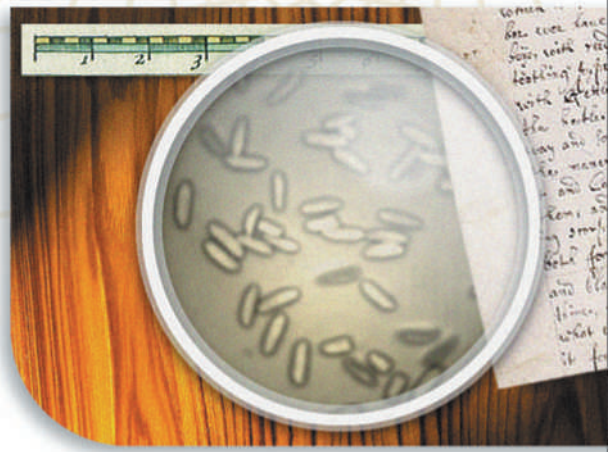
biology

VOLUME 4
Plants and Careers in Biology



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VOLUME 4
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Cumulative Index

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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

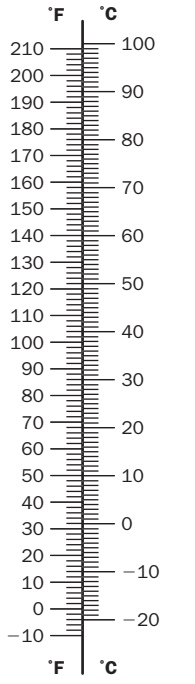
Definitions

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

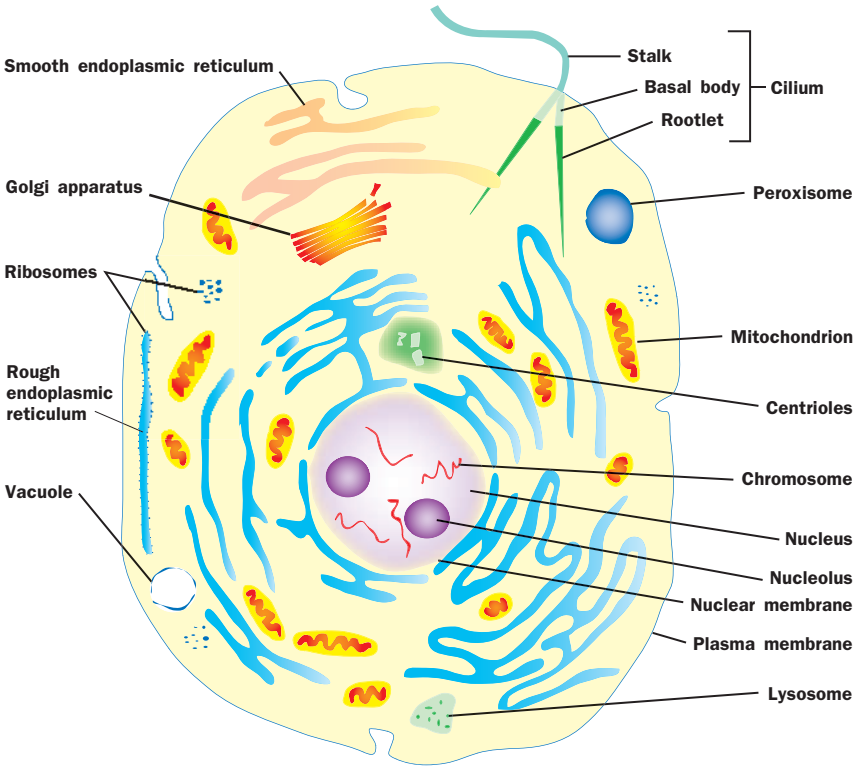


100°C = water boils
0°C = water freezes

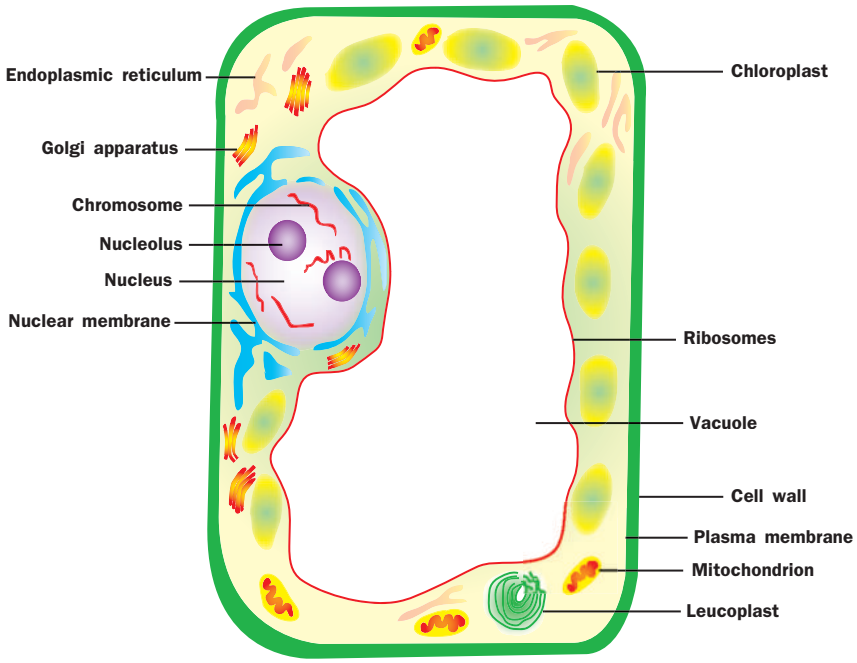
GEOLOGIC TIMESCALE

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

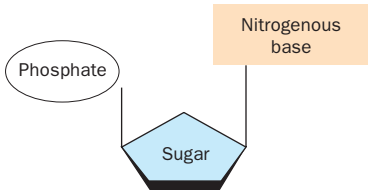


A TYPICAL PLANT CELL



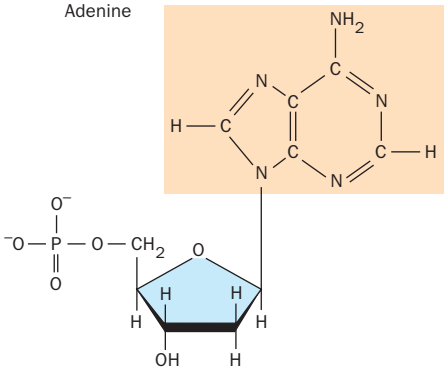
STRUCTURE OF DNA NUCLEOTIDES

Components of a nucleotide

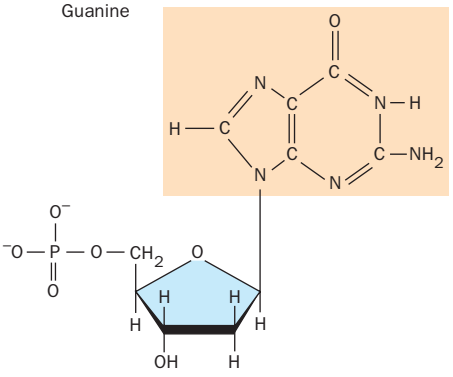


Purine-containing nucleotides

Adenine

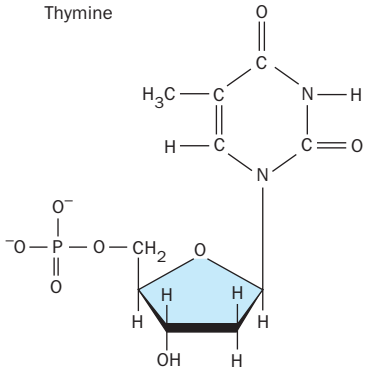


Guanine

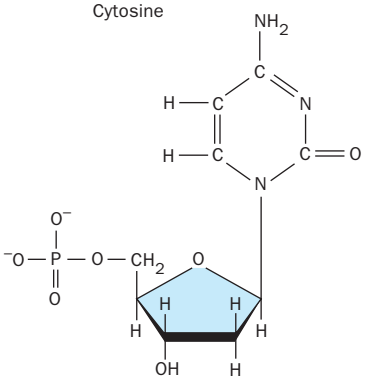


Pyrimidine-containing nucleotides

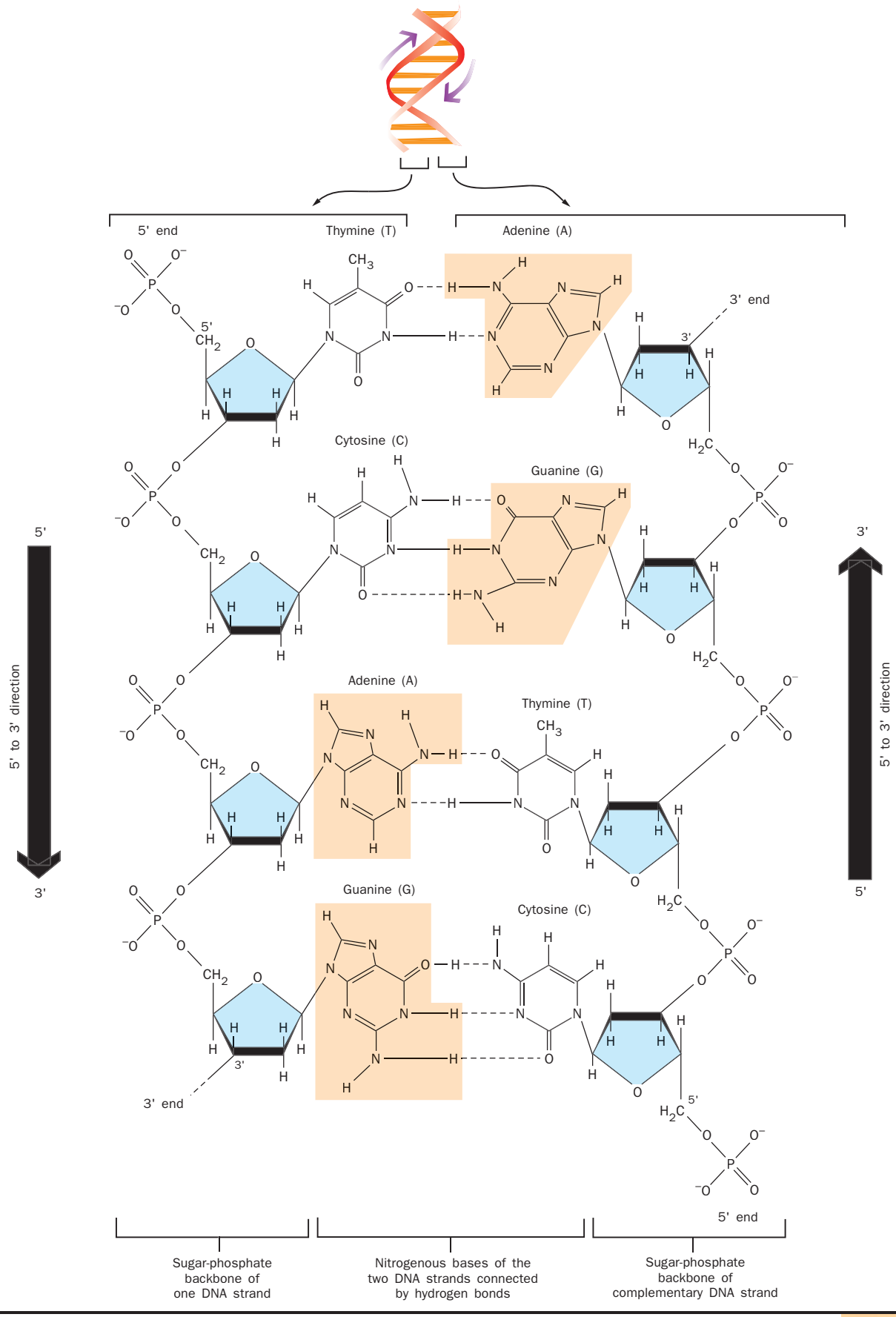
Thymine



Cytosine



DNA NUCLEOTIDES PAIR UP ACROSS THE DOUBLE HELIX



COMPARISON OF DNA AND RNA

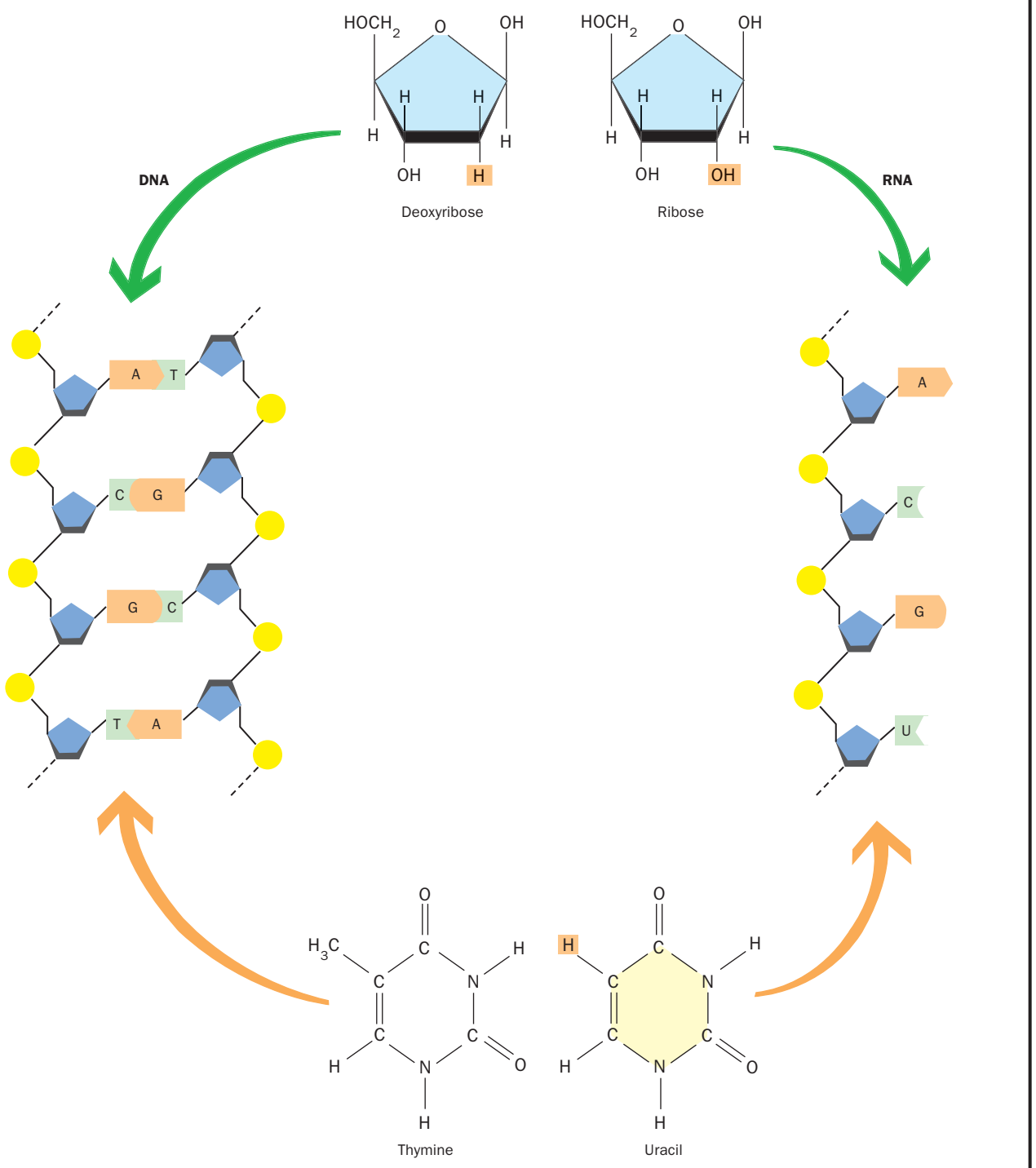


Table of Contents

VOLUME 1

D

VOLUME 2

E

M

N

O

P

VOLUME 4

P

R

S

T

V

W

Z

biology

Predation and Defense

Predatory behavior is that which results in the killing of another animal for food. Some predators, such as lions and tigers, are large and ferocious, while others can be small and benign in appearance, such as lady bugs. (Lady bugs, however, might seem ferocious to their prey, which are tiny insects called aphids.) Some predators, such as bears and crows, eat a mixed diet that includes a lot of plant material as well as other animals. Other animals, such as frogs, lizards, and most species of wild cats, are more strictly carnivorous, and their diet consists almost entirely of animals.

