bond bond between two amino acids

peptidoglycans polymer that is composed of polysaccharides and peptic chains

perianth combined sepals and petals

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

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

phage short for bacteriophage

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

pharynx throat

phase-contrast microscopy technique that manipulates passage of light through transparent specimens to reveal internal features

phenotype observable characteristics of an organism

pheromone molecule released by one organism to influence another organism's behavior

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

phosphodiester the link between two nucleotides in DNA or RNA

phosphorylate add a phosphate group to

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

phyletic gradualism the belief that evolutionary change is slow and steady

phylogenetic related to phylogeny, the evolutionary development of a species

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

physiology branch of biology that deals with the functions and activities of living matter

phytoplankton microscopic floating creatures that photosynthesize

pinnate featherlike

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

pipette lab instrument for precise measurement and transfer of small volumes of liquids

pistil female reproductive organ of a flower

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

plankton microscopic floating organisms

plant hybridization creation of offspring by union of two different types of plants, such as wheat and rye

plasmid small ring of DNA found in many bacteria

plasticity change form

plate tectonics the movement of large plates of Earth's crust

polar partially charged, and usually soluble in water

polar covalent bond in which electrons are unevenly shared

polymer molecule composed of many similar parts

polymerase enzyme complex that synthesizes DNA or RNA from individual nucleotides

polymerization linking together of similar parts to form a polymer

polypeptide chain of amino acids

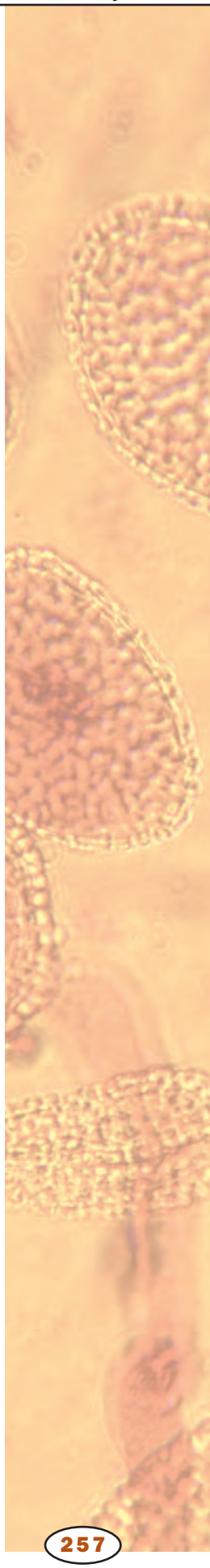
polysaccharide carbohydrate composed of many individual units of sugar

posterior toward the back

postmortem after death

prebiotic before the origin of life

Precambrian before the Cambrian era; before 600 million years ago



primer short nucleotide sequence that helps begin DNA replication

progeny offspring

prokaryote single-celled organism without a nucleus

promoter DNA sequence to which RNA polymerase binds to begin transcription

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

prostrate face downward

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

proteolysis breakdown of proteins

protoecology early ecology

protoplasm fluid portion of a plant cell within the cell wall

protostome "mouth first"; referring to the early development of the oral pore during gut tube formation

protozoa any of a phylum of minute protoplasmic animals present in almost every kind of habitat, some of which pose serious threats to humans and animals

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

psychosis severe mental disorder characterized by diminished connection with reality

psychotropic affecting consciousness, thought, or emotion

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

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

quarternary fourth level

radially symmetric symmetric, or similar, about a central point (a wheel is radially symmetric)

reproductive isolation isolation of a population from other populations of the same species due to inability to successfully reproduce; an early stage in species formation

respire use oxygen to burn cellular fuel

restriction enzyme enzyme that cuts DNA at a particular sequence

restriction fragments fragments of DNA created by restriction enzymes

reticular netlike

retrograde backward

reverse transcriptase enzyme that copies RNA into DNA

reverse transcription creation of DNA from an RNA template

ribonucleoprotein combination of RNA and protein

ribosome protein-RNA complex in cells that synthesizes protein

rickettsia (pl. -sias or siae) any of a family of polymorphic microorganisms that cause various diseases

RNA polymerase enzyme complex that creates RNA from DNA template

saline of, or relating to, salt

saprophyte plant that feeds on decaying parts of other plants

savanna open grassland with sparse trees

sclerophyll small, tough evergreen leaves

secretion material released from the cell

secretory pathway series of events within a cell by which molecules are brought to the plasma membrane for release from the cell

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

serotinous developing late in the season

serotype identity of an organism or virus based on reaction to an antibody

sessile attached and remaining in one place

silviculture cultivation of forest trees

sleep apnea difficulty breathing while asleep

solenoid cylindrical coiled structure

solute dissolved substance

solvation the process of dissolving

somatic nonreproductive; not an egg or sperm

somatostatin hormone produced by the hypothalamus that influences growth

spasticity of, or relating to, spasms

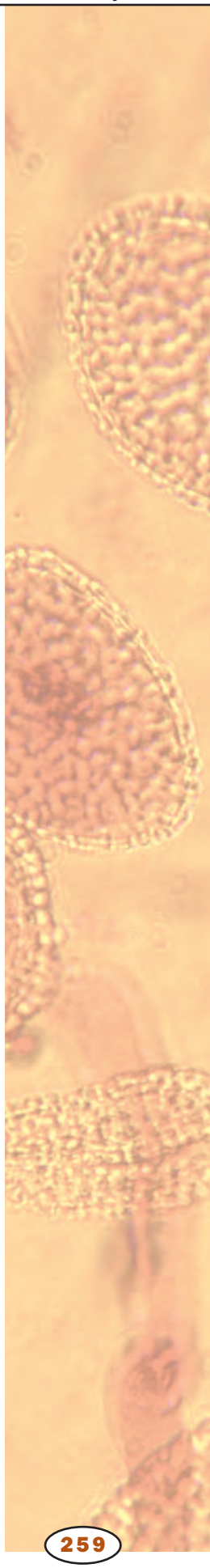
spectroscopy process using light or other emitted radiation to determine properties of a sample

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

spontaneous generation the theory that life began from nonliving matter

stasis state of no change

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



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

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

strong bond high-energy arrangement between two atoms involving electron-sharing; strong bonds require more energy to break than weak bonds

subcutaneous below the skin

substrate the molecule acted on by an enzyme; also a surface for attachment

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

superficial on the surface; not deep

symbiont organism living in close association with another organism

symbiosis close relationship between two species in which at least one benefits

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

synaptic transmission passage of chemicals between nerve cells to send messages or alter neuron firing

synchronously at the same time

synergism working together to create a larger product rather than a simple sum

systemic throughout the body

T cell white blood cell that controls the immune response

taxon a level of classification, such as kingdom or phylum

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

template master copy

teratogens substances that cause birth defects

tertiary third level

thermoregulation temperature regulation

transcribe creation of an RNA copy of a DNA gene

transcription messenger RNA formation from a DNA sequence

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

transduction conversion of a signal of one type into another type

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

translation synthesis of protein using mRNA code

translocation movement of sugars and other nutrients throughout a plant

transverse situated or lying across

trimer a structure composed of three parts

triploid possessing three sets of chromosomes

trophic related to feeding

trophic level feeding level in an ecosystem

true breeding giving only offspring identical to the parents

turgor internal pressure

ubiquitous found everywhere

ultrasonography use of sound waves to produce an image

ungulate hoofed mammals such as cattle

uninucleate possessing one nucleus

vas deferens tube through which sperm travel from testes to urethra

vector carrier

ventral to toward the belly side

ventricle fluid-filled chamber

venule any of the minute veins connecting the capillaries with the larger systemic veins

vesicle membrane-bound sac

vestigial no longer functional

visceral related to the viscera, or internal organs

viscous thick

vivipary production of live young

volatile easily vaporized

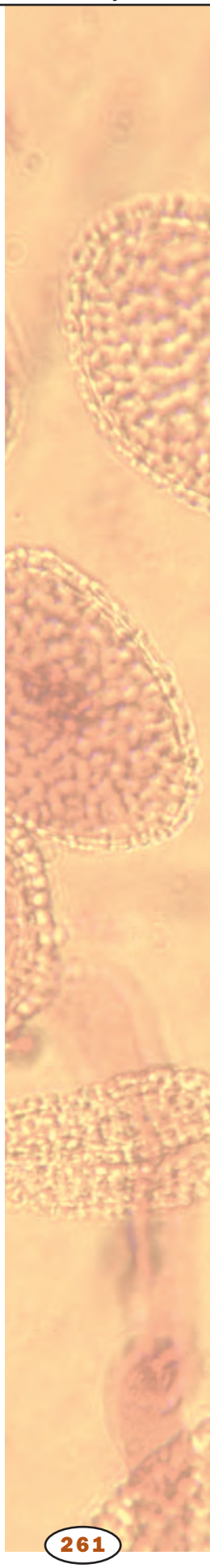
vulva external female genitalia

weak bond low-energy arrangement between two atoms involving electron-sharing; weak bonds require less energy to break than strong bonds