Characteristics of Predators

Predators usually possess excellent senses to find their prey and special abilities to capture the prey. Predatory birds, for example, possess outstanding eyesight and often hearing, as in the case of owls. Other predators, such as many species of mammals, have a very keen sense of smell that helps them locate prey. Many predators are very fast, and use their speed to help capture their prey. Cheetahs, predators of the African **savannas**, are the world's fastest runners; falcons, predators of other bird species, are the world's fastest fliers; and dolphins and barracudas are very fast swimmers.

savanna open grassland with sparse trees

Prey Defenses

Most species are potential prey for another animal at least sometime during their lives. Even lions and wolves can fall victim to other predators when they are very young. Most species possess several lines of defense against predators. Often the first line of defense is to avoid being detected by the predator. One way to do this is to minimize noise production and any visual cues that the predator might use to locate the prey. Frogs and crickets usually stop singing as another creature approaches. The resulting silence makes it more difficult for the predator to find them. Other prey have evolved camouflage coloration that blends into the background making it difficult for visual predators to find them. Many moths, common prey for birds, look like the bark of trees on which they rest during the day, and snowshoe hares, the primary prey for lynx, have brown fur in the summer but white fur in the winter when their northern environment is covered with snow. Because predators often use prey movements to detect them, many prey remain as still as possible when a predator approaches.

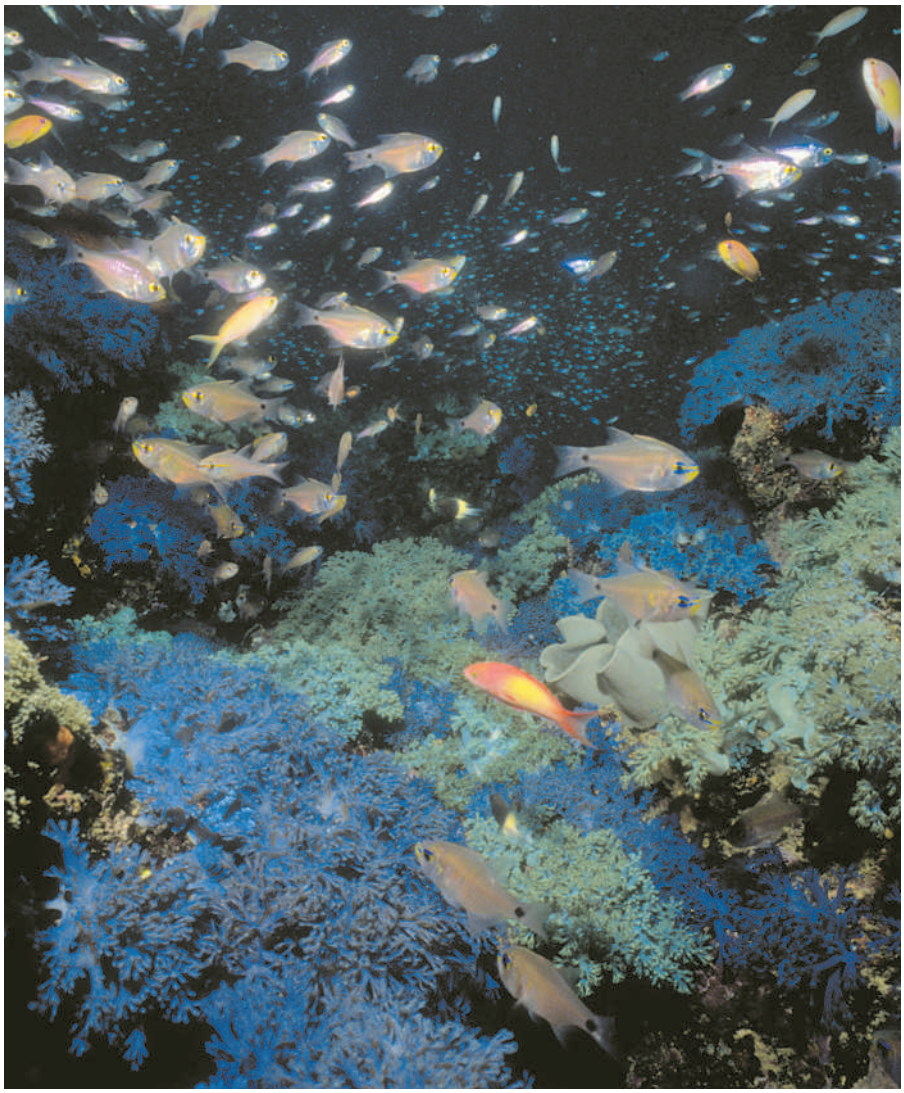
Predatory birds, such as this peregrine falcon (*Falco peregrinus anatum*), possess outstanding eyesight.

The prey usually has other lines of defense it can utilize if spotted. Many prey species are very fast runners, swimmers, or fliers, and they often can use their speed to escape. Even if a prey is spotted and caught, or cornered, the result is often not a foregone conclusion. Many prey successfully deter a predatory attempt by fighting back. An adult moose is usually successful at warding off an attack by a pack of wolves, even if the moose has been surrounded by the wolves. The moose is able to use its hooves as lethal weapons against the much smaller wolves, and the wolves generally give up once they realize the moose is healthy and a formidable adversary.

Some animals have morphological and behavioral adaptations that make it difficult for the predator to get the prey into their mouth. Many fish and insects have spines that prevent a predatory fish or bird from being able to eat them. Some prey, like the puffer fish, make themselves larger if threatened, again making it more difficult, often impossible, for the predator to ingest the prey.

Many prey have evolved to use social behavior as a predatory defense. For example, many species of fish and birds travel in groups, such as schools of fish and flocks of birds. These schools and flocks often move very quickly in a highly synchronized fashion. Scientists believe that these groups provide protection for individuals in the group. Most predators have to single out and focus on a single individual in order to successfully capture a prey. However, the fast-moving and synchronized flocks and schools are believed to make it difficult for the predators to accomplish this. In some cases, a group of prey is able to successfully fight off a predatory attack, whereas an individual prey probably would not be able to do this. For example, although a baboon on its own would probably succumb to a predatory attack from a leopard, a group of males in a baboon troop can usually ward off such an attack.

Some prey are easy for predators to find, easy for predators to capture, and easy for predators to ingest. Yet they seldom fall prey to predators because they employ a final line of defense: toxicity. They are poisonous. The poison dart frogs of the rain forests of Central and South America are an



Some species of fish swim in a highly synchronized fashion to defend themselves against their predators.

excellent example. These are small, brightly colored frogs that are easy to find, catch, and eat. However, they are very poisonous, and most birds quickly learn to avoid them. The indigenous people of these rainforests discovered that these frogs contain a potent toxin and learned to extract the toxin from the frogs. They then dipped the tips of their arrows in the toxin before going out on a hunting expedition. Ironically, by using the toxin that had evolved as an antipredatory defense, the people became more effective predators.

Evolution of Predator-Prey Relationships

Because the cost of being caught and eaten by a predator is so great, the intensity of natural selection on prey species has been very high throughout evolution. The selection pressure on the prey is probably higher than that on the predator. If a fox fails in its attempt to catch a rabbit, it just misses lunch. However, if a rabbit fails in its attempt to escape from a fox, it loses its life. Because of the intensity of selection on prey species, the variety and effectiveness of antipredatory defenses is especially impressive.

It is believed that predators and their prey have coevolved. This means that as the predators developed adaptations that enabled them to capture the prey more successfully, the selection pressure on prey intensified, resulting in the selection of more effective antipredator adaptations. In turn, these more effective antipredator adaptations are believed to have promoted the selection of more effective predatory adaptations. This reciprocal ongoing evolutionary cycle among predators and prey is sometimes referred to as an evolutionary arms race. SEE ALSO ECOSYSTEM; FEEDING STRATEGIES; MIMICRY, CAMOUFLAGE, AND WARNING COLORATION; POISONS

Mark. A. Davis

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Primate

The order Primates includes prosimians, monkeys, and apes. Primates are well studied, to a large extent because people are primates. (Humans are apes, within the superfamily Hominoidea.) There are some 240 species of primates alive today, ranging across South America, Africa, and Asia. Since nearly all primates are primarily arboreal (they live in trees), their geographic distribution is largely confined to forest or woodland and to warm regions where all of the trees do not lose their leaves and fruits at the same time.

Traditionally primates are divided into two groups: the Prosimians (lemurs of Madagascar and Africa, lorises of Asia, and tarsiers of Asia) and the Anthropoidea (monkeys and apes). Many primatologists prefer to classify them in two main groups: the Strepsirrhini (lemurs and lorises) and Haplorrhini (tarsiers, monkeys, and apes). The difference between the two classificatory systems is the placement of tarsiers, which demonstrate many evolved features relative to the prosimians.

Primates are a generalized group of mammals defined by a series of characters variously present in each species. Tendencies in the primates include:

- An emphasis on the sense of sight and a relative deemphasis on the sense of smell; forward-facing eyes that allow good depth perception; and, in the monkeys and apes, there is color vision.
- Grasping hands, with retention of all five digits; nails (not claws) on the ends of digits; sensitive tactile pads on grasping hands, opposable thumbs; and usually grasping feet.
- Large brains for body size; efficient nourishment of the fetus *in utero*, with usually one infant born at a time, and a prolonged childhood, allowing for more time to learn; longer lives and a great deal of sociality.
- Generalized diets, eating some combination of insects, fruit, and leaves (there are some specialists in each of those categories); baboons and chimpanzees also hunt vertebrates to a small degree, while humans hunt relatively more.

- Varying social and mating habitats. There are multi-male, multi-female groups (baboons); single male multi-female groups (some gorillas, some baboons); and monogamous (gibbons), polyandrous (tamarins and marmosets), polygynous, and promiscuous mating species (chimpanzees). Some are relatively solitary (for example, orangutans). In some cases males immigrate from their natal group and in others, females do.

The relationship between the primates and other orders is not resolved, despite attempts using **morphology** and comparisons of molecular biology. Molecular and anatomical comparisons have indicated sister groups, which include Chiroptera (bats), Rodentia (rodents), and Lagamopha (rabbits), among others.

The earliest fossils that are undisputed primates are from a warm epoch called the Eocene, found in North America, North Africa, and Asia, but not in South America or Antarctica.

There is special urgency to preserve primates because they inform scientists about humans and human evolution. About one-third of primate species are in danger of extinction because of rampant destruction of their forest habitats via logging and the bush-meat trade. SEE ALSO CHORDATA; HUMAN EVOLUTION

Martha Tappen

GOODALL, JANE (1934–)

British biologist whose long-term study of the behavior and social organization of chimpanzees in Tanzania has transformed scientific understanding of primate behavior. She showed, for example, that chimpanzees make and use tools and engage in highly complex social behaviors.

morphology related to shape and form

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Prion

Unlike all other infectious agents, prions contain no deoxyribonucleic acid (DNA) or ribonucleic acid (RNA). This radical difference has slowed the understanding and acceptance of the infectious properties of prions since their discovery. Prions are infectious agents composed of **protein** that cause fatal brain diseases. Prion diseases include scrapie in sheep, "mad cow disease" (bovine spongiform encephalopathy, or BSE) in cattle, and Creutzfeldt-Jakob disease (CJD) in humans. Prion diseases can be transmitted when an organism consumes infected brain material from another organism. This occurred in England (and elsewhere) when cows were fed processed remains of infected livestock. While the cause of most cases of CJD is unknown, a small number of European cases have been correlated with the consumption of contaminated beef.

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

First called "slow viruses," the unusual nature of these infectious agents became clear from experiments performed in the 1960s. For example, the agents were particularly resistant to sterilization procedures that inactivated bacteria and viruses.

In the early 1980s American **neurologist** Stanley Prusiner published biochemical purification studies suggesting that these **pathogens** were composed mainly of one type of protein and were thus fundamentally different—and by

neurologist doctor who treats brain disorders

pathogen disease-causing organism

implication, far simpler chemically—than conventional infectious pathogens of animals and plants. Prusiner coined the term prion (derived from *pro*teinaceous *in*fectious pathogen) to highlight this distinction. The single protein implicated as the causative agent was named the prion protein, PrP for short. Although the theory was first greeted with skepticism, Prusiner was vindicated by receiving the 1997 Nobel Prize in Biology or Medicine.

amino acid a building block of protein

conformation three-dimensional shape

α the Greek letter alpha

Generally, and as first suggested by Norwegian-American chemist Christian Anfinsen, the linear sequence of **amino acids** in a protein determines its unique three-dimensional structure, or "conformation." This **conformation** arises from folding of the peptide chain driven by thermodynamic considerations. A normal form of PrP made in healthy animals is called PrP^{C} and follows a predetermined pattern of folding. The folding results in three corkscrew ("**α**-helical") segments that compact down upon each other to form a globular core region. Surprisingly, analysis of the infectious form of the PrP referred to as PrP^{Sc} reveals a different shape. Compared to PrP^{C}, PrP^{Sc} has a diminished amount of α-helix and an increased amount of another folding pattern called α-sheet, despite the fact that they have the same amino acid sequence.

template master copy

These findings defined a new mechanism of disease resulting from proteins adopting alternative, inappropriate conformations. The exact means whereby PrP^{Sc} molecules are formed from PrP^{C} molecules is not fully understood. Nonetheless, it appears to involve a templating reaction where PrP^{C} molecules are first unfolded and then refolded into the shape characteristic of PrP^{Sc} using preexisting PrP^{Sc} molecules as **templates**. Since the generation of new PrP^{Sc} molecules is equated with (and perhaps the same as) the generation of new infectious particles, it can be seen that prions "replicate" in a strange and novel manner, namely by subverting the folding of a normal cell-surface protein. SEE ALSO NEUROLOGIC DISEASES; PROTEIN STRUCTURE

David Westaway

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Propagation

Plant propagation is the art and science of increasing numbers of plants utilizing both sexual and asexual methods. It is not an exaggeration to say that the continued existence of modern civilization depends upon plant propagation.

Sexual plant propagation is accomplished using seeds or spores. Many crops grown this way are essential for environmental quality, food, fiber, fuel, medicines, shelter, and myriad other plant-derived substances essential for quality of human life.

hybrid combination of two different types

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

Seeds may be harvested from wild plants or from those subject to carefully controlled cross-pollination, which produces plants known as **hybrids**. These hybrid plants may have characteristics superior to their parents such as increased **protein**, better flavor, and pest resistance. Sexual plant propa-

gation begins with seed harvesting and is separate from the creation of the cross-pollination process.

Seeds of most grains and vegetables require specific environmental conditions to germinate and grow. For these plants, proper seed harvest and storage to maintain **viability** and vigor are essential. Once a seed is sown, it can be expected to germinate in a period of time ranging from a few days to a few weeks.

viability ability to live

Many seeds require special events or processes to occur before they can germinate. These may include cycles of warm and/or cool, moist treatments (stratification), cracking or wearing away of seed coats (scarification), smoke, intense heat from fire, or even passing through the digestive tract of an animal. Seeds of many perennial flowers as well as most trees and shrubs originating in temperate climates require physical and/or chemical treatment to overcome dormancy.

Some natural and human-made plant hybrids will not retain their desirable traits if allowed to reproduce sexually, so they must be propagated by asexual means to produce clones. A common technique in asexual plant propagation is stimulating root growth on plant parts such as stems that have been cut off. This is known as cutting propagation and is the most common form of propagation used in ornamental nursery production.

An ancient yet common asexual propagation technique involves joining the top of one plant (the "scion") with the root system of another. This is called **grafting**. Grafting allows combinations of desirable root characteristics of a plant (such as pest resistance) with desirable shoot characteristics of another (such as flavorful fruit). Often grafting is the only economical means to produce plants with those desirable characteristics. Grafting is a skill commonly employed in the production of fruit and nut-producing plants.

grafting attachment and fusing of parts from different plants

Another asexual plant propagation method is micropropagation, or tissue culture. In micropropagation, a very small piece of plant tissue is placed on an artificial growth **medium** under conditions similar to a hospital laboratory. Once sufficient tissue increase has occurred, plants are hormonally stimulated into differentiating to create a plant that can be grown outside the laboratory. SEE ALSO CLONE; HORMONES, PLANT; HORTICULTURIST

medium nutrient source

Richard E. Bir

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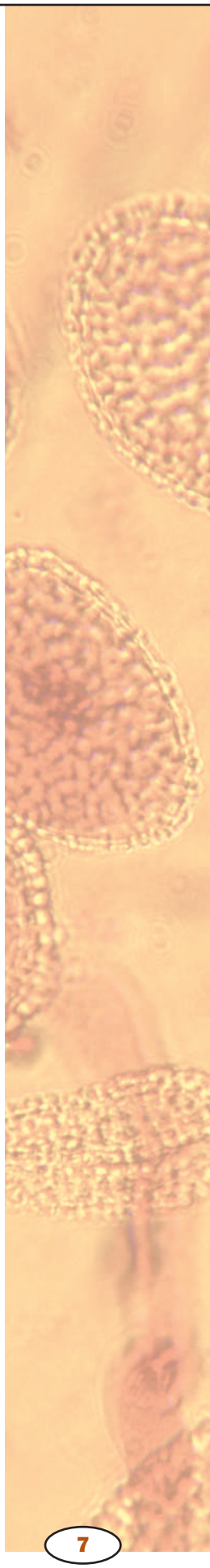
Protein Structure

Proteins are chains of **amino acids** that fold into a three-dimensional shape. Proteins come in a wide variety of amino acid sequences, sizes, and three-dimensional structures, which reflect their diverse roles in nearly all cellular

amino acid a building block of protein



functions. Each protein has a particular structure necessary to bind with a high degree of specificity to one or a few molecules and to carry out its function; thus, function is directly correlated to structure of the protein. Proteins make up about 50 percent of the dry weight of cells and are the most abundant of the **macromolecules** inside the cell and of the cellular membranes. Proteins (including their **lipoprotein** and glycoprotein forms) also constitute 10 percent of the weight of the blood plasma of living organisms, carrying various nutrients throughout the body and acting as signals to coordinate bodily functions between the different organs.

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

lipoprotein combination of protein and lipid, or fatlike molecule

The sizes of proteins vary greatly. The size is described by the molecular weight given in the units of a dalton. One dalton is the molecular mass of one hydrogen atom. The molecular weight of a protein is equal to the addition of the molecular weights of the amino acids constituting the protein. Some proteins are of relatively small molecular size, such as insulin, with a molecular weight of about 5,700 daltons. Others, like titin (a protein found in muscle), are very large. Some proteins consist of a single amino acid sequence (polypeptide chain), while others are **multimers** of the same or different subunits.

multimer composed of many similar parts

Organization of Protein Structure

There are four levels of protein structure: primary, secondary, tertiary, and quaternary. These levels also reflect their temporal sequence. Proteins are synthesized as a primary sequence and then fold into secondary → tertiary → and quaternary structures. The figures show these various types of structure, which are described as follows.

Amino acids (see Figure 1) are the building blocks (units) of proteins. Each amino acid has several common features: an amino and a carboxyl chemical group both bonded to the alpha carbon (Cα) and an R group that defines a particular amino acid. Some R groups are **hydrophobic** and tend to project to, and be buried in, the inside of a protein structure. Four amino acid R groups contain either a positive or negative charge and thus project to the water environment to the exterior of proteins. Other R groups are **polar** in nature and also tend to project to the outside.

hydrophobic "water-hating," such as oils

polar partially charged, and usually soluble in water

The amino acids of a protein are connected to each other by **peptide bonds**. During protein synthesis the amino group of the amino acid being added is coupled to the carboxyl group of the prior amino acid, and two hydrogen atoms and one oxygen atom are removed as a water molecule (H_2O) and the peptide bond is formed (see Figure 2).

peptide bond bond between two amino acids

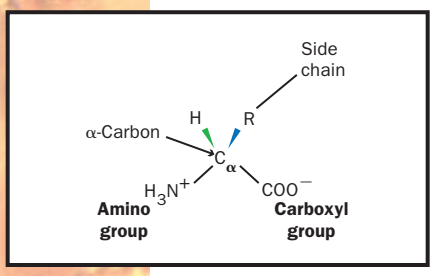


Figure 1. Structure of an amino acid.

Primary Structure of Proteins. The linear sequence of amino acids constitutes a protein's primary structure. The sequence is written from the amino-terminal end (the first amino acid) to the carboxyl-terminal end (the same sequence in which the protein is synthesized). All properties of a protein are derived from the primary structure, the linear sequence. Encoded in the sequence is the ability of the protein to fold into its secondary, tertiary, and quaternary structures, and thus to be able to carry out a function. The function of a protein is only expressed when the protein has achieved its three-dimensional shape.

Secondary Structures of Proteins. Secondary structures arise from noncovalent interactions between amino acids across the chain. There are only

two bonds that can rotate in space between each amino acid in the backbone of the primary sequence. These restricted movements, when repeated through several amino acids in a chain, yield the two main types of protein secondary structure: the alpha (α) helix and the beta (β) strand.

The α helix is shaped like a spiral staircase, with each step representing a single amino acid. Each 3.6 amino acids complete a 360-degree turn in the helix. If a helical portion of a protein contained 36 amino acids, there would be 10 complete turns in the helix. Each amino acid projects an R group to the outside of the staircase. **A** helices of proteins vary in length from 5 to 40 amino acids with an average of about 10. Certain proteins are made up entirely of α helices (and the loops connecting the helices) such as the subunits of **hemoglobin**, which contain 8 α helices.

As the name "strand" implies, the amino acids of the β strand form a linear structure. However, the bond angles along the peptide backbone produce a regular zigzag pattern within this linear structure. Adjacent R groups project in opposite directions. When amino acid sequences fold into a three-dimensional structure of β strands, one amino acid R group will then project to the interior of the protein and the adjacent R group will project to the outside (to the water environment).

β strands of proteins may be arranged adjacent to each other like strings on an instrument to form what is termed a β sheet. The β strands of a β sheet may be parallel in orientation (all the sequences running from amino- to carboxyl-terminal) or antiparallel (that is, the strands alternate in orientation).

To form a complete protein, the α helices or β strands must be joined together through the amino acid sequence. The amino acids that make up these joining regions are called "loops." For example, two adjacent antiparallel β strands of a β sheet are often connected by a loop consisting of two or three amino acids. Loops also connect segments of α helices and connect β strands that are adjacent to α helices in a protein sequence. Some loop regions can be very long, consisting of up to twenty-one amino acids; but, most commonly, they are between two and ten amino acids.

Tertiary Structures of Proteins. The three-dimensonal structure of a single **polypeptide** chain is termed its tertiary structure. Tertiary structures are different combinations of the secondary structures (α helices, β strands, and loops). Tertiary structure is subdivided into certain portions that are termed motifs and domains.

Motifs are simple combinations of secondary structure that occur in many different proteins and which carry out a similar function. An example is the helix-loop helix. It consists of two antiparallel α helices at about a 60-degree angle to each other connected by a loop. This motif, which binds the calcium **ion**, is found in several proteins that regulate cellular activity via changes in calcium ion concentrations. Many proteins that bind to deoxyribonucleic acid (DNA) and regulate **gene expression** incorporate a zinc finger motif. As the name implies, this motif binds the zinc ion using combinations of the amino acids cysteine and histidine. One type of zinc finger motif consists of a single α helix opposite two β strands in an antiparallel arrangement. The zinc ion is held between the α helix and the two β strands using two histidine R groups from the α helix and two cysteine R groups

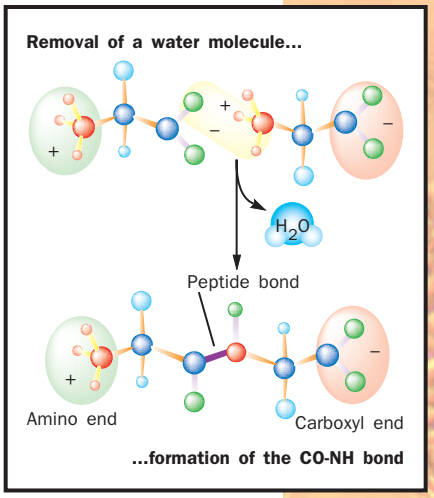


Figure 2. Formation of a peptide bond.

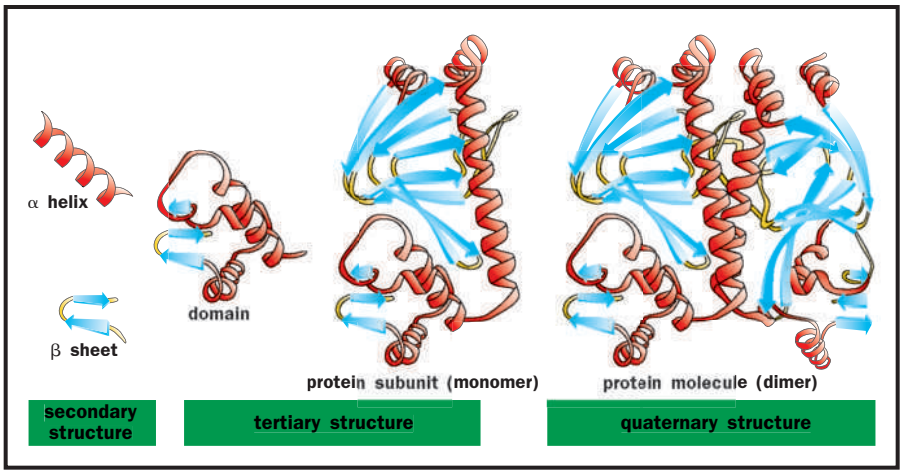
A the greek letter alpha

hemoglobin oxygen-carrying protein complex in red blood cells

polypeptide chain of amino acids

ion an electrically charged particle

gene expression use of a gene to create the corresponding protein



Levels of protein structure. Alpha helices and beta sheets are linked by less-structured loop regions to form domains, which combine to form larger subunits and ultimately functional proteins.

from the β strands. Another motif common to DNA binding proteins is the leucine zipper, in which two parallel α helices are adjacent to each other with the leucine side chains projecting from each helix binding together and thus binding the two helices together.

A single polypeptide chain may fold into one or more domains to yield the tertiary structure of a protein. The eight α helices of a subunit of hemoglobin connected by seven loop regions constitute the globin domain. Two β sheets (each of four antiparallel β strands) form a "β barrel" structure domain that is repeated in the **immunoglobulin** proteins. Each domain can express a distinct function and is sometimes arranged in a single protein to efficiently carry out an overall function that has several parts. For example, there are seven different chemical reactions that act in sequence to synthesize a fatty acid. In mammals, the fatty acid synthetase **enzyme** is a single polypeptide chain folded into seven domains, each domain carrying out one of the seven chemical reactions.

immunoglobulin an immune protein, also called an antibody

enzyme protein that controls a reaction in a cell

Quaternary Structures of Proteins. Two or more polypeptide chains may bind to each other to form a quaternary structure. The quaternary structure of hemoglobin, for example, consists of four polypeptide chains, two α, and two β subunits arranged in space in a defined manner.

How Does Protein Structure Determine Function? For almost all biological functions to be expressed, two molecules must bind to each other. An **antibody** protein must bind to an **antigen** to provoke an immune response, a **hormone** protein (for example, a growth factor) must bind to a cell surface receptor to trigger a cell reaction, an enzyme protein must bind to a **substrate** to **catalyze** a reaction, and a protein containing the leucine zipper motif must bind to DNA to regulate gene expression. In order for two molecules to bind, they must recognize each other and form a series of noncovalent bonds. Recognition of two molecules for each other is termed "structural complementarity"; that is, the three-dimensional structures must complement each other in the shapes of the interacting surfaces. Analogies that have been used are a key fitting into a lock or the wooden square of a simple child's game that fits into the square-shaped cutout of a puzzle board.

antibody immune system protein that binds to foreign molecules

antigen foreign substance that provokes an immune response

hormone molecule released by one cell to influence another

substrate the molecule acted on by an enzyme

catalyze aid in the reaction of

"Ligand" is the general term used to denote the molecule bound by the protein. When a protein binds to a ligand, many noncovalent bonds are formed. These may be ionic bonds between the charged **acidic** or **basic** groups of side chains of amino acids, or **hydrogen bonds** whereby a hydrogen proton is shared between two atoms, or a weak force of binding termed van der Waals bonding that can occur between any two atoms that are very close in space. Water may also be excluded from the surfaces of two molecules binding to each other, contributing what is called the hydrophobic effect. The number of such noncovalent bonds formed between two molecules directly relates to the strength (the **affinity**) of binding. Thus strength of binding can be strong, as in the case of a protein hormone binding to a cell surface receptor, or weak, as with binding to their substrate enzymes.

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

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

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

affinity attraction

Binding of ligands occurs on certain portions of the protein surface. All three types of secondary structure (or combinations of secondary structure) can be involved in binding a particular ligand. The immunoglobulin molecule uses a total of six loop structures, three each from the variable domains of the heavy and light chains to bind to an antigen. By a very large number of variations of the spatial relationships of these loop regions and differences in amino acid residues of the loops, immunoglobulins exhibit binding activities to a very large number of antigens that are encountered in the environment.

For instance, DNA-binding proteins often use α helices to recognize and bind to the nucleic acids of DNA sequences. Different sequences of amino acids along the α helices allow such gene regulatory proteins to recognize specific nucleic acid sequences of the DNA and thus to alter expression of a single or only a few genes. The hexokinase protein binds both **glucose** and **ATP** to form glucose-phosphate, the first step in the **metabolism** of glucose through the glycolytic pathway. The hexokinase protein has two domains, and the glucose spatially complements within a groove between the two domains and thus is bound by the enzyme. Galactose is another sugar very similar to glucose except for the spatial orientation of one of five **hydroxyl** groups common to glucose and galactose. This single hydroxyl orientation difference does not allow galactose to bind to hexokinase and thus hexokinase exhibits specificity of binding. Galactose is **phosphorylated** by another enzyme protein, galactokinase, which exhibits specificity for the galactose sugar; that is, galactokinase structurally complements and binds galactose, but not glucose.

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

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

metabolism chemical reactions within a cell

hydroxyl chemical group consisting of -OH

phosphorylate add a phosphate group to

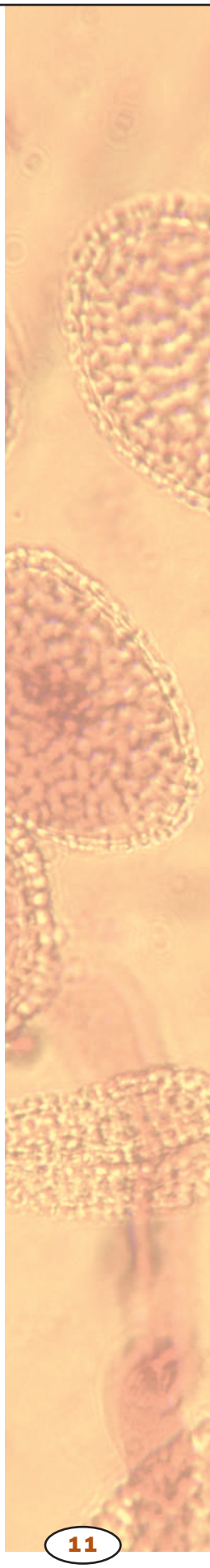
Protein Modifications

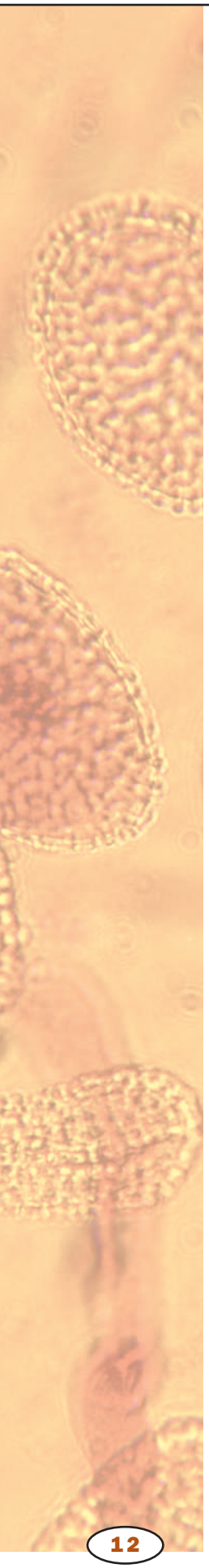
Proteins can be glycosylated (glycoproteins) or associated with **lipids** (lipoproteins).