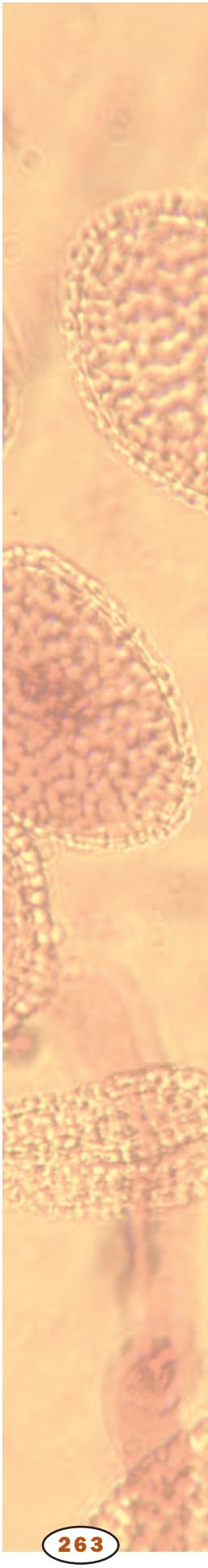
X-ray crystallography use of X rays to determine the structure of a molecule

xylem water-transporting system in plants

zygote fertilized egg



Topic Outline



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

Lipids
Lysosomes
Membrane Proteins
Metabolism
Mitochondrion
Nitrogen Cycle
Nitrogen Fixation
Nucleotides
Origin of Life
Oxidative Phosphorylation
Pauling, Linus
Peroxisomes
Pharmacologist
Poisons
Polymerase Chain Reaction
Prion
Protein Structure
Protein Synthesis
Radionuclides
RNA
Secondary Metabolites in Plants
Separation and Purification
Structure Determination
Vitamins and Coenzymes
Water

BIOLOGY AND SOCIETY

Alcohol and Health
Anabolic Steroids
Behavior, Genetic Basis of
Biological Weapons
Biology of Race
Carson, Rachel
Creationism
Desertification
Doctor, Specialist
Dubos, René
Endangered Species
Ethnobotany
Evolution, Evidence for
Extinction, Mammals
Fire Ecology
Gene Therapy
Global Climate Change
Human Genome Project
Human Population
Invasive Species
Organic Agriculture
Pauling, Linus
Pollution and Bioremediation
Psychiatric Disorders, Biology of
Psychoactive Drugs
Recombinant DNA
Reproductive Technology
Sexually Transmitted Diseases
Smoking and Health
Sociobiology
Transgenic Techniques

BIOMES

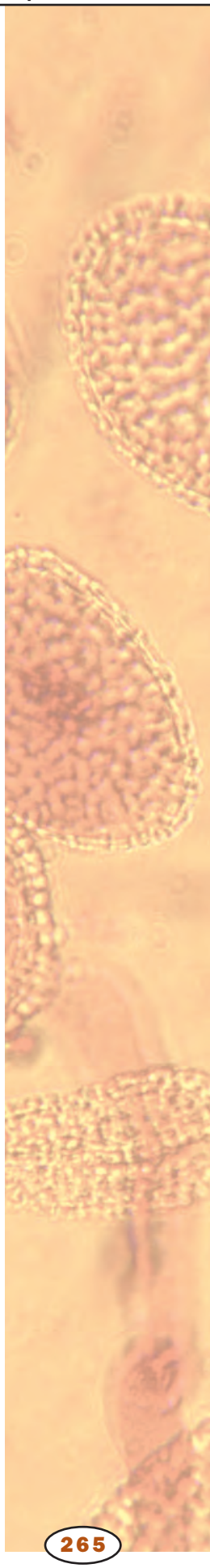
Biogeography
Biome
Coral Reef
Desert
Field Studies in Plant Ecology
Forest, Boreal
Forest, Temperate
Forest, Tropical
Global Climate Change
Grassland
Remote Sensing
Tundra