Glycoproteins. Glycoproteins have attached carbohydrate molecules (residues). Carbohydrate residues are added to the protein structure and modified during and following protein synthesis. There are many different carbohydrate sequences found in glycoproteins, many of which have functional consequences. In general, most proteins that are secreted from cells are glycosylated. Most of the proteins in serum are glycosylated as are the proteins found in saliva and the digestive juices of the gastrointestinal tract. **Carbohydrates** have many hydroxyl (-OH) groups that bind to water molecules, and thus increase stability. Thus the glycoproteins of saliva tend to

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





esophagus tube connecting throat to stomach

lubricate the food chewed, in part to allow easier swallowing of food and its passage through the **esophagus**. The glycoproteins secreted in the stomach protect the lining of that organ from its acidic environment. This protective role of carbohydrates is also apparent for the serum glycoproteins. The carbohydrates on the surface of the protein protect the protein from the actions of proteases that degrade protein structures.

Certain types of carbohydrate residues on glycoproteins also serve as signal mechanisms. If a tissue is injured or becomes infected, certain glycoproteins are recruited to the surfaces of endothelial cells (the cells that line all blood vessels), where they are recognized by white blood cells, as a signal that this is a site of injury requiring attention. Particularly in the last ten years, about three hundred functions of the carbohydrate portions of glycoproteins have been described.

Lipoproteins. Lipoproteins are complexes between a particular set of proteins (termed apoproteins) and lipids (phospholipids, triglycerides, cholesterol, and cholesterol esters). These lipids are transported throughout the body as the complex lipoproteins. Humans have nine different apoproteins of various molecular sizes and concentrations in the blood. Portions of the surfaces of apoproteins exhibit specificity and bind the various lipids, providing the scaffold upon which the lipoprotein particles are constructed. Their densities—high-density (HDL), low-density (LDL), and very-low-density lipoproteins (VLDL)—are used to characterize the protein. The apoproteins are synthesized in the cell (mainly in the liver) and acquire lipids to become HDL, LDL, or VLDL.

Proteins and Evolution

The presence of similar domain structures in different proteins, the duplication of domain structures in a single protein, and similarities in amino acid sequences (sequence homologies) indicate an evolutionary relationship of many proteins in a single species and between species. There are many examples of these relationships, of which a few will be described here.

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

The globin fold, as described above, consists of eight α helices (connected by loops) that form a pocket as an **active site**. A heme structure is bound in many globin fold proteins that binds and carries oxygen in an organism. The globin fold structure has been preserved in mammals, insects, and plants although the amino acid sequence similarities may be very low between such disparate species. Thus, natural selection has maintained similar structures to carry out similar functions even as the gene sequences have diverged to such a great extent between the different species.

The helix-turn-helix motif is common to many gene repressor proteins that bind to DNA sequences. Rigorous statistical analyses of the amino acid sequences of these motifs suggest that these repressor proteins all evolved from a common ancestral gene and that certain amino acid residues in the motif structure are crucial to maintain the helix-turn-helix structure of the motif.

Serine proteases (for example, chymotrypsin, a digestive enzyme in mammals) consist of two β barrel domains, the ends of which come together to form an active site. Within the active site is a catalytic triad, which consists of three amino acids (histidine, serine, and cysteine) arranged in space to catalyze the **hydrolysis** of a peptide bond. The two β barrels probably

hydrolysis splitting with water

evolved from duplication of a common gene. In humans, there are many serine proteases that cleave peptide bonds of different proteins. All have the same two β barrel domain structure with the same spatial catalytic triad. Specificity of binding and cleaving different proteins is achieved by altering the sequences around the catalytic triad such that different proteins complement the different binding sites.

Protein Structures and Disease

Some differences of amino acid sequences of proteins are directly related to disease. A well-defined example is that of sickle-cell disease. A single difference at position number 6 in the amino acid sequence of the β chain of hemoglobin (a valine amino acid is found in the person with sickle-cell disease instead of glutamic acid) results in aggregation of the hemoglobin molecules with consequent elongation (the sickle shape) and fragility of the red blood cells. The disease cystic fibrosis has now been defined as mutations in a particular gene that codes for a cell membrane protein that functions to pump chloride ions out of the cell. This protein in cystic fibrosis is defective in this function because the amino acid sequence is different from normal. SEE ALSO AMINO ACID; ENZYMES; GENETIC DISEASES; MEMBRANE TRANSPORT; NUCLEAR TRANSPORT; PROTEIN SYNTHESIS; PROTEIN TARGETING

Byron Anderson

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Protein Synthesis

Proteins are the workhorses of the cell, controlling virtually every reaction within as well as providing structure and serving as signals to other cells. Proteins are long chains of **amino acids**, and the exact sequence of the amino acids determines the final structure and function of the protein. Instructions for that sequence are encoded in **genes**. To make a particular protein, a messenger ribonucleic acid (mRNA) copy is made from the gene (in the process called **transcription**), and the mRNA is transported to the **ribosome**. Protein synthesis, also called **translation**, begins when the two ribosomal subunits link onto the mRNA. This step, called initiation, is followed by elongation, in which successive amino acids are added to the growing chain, brought in by transfer RNAs (tRNAs). In this step, the ribosome reads the **nucleotides** of mRNA three by three, in units called **codons**, and matches each to three nucleotides on the tRNA, called the anticodon. Finally, during termination, the ribosome unbinds from the mRNA, and the amino acid chain goes on to be processed and folded to make the final, functional protein.

amino acid a building block of protein

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

transcription messenger RNA formation from a DNA sequence

ribosome protein-RNA complex in cells that synthesizes protein

translation synthesis of protein using mRNA code

nucleotide the building block of RNA or DNA

codon sequence of three mRNA nucleotides coding for one amino acid

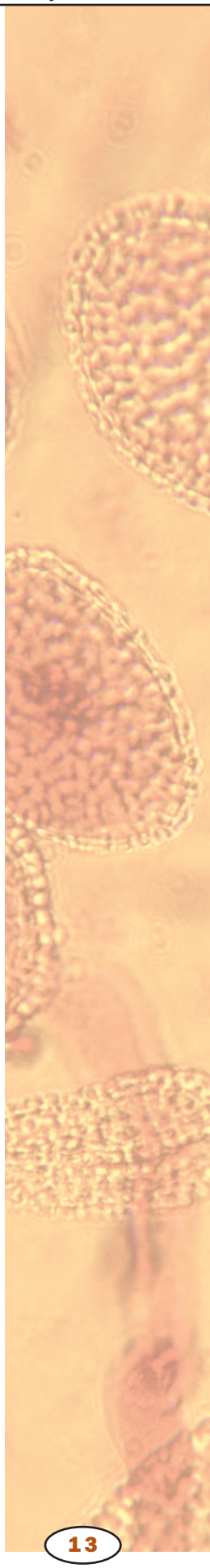
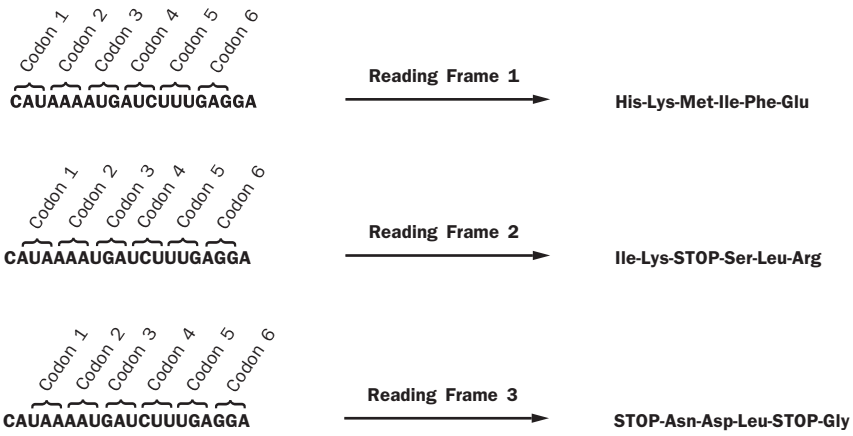


Figure 1.



The three different reading frames of an mRNA sequence code for three different proteins. Note that only reading frame 1 makes a full-length protein because the other two reading frames have stop codons which end translation.

Initiation

In the first step, initiation, the ribosome must bind the mRNA and find the appropriate place to start translating it to make the protein. If the ribosome starts translating the mRNA in the wrong place, the wrong protein will be synthesized. This is a particularly tricky problem because there are three different reading frames in which an mRNA can be read. Each unit of the **genetic code**, called a codon, is made up of three bases and codes for one amino acid. Completely different protein sequences will be read out by the ribosome if it starts translating with the start of the first codon at base 0, base 1, or base 2 (Figure 1). Thus, it is easy to see why the ribosome must have a way to find the correct starting point for translating each different mRNA.

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

In almost every known case, translation begins at the three-base codon that codes for the amino acid methionine. This codon has the sequence AUG. Ribosomes are made up of two parts, called subunits, that contain both protein and RNA components. It is the job of the smaller ribosomal subunit to locate the AUG codon that will be used as the starting point for translation (called the initiation codon). Although always starting at AUG helps solve the reading frame problem, finding the right AUG is not an entirely straightforward task. There is often more than one AUG codon in an mRNA, and the small ribosomal subunit must find the correct one if the right protein is to be made.

Initiation in Prokaryotes. In prokaryotes (bacteria) there is a nucleotide sequence on the upstream (5-prime, or 5′) side of the initiation codon that tells the ribosome that the next AUG sequence is the correct place to start translating the mRNA. This sequence is called the Shine-Delgarno sequence, after its discoverers. The Shine-Delgarno sequence forms base pairs with RNA in the small ribosomal subunit, thus binding the ribosomal subunit to the mRNA near the initiation codon.

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

complementary matching opposite

Next, a special tRNA forms **base pairs** with the AUG sequence of the initiation codon. The tRNA contains the **complementary** sequence to AUG

as its anticodon. This tRNA carries a modified version of the amino acid methionine (fMet-tRNA$_i$ or formylmethionyl initiator tRNA) and is already bound to the small ribosomal subunit. The interaction of codon and anticodon triggers a series of events that is not entirely understood but that results in the joining of the large ribosomal subunit to the small ribosomal subunit. The resulting complex is called an initiation complex; it is a whole ribosome bound to an mRNA and an initiator tRNA, positioned so as to make the correct protein from the mRNA.

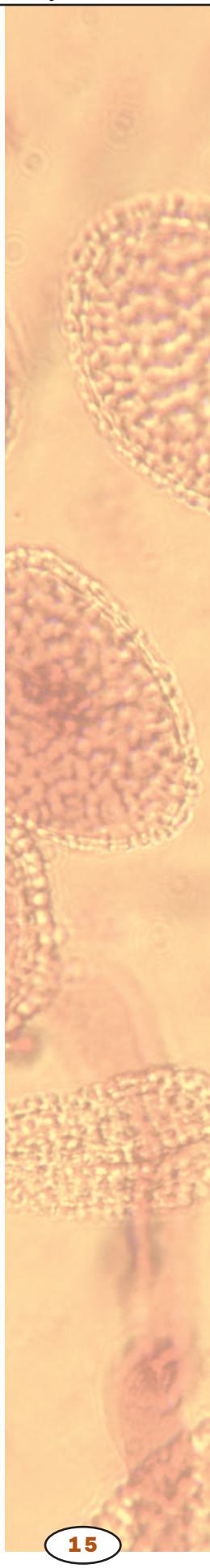
Initiation in Eukaryotes. In eukaryotes (animals, plants, fungi, and protists), the Shine-Delgarno sequence is missing from the small ribosomal subunit's RNA, and thus a different mechanism is used for locating the initiation codon. The strategy employed by eukaryotes is more complex and less well understood than that used by prokaryotes. In eukaryotes, the small ribosomal subunit is thought to bind to the 5′ end of the mRNA. This binding is mediated by a special structure on the 5′ end of eukaryotic mRNAs called a 7-methylguanosine cap and is also aided by a special tail of adenosine bases (the poly-A tail) on the 3′ end, both of which are added during RNA processing. A group of proteins called initiation factors binds to the 7-methylguanosine cap and poly(A) tail and appears to direct the binding of the small ribosomal subunit to the mRNA near the cap structure.

Once this has happened, the small ribosomal subunit can read along the mRNA and look for an AUG codon, a process called scanning. Recognition of the initiation codon is largely mediated by base-pairing interactions between the AUG codon and the anticodon sequence in a methionyl initiator tRNA (Met-tRNA$_i$; the methionine is not modified with a formyl group in eukaryotes as it is in **prokaryotes**). As in prokaryotes, this Met-tRNA is already bound to the small ribosomal subunit.

prokaryote single-celled organism without a nucleus

In most cases, the first AUG codon in a eukaryotic mRNA is used as the initiation codon, thus the small subunit locates the correct initiation codon simply by scanning along the mRNA starting at the 5′ end until it reaches the first AUG codon. However, the initiation AUG codon may be flanked by certain base sequences not found around other AUG codons not used for initiation. This preferred set of bases around the initiation codon is called the Kozak sequence, named after its discoverer, Marilyn Kozak. How the Kozak sequence helps direct the small ribosomal subunit to use one AUG codon instead of another is not known. As is the case in prokaryotes, once the correct AUG codon has been found, a complex series of steps takes place that results in the joining of the large ribosomal subunit to the small ribosomal subunit to produce an initiation complex: a complete ribosome assembled at the correct place on an mRNA with an initiator tRNA bound to it.

In both prokaryotes and eukaryotes there are proteins called initiation factors that are required for the correct assembly of an initiation complex. In prokaryotes there are three initiation factors, logically enough called IF1, IF2, and IF3. IF2 helps the fMet-tRNA$_i$ bind to the small ribosomal subunit. IF3's main role appears to be to ensure that an AUG, and not another codon, is used as the starting site of translation. That is, IF3 monitors the fidelity of the selection of the initiation codon. IF1 appears to prevent the initiator tRNA from binding to the wrong place in the small ribosomal subunit.



The antibiotic tetracycline prevents tRNA from binding to the A sites.

In eukaryotes, the situation is considerably more complex, with at least twenty-four protein components required for the initiation process.

Elongation

In the next phase of protein synthesis, elongation, the ribosome joins amino acids together in the sequence determined by the mRNA to make the corresponding protein. Amino acids are brought onto the ribosome attached to tRNAs. tRNAs are the adapter molecules that allow the ribosome to translate the information contained in the codon sequence of the mRNA into the amino acid sequence of a protein. This decoding happens by base pairing between the anticodon bases of the tRNA and the codon bases of the mRNA. When all three anticodon bases of the tRNA form base pairs with the next codon of the mRNA, the ribosome, with the aid of an elongation factor protein, recognizes that this tRNA has the correct amino acid attached to it and adds this amino acid to the growing protein chain. The process can then be repeated until the entire protein has been synthesized.

As just mentioned, elongation requires the help of elongation factor proteins. The tRNAs with attached amino acids (called aminoacyl tRNAs) are brought onto the ribosome by one such elongation factor. This factor is called EF-Tu in prokaryotes and EF1 in eukaryotes. Its job is to bring aminoacyl tRNAs onto the ribosome and then to help the ribosome make sure that this tRNA has the correct amino acid attached to it. The ribosome has three aminoacyl tRNA binding sites: the acceptor site (A), the peptidyl site (P), and the exit site (E). The tRNA that has the growing protein attached to it binds in the P site (hence the name peptidyl, for peptide). The incoming aminoacyl tRNA, containing the next amino acid to be added, binds in the A site. The A site is where decoding of the genetic code takes place; the correct aminoacyl tRNA is selected to match the next codon of the mRNA. Spent tRNAs that no longer have an amino acid or the growing peptide chain attached to them end up in the E site, from

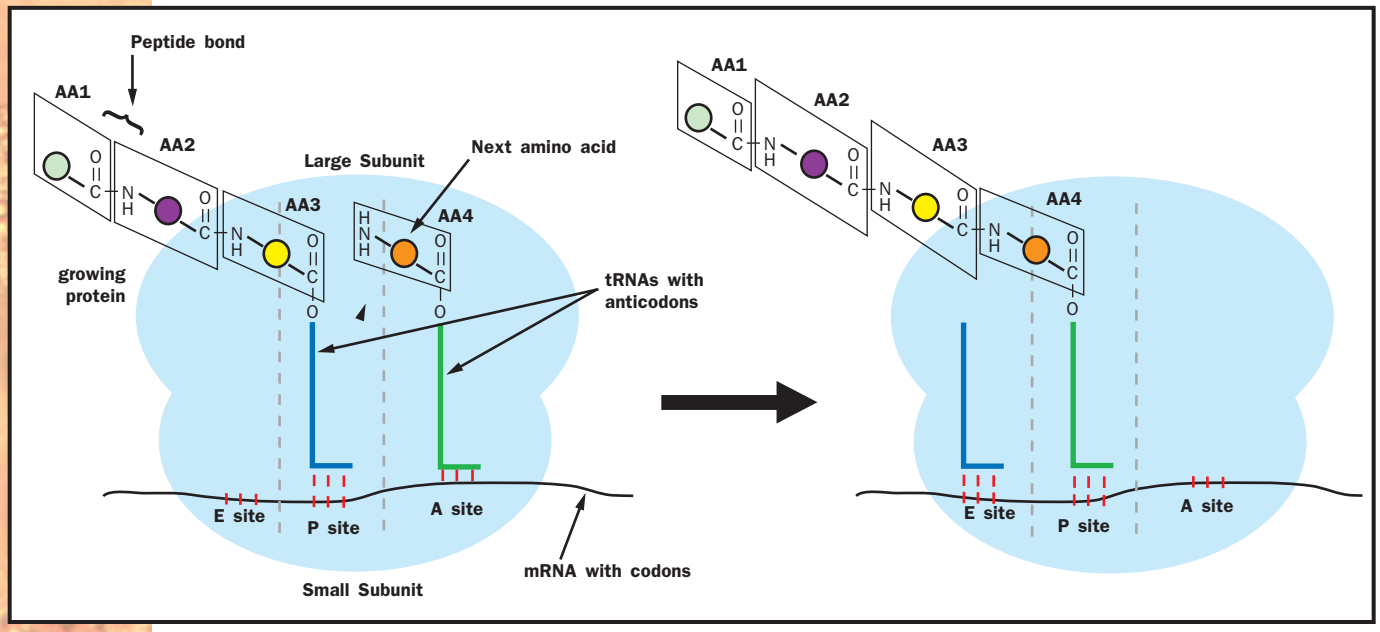


Figure 2. Peptide bond formation by the ribosome. The three lines between the mRNAs and the tRNA indicate base pairing between the codon of the mRNA and the anticodon of the tRNA.

Special Proteins Involved in Protein Synthesis

	Prokaryotes	Eukaryotes
Initiation	IF1 IF2 IF3	at least 24 protein components
Elongation	EF-Tu EF-G	EF1 EF2
Termination	RF1 RF2 RF3	eRF1 eRF3
Recycling	RRF	

which they fall off the ribosome back into the **cytoplasm**, where they can pick up new amino acids.

cytoplasm material in a cell, excluding the nucleus

Once the A site is occupied by the correct tRNA, the ribosome links the new amino acid to the growing peptide chain. It does this by catalyzing the formation of a peptide (amide) bond between the amino (NH_2) group of the new amino acid in the A site and the carbonyl (CO) group that attaches the growing protein chain to the tRNA in the P site (Figure 2). This results in an intermediate state of the ribosome, called a **hybrid** state, in which the tRNA in the P site has lost the growing protein chain and moved partially into the E site, and the tRNA in the A site now has the growing protein chain attached to it and has moved partially into the P site.

hybrid combination of two different types

To complete the round of elongation, a second elongation factor, called EF-G in prokaryotes and EF2 in eukaryotes, is needed. This elongation factor moves the tRNAs such that the spent tRNA that has lost the protein chain moves fully into the E site, and the tRNA with the growing protein chain moves fully into the P site. The mRNA is also shifted over one codon by EF-G, so that the next codon is in the A site. The A site is now empty of tRNAs and the next aminoacyl tRNA can be brought into it.

Many antibiotics (drugs that kill bacteria) affect the elongation phase of **prokaryotic** translation. Some decrease the fidelity (accuracy) with which the ribosome decodes the mRNA and the wrong amino acids get put into the proteins. This decrease in fidelity leads to an accumulation of proteins that do not work, which eventually kills the bacterium. Other antibiotics prevent the formation of the **peptide bond** or the movement of the tRNAs by EF-G after the peptide bond has been formed. The reason these drugs are effective on bacteria without killing the patient is that prokaryotic ribosomes have some different structural features than eukaryotic ribosomes, and thus these drugs can bind to the prokaryotic (bacterial) ribosomes but not the eukaryotic (that is, human) ribosomes. Since viruses use human ribosomes to reproduce, these antibiotics are not effective against them.

prokaryotic without a nucleus

peptide bond bond between two amino acids

Termination

The end of the code for the protein in the mRNA is signaled by one of three special codons called stop codons. These stop codons have the sequences

UAA, UAG, and UGA. In prokaryotes, the stop codons are bound by one of two release factor proteins (RFs) in prokaryotes: RF1 or RF2. These release factors cause the ribosome to cleave the finished protein off the tRNA in the P site. A third release factor, RF3, is responsible for releasing RF1 and RF2 from the ribosome after they have recognized the stop codon and caused the protein to be cleaved off the tRNA. Eukaryotes appear to have one protein, eRF1, that performs the functions of RF1 and RF2, and a second protein, eRF3, that performs the function of RF3. Once released, the protein can then go on to perform its function in the cell.

dissociate break apart

After the protein has been cleaved off the tRNA, the two ribosomal subunits must be **dissociated** from one another so that the ribosome can start translating another mRNA. This process is called recycling. In prokaryotes, recycling requires three proteins: one initiation factor (IF3), one elongation factor (EF-G), and a ribosome recycling factor called RRF. Once the subunits are dissociated from each other the whole process of translation can begin again.

Protein Folding

conformation three-dimensional shape

A functional protein is not a long, stretched-out chain of amino acids but rather a complex, three-dimensional structure. That is, each protein must fold up into a particular shape, or **conformation**, in order to perform its function in the cell. The evidence strongly suggests that all of the information required for the protein to fold into its correct three-dimensional structure is contained in the amino acid sequence of the protein (rather than, say, being determined by some other factor in the cell). However, as the protein is being synthesized on the ribosome there is a danger that the unfinished protein will begin to fold up incorrectly because the rest of the protein has not yet been made. It is also possible that the unfinished protein will interact with other unfinished proteins being made on other ribosomes and

aggregate clump together

form what is called an **aggregate**: a network of partially folded proteins that have interacted with each other rather than with themselves, thus producing a mess inside the cell. Such protein aggregates can be fatal for the cell. It is the job of a class of proteins called chaperones to bind to the growing protein chains as they are synthesized by ribosomes and prevent aggregates from forming or the proteins from folding incorrectly before they have been fully synthesized. Chaperones may also help proteins efficiently fold up into the correct three-dimensional structure once translation is complete.

Protein Modification

While the mRNA encodes the complete amino acid sequence of the corresponding protein, some proteins are altered after they are translated. This process is called post-translational modification. For example, some proteases (proteins that digest other proteins) are synthesized by the ribosome as precursor proteins (pro-proteins) that contain an extra sequence of amino acids at one end that prevents them from digesting any proteins until they get to the right place (usually outside of the cell). Once the proteases reach their destination, the amino acid sequences that prevent them from being active (called pro-sequences) are removed (by another protein), and the proteases can begin digesting other proteins. If these pro-sequences did not ex-

ist, the proteases would digest all of the useful proteins inside the cells that made them—which would not be a good thing.

Many proteins made by **eukaryotic cells** are modified by having sugars attached to various amino acids, a process called glycosylation. Proteins that are destined to be exported from the cell or are going to be inserted into the cell's membrane enter the **endoplasmic reticulum** (ER) as they are synthesized by ribosomes that bind to the surface of the ER and feed the new proteins into the ER through small pores. Inside the ER, sugars are added to the protein, which is then sent to the Golgi apparatus where some of the sugars are removed and additional sugars are added. The role of protein glycosylation is not well understood, but because many euykaryotic proteins are glycosylated, it is clearly important.

eukaryotic cell a cell with a nucleus

endoplasmic reticulum network of membranes within the cell

There are a number of additional ways that proteins can be modified after they are made. For example, many proteins can have one or more phosphate groups added to them by **enzymes** called **kinases**. These **phosphorylations** are often used by the cell to regulate the activity of specific proteins; the phosphorylated form of the protein often has different properties than the unphosphorylated form.

enzyme protein that controls a reaction in a cell

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

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

Protein Degradation

When a protein has outlived its usefulness or become damaged, it is degraded by the cell. In eukaryotes, a protein that is to be degraded has a number of copies of the small protein ubiquitin attached to it by a series of ubiquitin-adding enzymes. Ubiquitin serves as a tag that marks the protein for degradation. A tagged protein is then sucked into a large cellular machine called the proteasome, which itself is made up of a number of protein components and looks something like a trash can. Inside the proteasome, the tagged protein is digested into small peptide fragments that are released into the cytoplasm where they can be further digested into free amino acids by other proteases. The life of a protein begins in one cellular machine called the ribosome and ends in another called the proteasome. SEE ALSO ENDOPLASMIC RETICULUM; GENETIC CODE; GOLGI; PROTEIN STRUCTURE; RIBOSOME; RNA; RNA PROCESSING

Jon Lorsch

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Protein Targeting

Protein targeting refers to the methods cells use to get proteins to the proper location after synthesis. Proteins play a major role in most cellular processes but must be located properly to serve their functions. Knowing how newly synthesized proteins target within cells is essential for understanding protein function.

cytosol fluid portion of a cell, not including the organelles

endoplasmic reticulum network of membranes within the cell

ribosome protein-RNA complex in cells that synthesizes protein

substrate attachment site

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

cytoplasm material in a cell, excluding the nucleus

polymer molecule composed of many similar parts

complementary matching opposite

cytoskeleton internal scaffolding in a cell, composed of protein

affinity attraction

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

amino acid a building block of protein

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

nucleus membrane-bound portion of cell containing the chromosomes

eukaryotic cell a cell with a nucleus

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

lipid fat or waxlike molecule, insoluble in water

polypeptide chain of amino acids

Gunther Blobel won the 1999 Nobel Prize for his work on protein targeting.

Proteins are synthesized either in the **cytosol** or on the **endoplasmic reticulum**. When synthesized in the cytosol on free **ribosomes**, most proteins diffuse freely until they are bound to a particular **substrate** or assemble into a larger complex. Protein diffusion in the cytosol is usually rapid, so an unbound protein is capable of diffusing across the cell in only a few seconds.

One way cytosolic proteins are targeted within cells is by forming large macromolecular assemblies. Many proteins can exist either as **monomers**, which freely diffuse through the **cytoplasm**, or as **polymers**, which form large-scale structures that dynamically distribute to distinct locations in the cell. The cytoskeletal proteins actin and tubulin, for example, have a pair of **complementary** self-binding sites on their surfaces that allow them to polymerize into long helical filaments that stretch across the cell. These filaments form the **cytoskeleton** of the cell, which reorganizes continuously as the cell changes shape, divides, and responds to its environment.

Conformational changes in a protein often lead to changes in the protein's **affinity** toward a particular substrate. This process can play a crucial role in regulating the intracellular localization of a protein. An example of this type of regulation is protein **phosphorylation**, or addition of a phosphate group. This can dramatically change a protein's affinity for a substrate and can thereby lead to rapid changes in the protein's location. This type of regulation of protein localization is crucial for enabling cells to coordinate their activities under different growth conditions and during cell division.

Some cytoplasmic proteins are targeted to a particular site in the cell because they contain a specific **amino acid** sequence that causes them to bind to receptors located at that site. An example of such a targeting sequence is the so-called nuclear localization signal (NLS), which consists of two short stretches of **basic** amino acids divided by a 10–11 amino acid spacer region. This sequence of amino acids allows a protein possessing it to bind to nuclear localization receptors found in the **nucleus**. Once a protein containing an NLS signal binds to a nuclear receptor it is no longer able to freely diffuse and becomes "localized" to the nucleus.

Many proteins are embedded within or associated with membranes. In **eukaryotic cells**, membranes form the boundaries of a variety of distinct compartments, including the nucleus, **mitochondria**, endoplasmic reticulum (ER), and Golgi complex. Some proteins are synthesized in the cytosol and are then modified with a **lipid** "anchor," and association with membranes is simply a matter of embedding in the membrane's outer lipid layer. Signaling molecules, such as the GTP-binding protein Ras, localize to membranes in this manner.

All other proteins that target to intracellular membranes require sorting signals that direct their transport from the cytosol. For example, proteins targeted to mitochondria contain a specific peptide sequence of 20–80 amino acids that mediates their import. This sequence is found at the amino terminus of the protein and after import is rapidly removed by a protease.

Proteins localized within those membranes involved in endocytosis and exocytosis are first targeted to the ER, and then use membrane transport pathways to reach other compartments. Targeting of proteins to the ER begins before the **polypeptide** chain is completely synthesized. This is in contrast to import of proteins to mitochondria, chloroplasts, and peroxisomes,

which occurs after synthesis is completed. An ER signal peptide, localized at the amino terminus of these proteins, directs the ribosome to attach to the ER membrane before the protein has been completely translated. The ER signal peptide is guided to the ER membrane by a signal-recognition particle (SRP), which binds to the signal peptide, and an SRP receptor in ER membranes.

From the ER proteins use a variety of mechanisms to reach different final destinations in the cell. Proteins destined for the **nuclear envelope** simply diffuse there and stick, since the nuclear envelope is in direct continuity with the ER. To reach the Golgi complex, plasma membrane, endosomes, and lysosomes, however, proteins must enter the **secretory pathway** and use membrane trafficking pathways. For membrane proteins, entry into the secretory pathway is thought to require their concentration and sorting at ER exit sites. In contrast, proteins that are soluble in the ER lumen (inner space) move out by a bulk flow process. After leaving the ER, most soluble proteins are eventually secreted by the cell. Many membrane proteins are directed to specific **organelles** within the secretory and endocytic pathways because they contain specific sorting signals in their cytoplasmic tails, which function much like zip codes. Alternatively, sorting may be due to properties of a protein's transmembrane domain, a region of the protein that gives its affinity for different lipid environments characteristic of different organelles. SEE ALSO CELL CYCLE; CYTOSKELETON; ENDOCYTOSIS; EXOCYTOSIS; MEMBRANE PROTEINS; PROTEIN SYNTHESIS

Jennifer Lippincott-Schwartz

nuclear envelope double membrane surrounding the cell nucleus

secretory pathway series of events within a cell by which molecules are brought to the plasma membrane for release from the cell

organelle membrane-bound cell compartment

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

symbionts organisms living in close association with another organism

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

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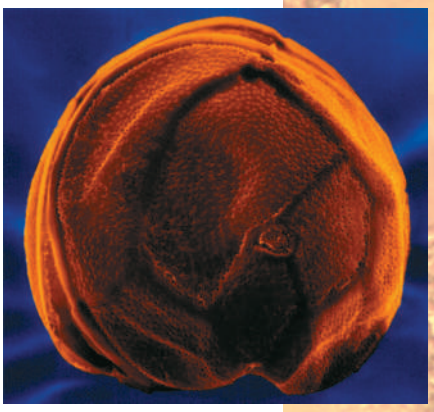
Protista

The Protista, or Protoctista, are a kingdom of simple eukaryotic organisms, usually composed of a single cell or a colony of similar cells. Protists live in water, in moist terrestrial habitats, and as **parasites** and other **symbionts** in the bodies of multicellular eukaroytes.

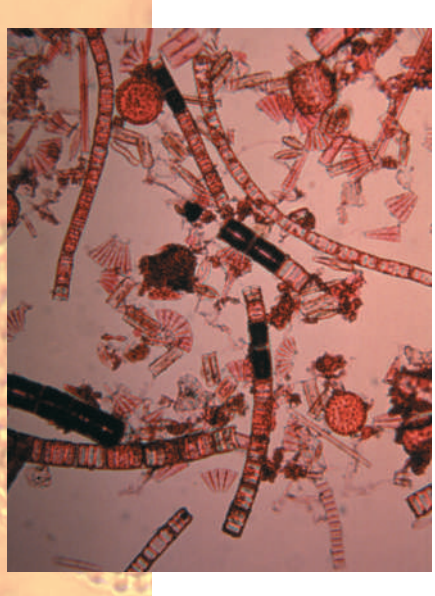
Other eukaryotic kingdoms—the Plantae, Fungi, and Animalia—are each believed to be **monophyletic**. That is, all plants evolved from one ancestral plant, all animals from one ancestral animal, and all fungi from one ancestral fungus. The Protista, however, are not; they are almost certainly polyphyletic and did not arise from a single ancestral protist. Rather, the Protista are a category of miscellaneous eukaryotes, not closely related to each other and not sharing many characteristics, but not fitting any other kingdom of life. Some authorities divide the Protista into as many as twenty-seven phyla, and some feel the Protista should be discarded as a kingdom name, and these organisms divided into as many as twelve kingdoms.