BIOTECHNOLOGY

Antibodies in Research
Antisense Nucleotides
Bacterial Genetics
Bioinformatics
Biological Weapons
Biotechnology
Clone
Electrophoresis
Forensic DNA Analysis
Genomics
Human Genome Project
Hybridization
Polymerase Chain Reaction
Recombinant DNA
Reproductive Technology
Reverse Transcriptase
Separation and Purification
Structure Determination
Transgenic Techniques

CAREERS

Agronomist
Biochemist
Botanist
College Professor
Dentist
Doctor, Family Practice
Doctor, Specialist
Emergency Medical Technician
Entomologist
Epidemiologist
Forester
Health and Safety Officer
High School Biology Teacher
Horticulturist



Laboratory Technician
Marine Biologist
Medical Assistant
Microbiologist
Microscopist
Nurse
Nurse Practitioner
Nutritionist
Pharmaceutical Sales Representative
Pharmacologist
Physician Assistant
Plant Pathologist
Psychiatrist
Public Health Careers
Science Writer
Veterinarian
Wildlife Biologist
Zoology Researcher

CELL FUNCTION

Active Transport
Cancers
Cell Cycle
Cell Motility
Control Mechanisms
Control of Gene Expression
Cytokinesis
Endocytosis
Enzymes
Exocytosis
Glycolysis and Fermentation
History of Plant Physiology
Hormones
Ion Channels
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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
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Life, What Is
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Muscle
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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

Lymphatic System
Physiological Ecology
Respiration
Smoking and Health
Temperature Regulation

DIGESTION AND EXCRETION

Digestion
Digestive System
Excretory Systems
Human Nutrition
Kidney
Liver
Metabolism
Osmoregulation
Physiological Ecology

DISEASE AND HEALTH

AIDS
Alcohol and Health
Anabolic Steroids
Autoimmune Disease
Bacterial Diseases
Birth Control
Blood Sugar Regulation
Cancers
Cardiovascular Diseases
Clinical Trials
Disease
Environmental Health
Female Reproductive System
Fungal Diseases
Gene Therapy
Health
Health and Safety Officer
Herbal Medicine
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Stress Response
Transplant Medicine
Vaccines
Viral Diseases
Vitamins and Coenzymes

DNA, RNA, CHROMOSOMES

Antisense Nucleotides
Chromosome Aberrations
Chromosome, Eukaryotic
Crick, Francis
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DNA Sequencing
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Genome
Medical/Science Illustrator
Meiosis
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Recombinant DNA
Replication
Sex Chromosomes
Transfer RNA
Watson, James

ECOLOGY

Biogeochemical Cycles
Biogeography
Biome
Carbon Cycle
Community
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Desertification
Ecological Research, Long-term
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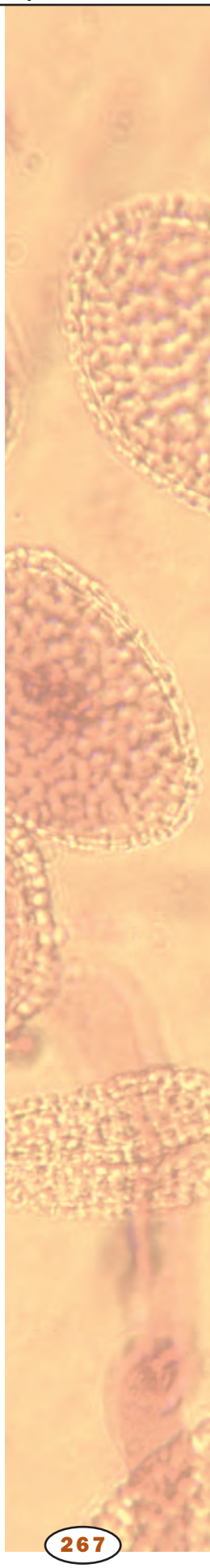

Grassland
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Population Dynamics
Predation and Defense
Remote Sensing
Rivers and Streams
Symbiosis
Theoretical Ecology
Tundra
Water Cycle
Wetlands

ENDOCRINE SYSTEM

Adrenal Gland
Anabolic Steroids
Birth Control
Blood Sugar Regulation
Endocrine System
Female Reproductive System
Hormones
Hypothalamus
Pancreas
Pituitary Gland
Sex Determination
Stress Response
Thyroid Gland

EVOLUTION AND ADAPTATION

Adaptation
Amniote Egg
Angiosperms
Biodiversity
Biogeography
Buffon, Count (Georges-Louis Leclerc)
Cambrian Explosion
Cell Evolution
C4 and CAM Plants
Convergent Evolution
Creationism
Darwin, Charles
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Evolution of Plants
Extinction, Mammals
Extreme Communities
Hardy-Weinberg Equilibrium
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History of Evolutionary Thought
Human Evolution
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Scaling
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Sociobiology
Speciation
Species

EXPERIMENTAL TECHNIQUES

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Transplant Medicine
Van Helmont, J. B.
Watson, James
Zoology Researcher

FUNGI

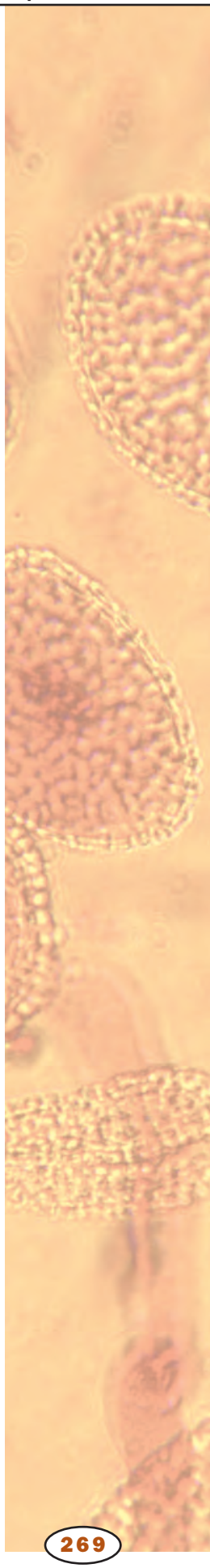
Biodiversity
Cell
Cell Wall
Fungal Diseases
Fungi
Lichen
Mycorrhizae
Plant Pathogens and Pests
Symbiosis
Taxonomy, History of

GENE—PROTEIN

Antisense Nucleotides
Chromosome, Eukaryotic
Control Mechanisms
Control of Gene Expression
DNA
Endoplasmic Reticulum
Gene
Genetic Code
Genetic Control of Development
Genetic Diseases
Hormones
McClintock, Barbara
Mutation
Nuclear Transport
Nucleolus
Nucleotides
Nucleus
Prion
Protein Structure
Protein Synthesis
Protein Targeting
Recombinant DNA
Retrovirus
Reverse Transcriptase
Ribosome
RNA
RNA Processing
Transcription
Transfer RNA
Transposon
Virus

GENETICS

Bacterial Genetics
Bacterial Viruses
Behavior, Genetic Basis of
Biology of Race
Chromosome Aberrations
Chromosome, Eukaryotic
Clone
Control of Gene Expression
Crick, Francis
DNA
DNA Sequencing
DNA Viruses
Forensic DNA Analysis
Gene
Gene Therapy
Genetic Analysis
Genetic Code
Genetic Control of Development
Genetic Counselor
Genetic Diseases
Genome
Genomics
Hardy-Weinberg Equilibrium
History of Biology: Inheritance
Human Genome Project
Hybrid
Hybridization
Hybridization, Plant
Linkage and Gene Mapping
McClintock, Barbara
Meiosis
Model Organisms: Cell Biology and Genetics
Nucleotides
Patterns of Inheritance
Pedigrees and Modes of Inheritance
Population Genetics
Prion
Radiation Hybrid Mapping
Recombinant DNA



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

Symbiosis
Theoretical Ecology
Von Humboldt, Alexander

LIFE CYCLES

Aging, Biology of
Alternation of Generations
Amniote Egg
Cell Cycle
Cnidarian
Development
DNA Sequencing
Female Reproductive System
Ferns
Fetal Development, Human
Growth
Life Cycle, Human
Life Cycles
Male Reproductive System
Reproduction in Plants
Seedless Vascular Plants
Seeds
Sexual Reproduction
Slime Molds