Historically, the Protista were divided into three main categories: the plantlike algae, animal-like protozoans, and funguslike slime molds. This classification persists in many elementary textbooks; however, current molecular evidence indicates that these are not natural groups related by common descent, but groups with merely **superficial**, deceptive similarities.



A scanning electron micrograph of the dinoflagellate *Gambierdiscus toxicus*.

superficial on the surface; not deep



Diatoms, unicellular algae encased in siliceous walls, often display delicate lacy designs.

Classifying them together is probably no more scientific than it would be to classify bees, birds, and bats in one group simply because they all have wings and fly. The two flagellated protozoan groups called trypanosomes and dinoflagellates, for example, are probably less related to each other than a human is to a fish. Genetic evidence (base sequences in their **mitochondrial** deoxyribonucleic acid [mtDNA] and ribosomal ribonucleic acid [rRNA]) now indicates that the following are more natural (evolutionarily related) groups of Protista.

Basal Protista

These are the most primitive protists. Some lack mitochondria and suggest what the first eukaryotes may have been like, while others have primitive mitochondria that closely resemble bacteria. Some **basal** Protista without mitochondria are *Trichomonas*, a vaginal parasite of humans; *Giardia*, an intestinal parasite; and *Entamoeba*, the cause of amoebic dysentery. The lack of mitochondria is not necessarily the primitive (original) condition of all these protists, however. Although *Giardia* lacks mitochondria, it does have mitochondrial genes. Apparently it once had mitochondria, and these genes transferred to its nuclear DNA before the mitochondria were lost.

Basal Protista with mitochondria include *Trypanosoma*, a genus of blood parasites that cause African sleeping sickness and other diseases; *Euglena*, a green freshwater flagellated protozoan with chloroplasts; and *Physarum*, a common terrestrial slime mold.

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

basal lowest level

Alveolates

Alveolates are named for flattened sacs called alveoli just beneath their plasma membranes. They have mitochondria with tubular cristae rather than the flattened cristae typical of most mitochondria. Alveolates include dinoflagellates, aquatic forms with two flagella and a cell wall made of armorlike **cellulose** plates; *Paramecium* and other familiar ciliates; and the Apicomplexa, a group of **intracellular** parasites that includes *Plasmodium*, the cause of malaria, and *Toxoplasma*, the cause of toxoplasmosis.

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

intracellular within a cell

Stramenopiles

Stramenopiles include water molds, golden and brown algae, and diatoms. The funguslike water molds (oomycetes) live in fresh water and soil, feeding on living or decaying organisms. Despite their name, some of them are important pests of row crops, including potato blight, downy mildew, and white rust. The golden algae (*Chrysophyta*) and brown algae (*Phaeophyta*) include many familiar seaweeds easily found on rocky coasts. Kelp is a gigantic marine brown alga (*Macrocystus*) that grows up to 30 meters (100 feet) long and forms dense "forests" in some coastal waters. Diatoms are microscopic unicellular algae encased in siliceous (glasslike) walls, often with delicate lacy designs like tiny jewel boxes or Christmas ornaments.

Red Algae

The red algae (*Rhodophyta*) include most seaweeds and are most abundant in tropical seas. Coral reefs are made not only by corals but also by coralline

red algae that deposit calcium carbonate in the reef. Some red algae produce **viscous polysaccharides** such as **agar** and carrageenan, used to thicken ice cream, desserts, salad dressings, toothpaste, cosmetics, paints, and bacterial culture media.

viscous thick

polysaccharide carbohydrate composed of many individual units of sugar

agar gel derived from algae

Green Algae

The green algae (*Chlorophyta*) include the single-celled *Chlamydomonas*, the spherical colonies of *Volvox*, and large seaweeds such as *Codium magnum*. Some unicellular green algae, notably *Chlorella*, live within the cells of animals, imparting a green color to some sponges, hydras, and flatworms. The plant kingdom probably evolved from a green alga.

The Study of Protista

Biologists in several subdisciplines of biology specialize in the Protista or have interests that overlap with this kingdom. Microbiologists study bacteria and some unicellular protists. Phycologists specialize in algae. Protozoologists study protozoans. Mycologists specialize in fungi but also often study water molds and slime molds, formerly classified as fungi. Parasitologists study disease-producing protists. SEE ALSO ALGAE; CORAL REEF; FUNGI; MITOCHONDRION; PLANT PATHOGENS AND PESTS; PROTOZOA; PROTOZOAN DISEASES; SLIME MOLDS

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Protozoa

Protozoa (meaning "first animals") are heterotrophic, single-celled or colonial eukaryotes. Individuals are microscopic and range in size from a few to hundreds of micrometers, depending on the species. Most protozoa are animal-like (heterotrophic) because their carbon and energy must be obtained by eating or absorbing **organic** compounds originating from other living organisms. As eukaryotes they have several **organelles**, including at least one **nucleus** that contains most of the cell's deoxyribonucleic acid (DNA).

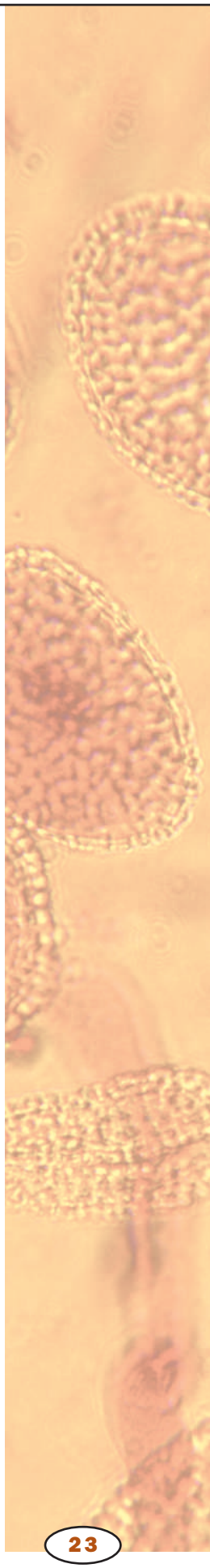
organic composed of carbon, or derived from living organisms

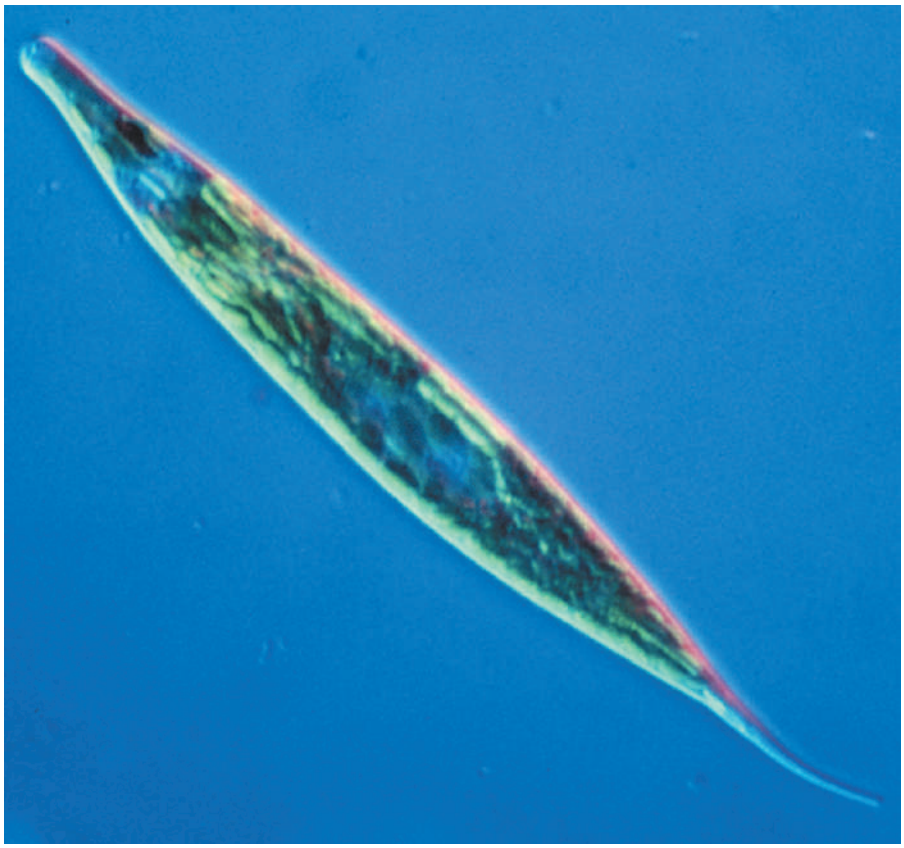
organelle membrane-bound cell compartment

nucleus membrane-bound portion of cell containing the chromosomes

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

Beyond this broad description, it is difficult to define protozoa because they are so diverse and only distantly related to each other. While the term "protozoa" is commonly used, it has little basis in evolutionary history, or phylogeny, of these organisms. Taxonomic systems try to assign organisms to a **monophyletic** group, that is, one that includes an ancestor and all of its descendants. Plants, animals, and fungi are monophyletic groups; protozoans are not. (The understanding of evolutionary relationships of unicellular eukaryotes is in a state of flux.) Further complicating a precise definition of protozoa is the close relationship between some protozoa and





A photomicrograph of the protozoa *Euglena.*

EUGLENA

Species in the genus *Euglena* are photosynthetic members of a diverse group of pigmented and colorless flagellates in the order Euglenida. Both protozoologists and botanists traditionally have studied them. The cylindrical shape of the body is maintained by a flexible pellicle composed of the cell membrane and a layer of protein strips. *Euglena* have large, bright green chloroplasts and two flagella that arise from within a pocket on the anterior end. Usually only one flagellum is long enough to emerge from the reservoir. Beside the reservoir is a small, red-pigmented spot, the stigma, which is associated with a light-sensing region. Many euglenids have visible rods or rings made of paramylum, which, like starch, is a glucose storage molecule.

Euglena swim with a gyrating motion using their emergent flagellum, which pull the organism forward like a propeller. When not swimming, *Euglena* often alternately contract and elongate the pellicle, causing a bulge to move from one end of the cell to the other in a characteristic "euglenoid motion." Euglena are most common in organically rich freshwater environments.

unicellular algae. Modern taxonomic treatments recognize these similarities and group protozoa, photosynthetic unicellular algae, and slime molds together as protists or protoctists. Whichever term one prefers, the classification is not monophyletic. Despite the fact that protozoa is not a proper taxonomic name, it is a useful, functional term. Ecologists differentiate between autotrophic and heterotrophic components of an ecosystem, and it is natural to separate the animal-like protozoa from the photosynthetic algae based on their nutritional mode. (However, *Euglena*, which can be induced to lose their chloroplast, illustrate why unicellular algae are included with protozoa.)

As is appropriate for heterotrophic organisms that capture food, most protozoa are motile (able to move). The way they move is one of the important characteristics historically used to divide them into major groups: amoebae, flagellates, and ciliates. Apicomplexa, formerly called Sporazoa, is a fourth group of generally **obligate** parasitic protozoa. Amoebae crawl along surfaces by extending a **cytoplasm**-filled pseudopod (false-foot) that bulges outward from any edge of the cell. Flagellates and ciliates use specialized organelles, flagella and cilia, that differ primarily in length and number, to propel the cells through water. Flagella are whiplike structures that usually occur one to a few per cell and have an undulating motion. Cilia are shorter and move in concert, like oars, with alternating power and recovery strokes. Sporozoa are either nonmotile or very slow.

Other organelles that are widely distributed among protozoa include food vacuoles, in which ingested particles are digested, and lysosomes that

fuse with food vacuoles and supply digestive enzymes. Contractile vacuoles, common in freshwater protozoa, eliminate water that moves into the cells by **osmosis**. Extrusomes are associated with the membrane of many protozoa and contain material that can be ejected from the cell. Some extrusomes secrete an amorphous material that is involved in formation of a capsule or cyst, and others discharge a pointed projectile that may serve for protection or predation. The thousands of "trichocysts" distributed over the surface of the ciliate *Paramecium* are extrusomes that discharge rapidly in response to physical stimulation and are probably effective deterrents to some predators. Ciliates are unique among protozoa in having two kinds of nuclei: the micronucleus, which is involved only in sexual reproduction; and the macronucleus, which is involved only in the production of messenger ribonucleic acid (RNA) for cell function.

Most protozoa reproduce most of the time by equal binary fission, in which a cell divides into two daughter cells after the chromosomes have been duplicated and distributed between them. This asexual mode of reproduction leads to rapid population growth of a clone of genetically identical cells. However, sex is widespread in protozoa and complicated life histories do exist. Sexuality is associated with environmental change and interrupts asexual reproduction; sex in protozoa usually marks the end of the existence of a genetically unique individual, when it becomes the gamete (reproductive cell) or gametes.

Protozoa are ubiquitous (found everywhere); they are present in all aquatic or moist environments, and their cysts can be found in even the most inhospitable parts of the biosphere. Most are free-living and eat bacteria, algae, or other protozoa. Protozoa are important components of aquatic and soil ecosystems, where they eat bacteria that are too small to be efficiently captured by most animals and are in turn eaten by other organisms. Bacterivorous protozoa also are abundant in activated sludge sewage treatment plants and, in fact, are necessary for their proper functioning. There are several protozoa of medical and economic importance. Examples include the flagellate *Trypanosoma*, which causes African sleeping sickness; the amoeba *Entamoeba histolytica*, which can attack the intestinal wall and cause amoebic dysentery, and the sporozoans of the *Plasmodium* species, which cause malaria.

Protozoa have many features linking them to the other kingdoms of life. Scientists widely believe that animals evolved from protozoan ancestors, probably colonial choanoflagellates. New tools and methods from molecular biology are leading to a better understanding of the evolutionary relationships to multicellular organisms and among protozoa. SEE ALSO ALGAE; CELL MOTILITY; CYTOSKELETON; LYSOSOMES; OSMOREGULATION; PLANKTON; PROTISTA; PROTOZOAN DISEASES

Robert W. Sanders

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AMOEBA

Most amoebae live on surfaces in moist soil or aquatic sediment. They are easily overlooked because they are small, predominantly transparent, and slow moving. Amoebae are characterized by the flow of granular cytoplasm into lobes of cell membrane (pseudopodia) that serve the dual functions of motility and food capture. These protozoa typically lack a fixed external anatomy and are flexible but can be categorized by the shape and number of the pseudopodia. Pseudopodia can occur as multiple rounded or needlelike projections or as a single advancing front. When a food particle is encountered, pseudopodia surround it with a membrane-enclosed sac that pinches off internally to form a food vacuole. In addition to food vacuoles, a contractile vacuole and a single large nucleus or many small nuclei can be distinguished. Some amoebae excrete tests, or shells. The marine foraminiferans harden their shells with calcium carbonate, and fossilized foram shells make up a large proportion of some marine sediments and terrestrial deposits (like the White Cliffs of Dover, England).

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

cytoplasm material in a cell, excluding the nucleus

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

Protozoan Diseases

Protozoans are a group of eukaryotic single-celled organisms. Several species of protozoans infect humans and inhabit the body as commensals or **parasites**. The parasitic protozoans of major medical importance include certain species of amoebae, flagellates, and sporozoans.

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

Amoebae

The most notorious amoeba of humans is *Entamoeba histolytica*, an inhabitant of the large intestine. Although often harmless, it can become invasive, penetrating into the **mucous membrane** of the intestine, multiplying and eroding the tissue. The result is a disease called amebiasis, characterized by intense abdominal pain, blood and mucus in the stool, diarrhea, and dehydration (a syndrome called amebic dysentery). Amebiasis can be fatal, especially to infants and children.

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

In addition to the intestinal infection, the amoebae sometimes get into the bloodstream and establish secondary sites of infection in the liver, brain, or elsewhere. *Entamoeba histolytica* is acquired from food or water contaminated with sewage. Several other amoebae, such as *Entamoeba coli*, inhabit the human intestine with little or no harm to the host, but their presence indicates that the person has ingested food or water contaminated with human feces and may be at risk of more serious infections.

Flagellates

The world's most common cause of water-borne diarrhea is the flagellate *Giardia lamblia*. Outbreaks of giardiasis are common in schools, mental hospitals, prisons, and other crowded institutions, but occur in circumstances as diverse as luxury resorts, backcountry camping, and impoverished villages. Giardia attaches to the surface of the small intestine, often in numbers great enough to seriously interfere with nutrient absorption. Unabsorbed nutrients then pass to the large intestine and cause gas production, painful abdominal cramps, and diarrhea.