NERVOUS SYSTEM

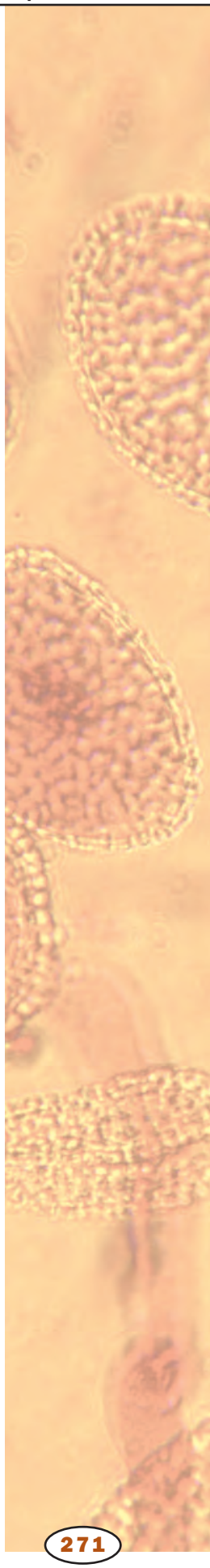
Biological Weapons
Brain
Central Nervous System
Chemoreception
Eye
Hearing
Hypothalamus
Ion Channels
Nervous Systems
Neurologic Diseases
Neuron
Pain
Peripheral Nervous System
Psychiatric Disorders, Biology of
Psychiatrist
Psychoactive Drugs
Spinal Cord
Stress Response
Synaptic Transmission
Touch
Vision

PLANT ANATOMY AND PHYSIOLOGY

Alternation of Generations
Anatomy of Plants
Beer-making, Botany of
C4 and CAM Plants
Cell Wall
Chloroplast
De Saussure, Nicolas
Differentiation in Plants
Flowers
Fruits
Grain
History of Plant Physiology
Hormones, Plant
Hybridization-Plant
Ingenhousz, Jan
Leaves
Meristems
Mycorrhizae
Nitrogen Fixation
Photoperiodism
Photosynthesis
Plant Development
Plant Nutrition
Plant Pathogens and Pests
Poisonous Plants
Pollination and Fertilization
Propagation
Reproduction in Plants
Rhythms of Plant Life
Roots
Secondary Metabolites in Plants
Seed Germination & Dormancy
Seeds
Senescence
Shoots
Soil
Translocation
Tropisms and Nastic Movements
Van Helmont, J. B.
Water Cycle
Water Movement in Plants
Wine-making, Botany of
Wood and Wood Products

PLANT DIVERSITY

Angiosperms
Biodiversity
Biogeography
Bryophytes
C4 and CAM Plants
Conifers
Eudicots
Evolution of Plants
Ferns
Grasses
Gray, Asa
Gymnosperms
Hybridization-Plant
Monocots



Plant
Seedless Vascular Plants
Torrey, John
Vavilov, Nikolay
Von Humboldt, Alexander

PROTISTS

Algae
Beer-making, Botany of
Cell
Coral Reef
Evolution of Plants
History of Biology: Cell Theory and Cell Structure
Leeuwenhoek, Anton
Lichen
Model Organisms: Cell Biology and Genetics
Plankton
Protista
Protozoa
Protozoan Diseases
Slime Molds

REPRODUCTION AND DEVELOPMENT

Aging, Biology of
Birth Control
Cell Cycle
Cytokinesis
Development
Female Reproductive System
Fetal Development, Human
Genetic Diseases
Life Cycle, Human
Life Cycles
Male Reproductive System
Meiosis
Mitosis
Reproductive Technology
Sexual Reproduction
Sexually Transmitted Diseases

SKIN, MUSCLE, AND BONE

Body Cavities
Bone
Connective Tissue
Epithelium
Growth
Locomotion
Muscle
Musculoskeletal System
Skeletons
Skin

TAXONOMY AND BIODIVERSITY (SEE ALSO ANIMAL DIVERSITY AND PLANT DIVERSITY)

Animalia
Archaea
Biodiversity
Eubacteria
Evolution of Plants
Fungi
Kingdom
Lamarck, Jean-Baptiste
Leeuwenhoek, Anton
Linnaeus, Carolus
Plant
Protista
Speciation
Species
Taxonomy, History of

VIRUSES AND PRIONS

AIDS
Bacterial Viruses
Plant Pathogens and Pests
Prion
Retrovirus
Reverse Transcriptase
Sexually Transmitted Diseases
Viral Diseases
Virus