In Africa, tsetse flies transmit another parasitic flagellate, *Trypanosoma*, which causes African sleeping sickness. Victims become fatigued, emaciated, and eventually lapse into a coma and die. Even though it does not occur in the United States, trypanosomiasis is one of the world's leading public health problems.

Sporozoans

Malaria is another leading cause of death in tropical countries. It is caused by four species of the protozoan genus *Plasmodium*. Transmitted by mosquitoes, Plasmodium multiplies in the liver and then invades the red blood cells, destroying them so extensively as to cause severe **anemia**. The victim experiences alternating fever and chills as the parasites emerge together from infected red cells, invade new ones, multiply, and repeat the cycle until finally the victim is overcome by exhaustion.

anemia lack of oxygen-carrying capacity in the blood

Another sporozoan disease is toxoplasmosis, caused by *Toxoplasma gondii*. Toxoplasma can be contracted from unpasteurized milk, undercooked meat, or house cats. It causes little pathology in adults, but when a pregnant woman

An electron micrograph of *Plasmodium falciparum,* one of the parasites that causes malaria.

is infected, it can cause serious fetal deformities resulting in infant blindness, hydrocephalus, and physical and mental retardation.

Any **parasitology** textbook can provide further details on these and related parasitic protozoans, how they infect humans, mechanisms of disease, and how to control or avoid them. SEE ALSO DIGESTIVE SYSTEM; PARASITIC DISEASES; VACCINES

parasitology study of parasites

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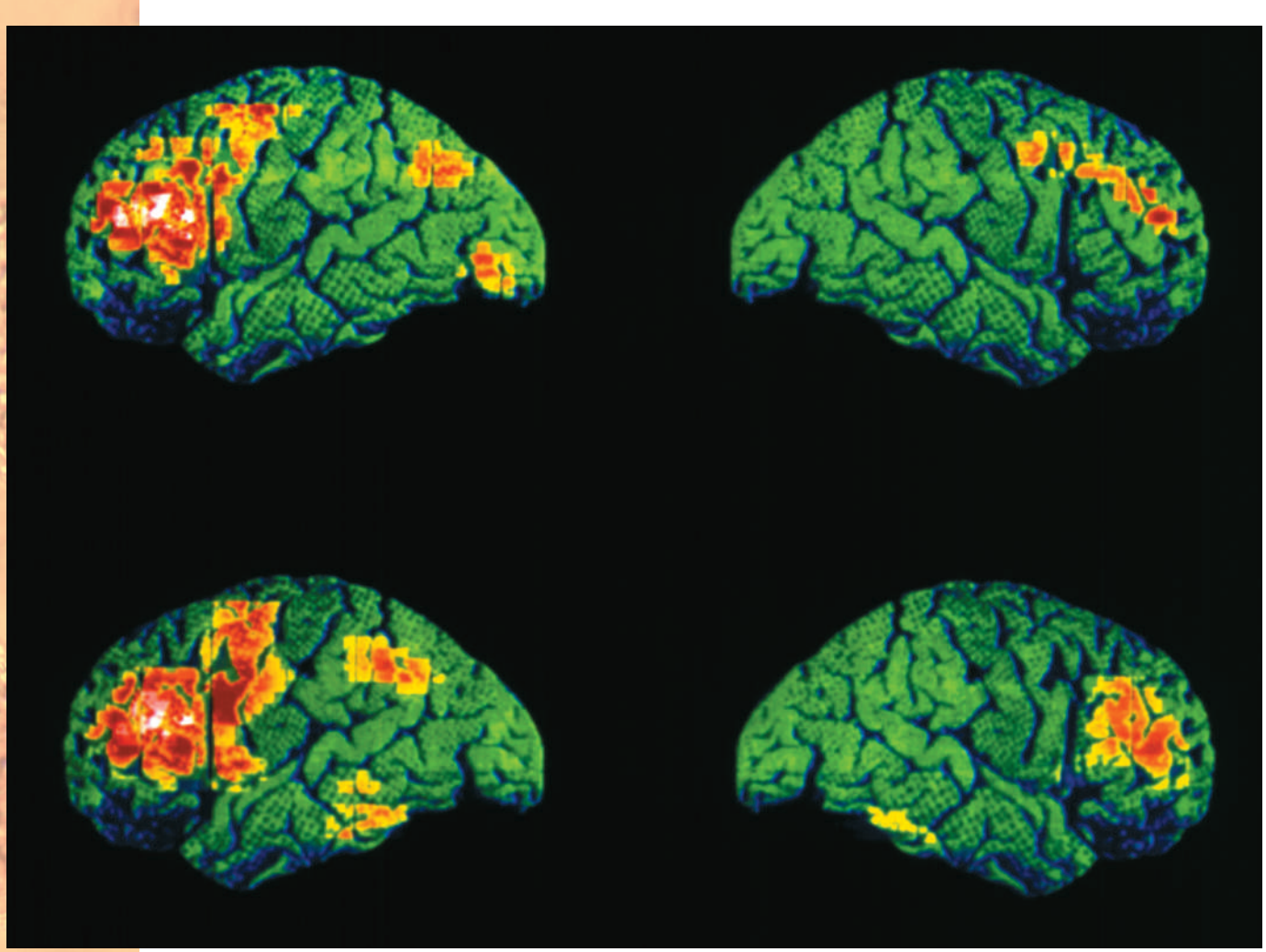
Psychiatric Disorders, Biology of

Mental illnesses affect millions of people each year, and billions of dollars are spent on their treatment and legal fees in the United States alone. Even



Colored positron emission tomography (PET) brain scans of a healthy person (top of image) and a person with schizophrenia (bottom).

more devastating is the impact these illnesses have on people, both those who are ill and those with whom they interact. Much ground has been gained in the areas of psychiatric research, diagnosis, and treatment options, but medical professionals still have a great deal more to learn. Current research shows that there is a strong biological component to many psychiatric disorders. Yet, it would be irresponsible to assume that biology, in either the form of physiology or genetics, can completely explain the basis for mental illnesses.

Humans and the human brain are complex entities. Humans are affected not only by their internal environment (biology) but by the external environment as well. There is no ethical method of separating one from the other when studying humans. Most researchers agree that in the "nature versus nurture" debate, both heredity and environment play a significant role in the development of human personality, whether "normal" or "abnormal."

Mental health disorders are classified into groups with some overlap. The major groups of disorders as they are classified are: anxiety, bipolar, borderline personality, depression, obsessive-compulsive, phobic, narcissistic, schizophrenic, substance abuse, and eating disorders. This article focuses on three of the more common and devastating ones.

Schizophrenia

Schizophrenia is a group of disorders characterized by some form of **psychosis** or disconnected thought processes. The symptoms associated with schizophrenia vary, and can affect thinking, behavior, and emotions. Schizophrenics suffer from delusions, **hallucinations**, and/or emotional unresponsiveness. Many people have the misconception that people suffering from schizophrenia have "split personalities," which is not the case. This misconception probably arose because some patients may hear voices that seem to arise from inside the head.

psychosis severe mental disorder characterized by diminished connection with reality

hallucination altered sensory experience resulting in the perception of objects that are not real

It is estimated that about 1 percent of the world population suffers from schizophrenia. The disease usually first becomes evident in men between the ages of fifteen and twenty-five, and in women between twenty-five to thirty-five. It usually starts slowly and progresses over time to a severely disabling state. While no single factor has been identified as causing schizophrenia, research has shown that there may be a strong genetic predisposition for the disease. Additionally, there may be structural differences in the schizophrenic brain. This group of disorders is now recognized officially as a brain disorder instead of a psychological problem. Current treatments include medications, community support services, and electroshock therapy.

Bipolar Disorder

The defining characteristic of bipolar disorder (formerly called "manic-depressive" disorder) is intense mood swings. During the manic phase of the disease, the person experiences a state of extreme euphoria (feeling good). He or she has bursts of energy or may become highly irritable. During the depressive phase, the person becomes increasingly despondent and inconsolable.

It is estimated that between 15 and 20 percent of those with untreated bipolar disorder commit suicide, usually during a depressive cycle. Research has demonstrated a genetic link between this disorder and genes on **chromosomes** 18 and 21, though the significance of this is not fully understood. Treatment for bipolar disorder includes behavioral therapy, medications, and close supervision or support, especially during depressive phases.

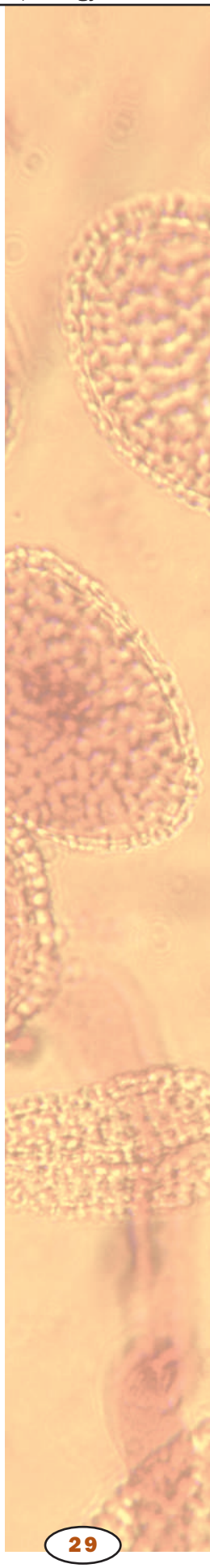
chromosome "colored body" in the cell nucleus; made of DNA and protein, and divided functionally into genes and non-gene regions

Substance Abuse

Substance abuse is defined as the maladaptive negative pattern of substance use that leads to impairment or distress. Estimates for the costs of substance abuse disorders on society are staggering and range from $117 billion to $235 billion per year. The personal costs to those afflicted are numerous as well. These disorders often cause severe impairments and complications. Those afflicted may have a deterioration of their general health because of malnutrition and poor hygiene. They are more likely to suffer from trauma and sudden death, to contract transmittable or **communicable** diseases, and to suffer from toxic or allergic reactions to ingested substances. Substance abusers are more likely than nonabusers to exhibit increased levels of aggression and violence, which lead to legal involvement.

communicable transmissible from person to person

The biological research on substance abuse includes studies on genetics and the physiology of the brain. Results are inconclusive, but there may



be a genetic component in some forms of alcoholism. Current studies are looking at the functioning of the brains of addicts in comparison to nonaddicts. Initial reports show that there are some structural differences as well as some differences in the ways the brain uses certain **neurotransmitters**, such as dopamine and serotonin.

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

Substance abuse is often a comorbidity (simultaneous occurrence of two or more disorders) associated with many other mental illnesses. In such cases, both the underlying psychiatric disorder and the substance abuse must be treated in order to achieve remission. There are many treatment methods, some controversial, for substance abuse. All claim therapeutic success, but many lack objective substantiation. Treatments can include therapy and/or medications and are most successful when used in combination. SEE ALSO ALCOHOL AND HEALTH; BRAIN; NEUROLOGIC DISEASES

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Psychiatrist

A psychiatrist is a physician who treats mental illness. The types of illnesses treated by psychiatrists include clinical depression, bipolar disorder (manic depression), obsessive-compulsive disorder (OCD), attention deficit disorder (ADD), drug and alcohol abuse, and many more. Mental illnesses that are categorized as psychoses involve chemical imbalances in the brain that require medication in addition to behavioral therapy. The psychiatrist is trained as a physician and is therefore qualified to prescribe the appropriate medication, but is also trained to administer behavioral therapies. In addition, psychiatrists often work cooperatively with psychologists (specialists who do not have an M.D. [Doctor of Medicine] degree).

Psychiatrists work in a variety of settings. Most hospitals employ psychiatrists to service the psychiatric ward and the emergency room. In addition, psychiatric hospitals (specializing in the care of the mentally ill) and detoxification facilities (specializing in the care of recovering addicts) rely on psychiatrists to administer treatment to their patients. Many psychiatrists also work in private practices, and some are employed by state governments to administer psychiatric treatment to prison inmates.

A psychiatrist must complete four years of medical school and a four-year residency in the field of psychiatry. A strong background in the sciences and math is an absolute requirement for medical school, and additional background in psychology is useful preparation for a career in psychiatry. High school and undergraduate courses in biology and psychology (specifically neuropsychology classes that discuss the link between brain function and behavior) allow one to explore one's interest level in this field. Strong interpersonal skills and compassion are essential qualities of a good psychiatrist. SEE ALSO DOCTOR, SPECIALIST; PSYCHIATRIC DISORDERS, BIOLOGY OF

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Psychoactive Drugs

Psychoactive drugs are a class of chemical substances that act on the **central nervous system** and can alter behavior and **cognition**. All psychoactive drugs are highly fat-soluble and thus cross the blood-brain barrier readily. Psychoactive drugs alter **synaptic transmission** by altering neurotransmitter amounts and availability or by affecting receptor activity. In addition to the drug's primary effects on behaviors such as arousal, thought processes, mood, perception, and consciousness, psychoactive drugs can produce a variety of nonbehavioral effects that may more directly affect health and, in some instances, can lead to death.

central nervous system brain and spinal cord

cognition mental processes of thought and awareness

synaptic transmission passage of chemicals between nerve cells to send messages or alter neuron firing

Although there are several different classification schemes for psychoactive drugs (pharmacological, legal, medical), the most common organization is based on their effect on behavior and cognition. According to this scheme, psychoactive drugs can be classified into four broad categories: (1) sedatives and hypnotics, (2) stimulants, (3) opiates, and (4) hallucinogens and psychedelics.

Sedatives and Hypnotics

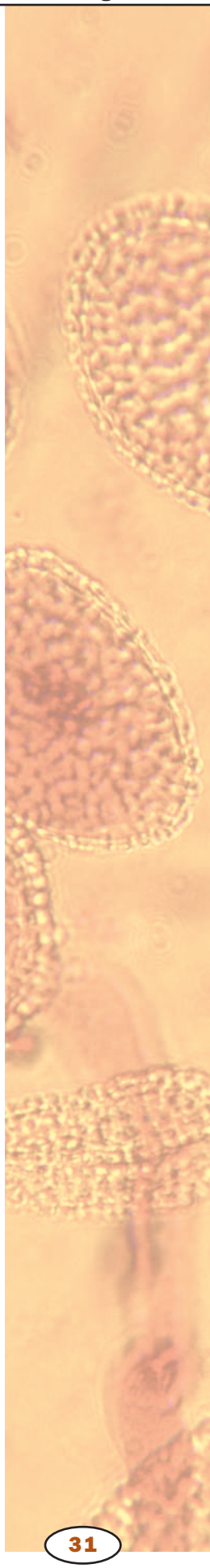
Sedatives and hypnotics depress or inhibit brain activity and produce drowsiness, sedation, or sleep; relieve anxiety; and lower inhibition. Although the depressant compounds do not share a common **neural** mechanism of action, most of them either decrease the metabolic activity in the brain or increase the transmission of the principal inhibitory neurotransmitter of the brain, gamma-aminobutyric acid (GABA).

neural related to nerve cells or the nervous system

All sedatives have the potential for addiction and dependency. Common depressants include barbiturates, such as Seconal; benzodiazepines, such as Xanax and Valium (commonly called minor tranquilizers); nonbarbiturate sedatives, such as methaqualone; newer nonbenzodiazepines, such as buspirone, antihistamines, and anesthetics; and alcohol. In low doses, alcohol can act as a stimulant; however, with increased dosage alcohol's main effect is depressive.

Stimulants

Stimulants produce behavioral arousal. As with the sedatives and hypnotics, there are a variety of substances, each with a different neural mechanism of action. Examples of stimulants are amphetamine, cocaine, antidepressants, caffeine (the most widely used psychoactive drug in the world), nicotine or tobacco, appetite suppressants, and a variety of exotic plant products. Stimulants vary in strength, legal status, and the manner in which they are taken; however, all stimulants have addictive potential.



The milky juice of unripe seed pods is used to make opium from the opium poppy plant.

Opiates

All drugs in the opiate class act on opiate receptors in the brain. They mediate relief from pain and produce feelings of euphoria. Opiates, which are referred to as narcotics by scientists and medical practitioners, are highly addictive and can either be natural, semisynthetic, or synthetic. Natural opiates such as opium are derived from the opium poppy. The active ingredients of opium are morphine and codeine. The most common semisynthetic opiate is heroin, which is five to ten times more potent than morphine. Examples of synthetic opiates include methadone and the prescription pain medication Demerol.

Hallucinogens and Psychedelics

hallucination altered sensory experience resulting in the perception of objects that are not real

Hallucinogens and psychedelics do not share a common mechanism of action, but all induce **hallucinations**. These drugs can either be natural such as mescaline, which is derived from the peyote cactus, or synthetic such as lysergic acid diethylamide (LSD), but they are typically classified pharmacologically according to the affected neurotransmitter system.

ecstasy Methylenedioxymeth amphetamine (MDMA) is a synthetic, psychoactive drug possessing stimulant and hallucinogenic properties

Cholinergic psychodelics (drugs altering acetylcholine transmission) include physostigmine, scopolamine, and atropine. Drugs that alter norepinephrine transmission include mescaline and **ecstasy**. Drugs that alter serotonin transmission include LSD and psilocin. Other drugs in this category include the psychedelic anesthetics phencyclidine (PCP) and ketamine.

Marijuana, which is derived from the hemp plant *Cannabis sativa*, is often classified as a psychedelic substance, although only in very high doses does it produce sensory distortions. Marijuana's most common behavioral symptom is sedation. Unlike other drug classes, and with the exception of the cholinergic psychedelics, hallucinogenic and psychedelic drugs are generally nonlethal even when taken in large doses.

Other Drugs that Affect the Central Nervous System

Additionally, there are a number of other drugs that affect central nervous system functioning. These compounds are used to treat a variety of psy-

chological and neurological disorders and include antidepressants, antipsychotic medication, and drugs for epilepsy, Parkinson's disease, the **dementias** (such as Alzheimer Disease), and **spasticity**.

dementia neurological illness characterized by impaired thought or awareness

spasticity of, or relating to spasms

Categorizing Drugs into Five Schedules

A different approach to the classification of psychoactive drugs is taken by the legal system, which considers all illegal drugs or controlled substances "narcotics." According to the Comprehensive Drug Abuse Prevention and Control Act of 1970, drugs are categorized into five schedules according to the perceived risk of dependency.

Schedule I drugs, such as heroin, marijuana, and most psychedelics, have a high risk of dependency and no widely accepted medical use. These drugs are forbidden and cannot be obtained even by prescription (although marijuana is available in some states). Schedule II drugs, such as morphine, codeine, amphetamines, and certain barbiturates, have a high risk of dependency but are accepted by the medical community for treatment. Schedule III drugs have a risk of moderate physical dependency or high risk of psychological dependency and include preparations with limited opiates (morphine) and barbiturates not in Schedule II.

Schedule IV drugs, which include the benzodiazepines, have a slight risk of mild physical or psychological dependency. Schedule V drugs have less risk of mild physical or psychological dependency. Finally, alcohol and tobacco are not classified under this law. They fall under the jurisdiction of the Bureau of Alcohol, Tobacco and Firearms (ATF), which is a division of the U.S. Department of the Treasury. SEE ALSO ALCOHOL AND HEALTH; DRUG TESTING; NERVOUS SYSTEMS; NEURON; SYNAPTIC TRANSMISSION

Arne Dietrich

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Pteridophytes

Pteridophtyes are a **phylum** of plants. They are the vascular plants (those having **xylem** and **phloem** tissues) that reproduce by releasing spores rather than seeds, and they include the highly diverse true ferns and other graceful, primarily forest-dwelling plants. There are about eleven thousand different species of pteridophytes, making them the most diverse land plants after the flowering plants (angiosperms). Pteridophytes may represent the closest living relatives (sister group) to the seed plants. (Seed plants include the angiosperms, the conifers, and a smaller assortment of other plants.)

As in seed plants, the greatest diversity of pteridophytes is found in the tropics, with only about six hundred species adapted for life in temperate climates. Species living today are relics of ancient **lineages** that once dominated

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

xylem water-transporting system in plants

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

lineage ancestral line

Ferns reproduce by releasing spores rather than seeds.

CLASSIFICATION OF THE PTERIDOPHYTES

Phylum Pteridophyta
Class Lycopodiopsida
Order Lycopodiales, the club mosses* and ground pines, approximately 400 species
Order Selaginellales, the spike mosses*, approximately 450 species
Order Isoetales, the quillworts, approximately 130 species

Class Equisetopsida, the horsetails or scouring rushes*, 15 species

Class Psilotopsida, the wisk ferns, approximately 12 species

Class Filicopsida, the true ferns, approximately 10,000 species

* The common names "mosses" and "rushes" applied to these species do not mean that these groups are related to the mosses and rushes, any more than a pineapple is related to pines or a breadfruit has some affinity to wheat. True mosses are nonvascular plants whose most commonly recognized life form is a gametophyte, and true rushes are grasslike flowering plants. Instead, these common names indicate that the club "mosses" and spike "mosses" are often small plants that hug the ground, and scouring "rushes" have long, grasslike stems.

the land surface. There is a rich fossil record showing that pteridophytes have ancestors dating back nearly four hundred million years. Before there were seed plants, there were pteridophytes such as large, treelike (up to 36.5 meters [120 feet] tall) *Lepidodendron*, an ancestor of modern club mosses (which are no more than .30 meter [1 foot] tall), and shrubby *Sphenophyllum*, a forebear of today's horsetails. Some of the ancient predecessors of modern ferns were also preserved, but there are comparatively few fossils for interpreting relationships among the approximately eleven thousand species of true ferns. These relatively young species probably arose along with the other most recent lineages of vascular plants, the angiosperms or flowering plants, another group lacking an extensive fossil record.

Pteridophytes range greatly in size. There are tiny floating ferns used as "green fertilizer" in rice paddies because they partner with bacteria that pull nitrogen from the air and "fix" it in chemical compounds that other plants can use. In some tropical forests, the largest plants are tree ferns that can be up to 30 meters (100 feet) tall and have huge spreading leaves up to 4.5 meters (15 feet) in length. Pteridophytes also show a transition from simple to complex leaves. Some pteridophyte groups, including the club mosses and horsetails (classes Lycopodiopsida and Equisetopsida), have simple microphyllous leaves, featuring a single, unbranched vein and modest vascular supplies that do not cause breaks or gaps in the stem vasculature. The true ferns (class Filicopsida), however, have larger, more complex macrophyllous leaves whose veins are usually extensively branched, placing such large demands on the plant's vasculature that distinctive gaps form in the xylem and phloem of the stem.

All pteridophytes have a true alternation of generations, in which a dominant sporophyte generation produces spores through **meiosis**, and a free-living **gametophyte** generation forms **gametes** (egg and sperm) by **mitosis**. Ferns can be used to illustrate the life cycle stages common to all pteridophytes. **Diploid** (2n) fern sporophytes are familiar to most people and are often found as quiet accompaniments in floral arrangements. When mature, the undersides of fern leaves produce clusters of capsular structures called sporangia, within which meiosis forms the **haploid** (n) spores. These spores are released from the sporangia, often when dry wind currents cause the active snapping of the capsules, lofting the spores into the air.

Spores that are wind-borne to shady, moist habitats germinate and yield multicellular, but microscopic, gametophytes, the sexual stage of the life cycle. These short-lived, delicate plants mature and produce egg-forming archegonia and sperm-producing antheridia. When water is present, multiflagellated sperm swim from mature antheridia, are chemically attracted to the necks of the archegonia, and fertilize the eggs. Although frequently bisexual (hermaphroditic), in most cases the sperm produced by a gametophyte cannot successfully fertilize its own eggs and must swim to archegonia on neighboring, genetically different gametophytes. The diploid **zygotes**, produced by the fusion of haploid egg and sperm, divide mitotically and differentiate into mature sporophytes, completing the life cycle.

Although most pteridophytes are homosporous (produce spores that are all the same size), a few groups are heterosporous with large megaspores and small microspores. The megaspores produce megagametophytes that

meiosis cell division that forms eggs or sperm

gametophyte a haploid plant that makes gametes by mitosis

gamete reproductive cell, such as sperm or egg

only form eggs, and microspores only produce microgametophytes and sperm. Heterospory evolved independently in several groups of vascular plants, including all members of the orders Selaginellales and Isoëtales and those in a few fern groups (the families Marsileaceae and Salviniaceae of the class Filicopsida). The most successful origin of heterospory ultimately resulted in the great diversity of seed plants.

No pteridophytes are cultivated as crop plants, but the leaf buds ("fiddleheads") of some ferns are commercially harvested and canned or frozen. Fern leaves used in floral arrangements are a major industry in Florida, and in some cultures tree fern stems are used to make elegant, naturally sculpted bowls. The contrasting colors of the vascular tissue in the stems and leaf bases of these plants create complex and pleasing designs. In the past, club moss spores provided the powder used to coat rubber gloves and prophylactics, and photographers used masses of these same spores as flash powder, since they could be easily and quickly ignited. SEE ALSO ALTERNATION OF GENERATIONS; ANGIOSPERMS; BRYOPHYTES; NITROGEN FIXATION; PLANT; REPRODUCTION IN PLANTS; SEEDLESS VASCULAR PLANTS

Christopher Haufler

mitosis separation of replicated chromosomes

diploid having pairs of chromosomes in the nucleus

haploid having single, nonpaired chromosomes in the nucleus

zygote fertilized egg

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Public Health Careers

Public health takes a population–based approach to address the physical, mental, and environmental health concerns of communities. With such information the appropriate health promotion and disease prevention is applied to improve and enhance quality of life. This can take place at the local public health clinic, at regional or national agencies, international organizations, or in the private sector. Each presents unique challenges to understand the health issues and health hazards, to provide access to quality health care at affordable cost, and to educate and promote sound health behaviors.

What do people involved in public health do? It depends on the specific career choice. You could give vaccinations at an inner city clinic, develop educational programs, investigate environmental problems, help determine how to get people to adopt healthier lifestyles, administer health service programs, or create health policies.

What education is needed to become part of public health? At the present time, registered nurses need an associate's degree in nursing, a bachelor of science degree in nursing, or a diploma from a hospital program. Other medical personnel, social workers, and therapists need a bachelor's degree in a specialized field or postgraduate education in an appropriate program.

AMERICAN PUBLIC HEALTH ASSOCIATION

As the oldest and largest public health professional association in the world, American Public Health Association (APHA) has more than 50,000 members representing more than 50 occupations. It provides a forum for the exchange of ideas, study, and action on a variety of issues that affect personal and environmental health. Researchers, health providers, administrators, teachers, and others work together on items as diverse as funding possibilities, pollution control, disease, and smoke-free societies.

Programs leading to a master's in public health degree allow the student to specialize in areas such as epidemiology, biostatistics, environmental health, health education, health policy/administration, occupational medicine, nutrition (as a registered dietitian), or maternal and child health.

What can help prepare a person for a career within public health?

1. Visit, interview, and/or volunteer with people or sites involved in the areas of interest. Find out education and experience requirements from them and plan high school classes accordingly.
2. Develop strong communication skills with individuals and in front of groups.
3. Learn a second language.
4. Learn to work with diverse populations.
5. Learn to handle stressful situations.
6. Develop a strong concern for others.

Karen E. Jensen

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Radiation Hybrid Mapping

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

genome total genetic material in a cell or organism

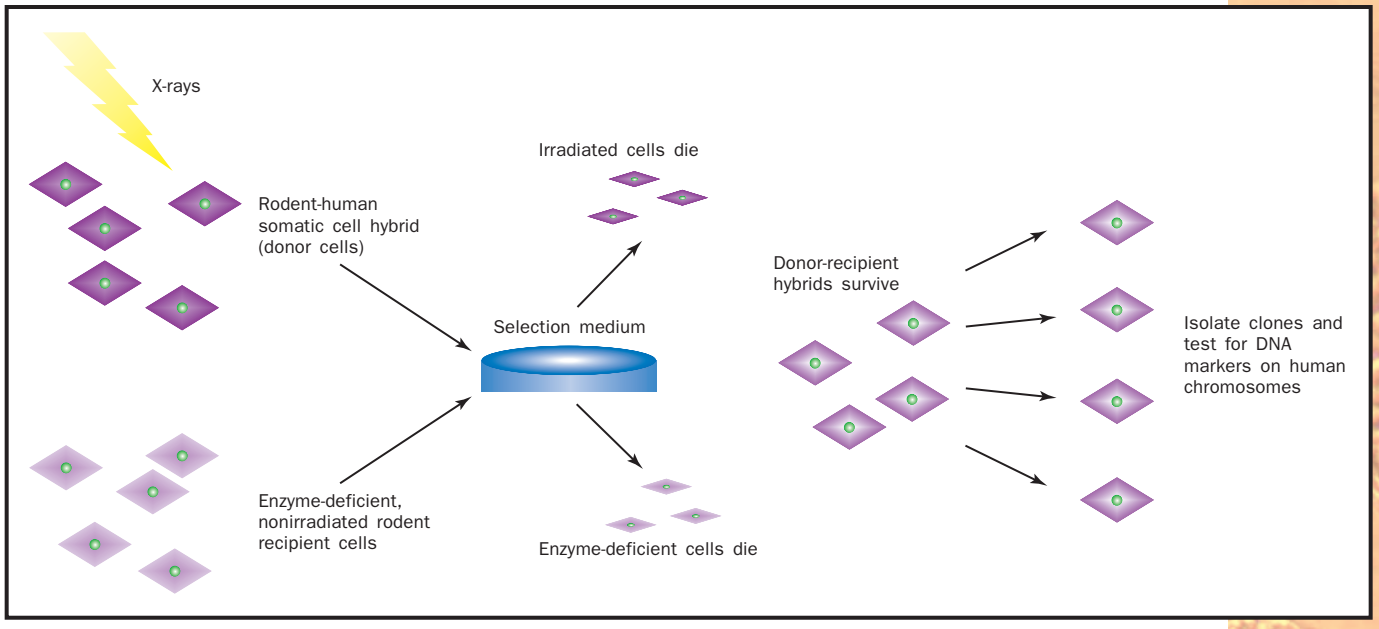
Radiation hybrid mapping is a genetic technique that was originally developed for constructing long-range maps of mammalian **chromosomes**. It is based on a statistical method to determine not only the distances between deoxyribonucleic acid (DNA) markers but also their order on the chromosomes. DNA markers are short, repetitive DNA sequences, most often located in noncoding regions of the **genome**, that have proven extremely valuable for localizing human disease genes in the genome.

Theory and Application

In radiation hybrid mapping, human chromosomes are separated from one another and broken into several fragments using high doses of X rays. Similar to the underlying principle of mapping genes by linkage analysis based on recombination events, the farther apart two DNA markers are on a chromosome, the more likely a given dose of X rays will break the chromosome between them and thus place the two markers on two different chromosomal fragments. The order of markers on a chromosome can be determined by estimating the frequency of breakage that, in turn, depends on the distance between the markers. This technique has been used to construct whole-genome radiation hybrid maps.

Technique

A rodent-human somatic cell hybrid ("artificial" cells with both rodent and human genetic material), which contains a single copy of the human chro-



Radiation hybrid mapping process.

mosome of interest, is X-irradiated. This breaks the chromosome into several pieces, which are subsequently integrated into the rodent chromosomes. In addition, the dosage of radiation is sufficient to kill the **somatic** cell hybrid or donor cells, which are then rescued by fusing them with nonirradiated rodent recipient cells. The latter, however, lack an important **enzyme** and are also killed when grown in a specific medium. Therefore, the only cells that can survive the procedure are donor-recipient hybrids that have acquired a rodent gene for the essential enzyme from the irradiated rodent-human cell line (see Figure above).

somatic nonreproductive; not an egg or sperm

enzyme protein that controls a reaction in a cell

From these donor-recipient hybrids, clones can be isolated and tested for the presence or absence of DNA markers on the human chromosome of interest, and the frequencies with which markers were retained in each clone can be calculated. This process is complicated by the fact that hybrids may contain more than one DNA fragment. For example, two markers retained in one hybrid may result from retention of the two markers on separate fragments or from no break between the markers. However, the frequency of breakage, theta, can be estimated using statistical methods, and a lod score (logarithm of the likelihood ratio for linkage) can be calculated to identify significantly linked marker pairs. SEE ALSO LINKAGE AND GENE MAPPING

Christine Klein

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Radionuclides

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

Radionuclides or radioisotopes are radioactive **isotopes** of elements that are extremely important tools in biochemistry and cell biology. Radionuclides allow scientists to tag specific molecules without altering the structure or function of the studied compounds. Radioactive isotopes of elements normally found in biological systems include carbon 14, hydrogen 3 (tritium), sulfur 35, and phosphorous 32. These unstable atoms decay over time (from seconds to centuries), emitting radioactive particles that can be detected by laboratory instruments.

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

Because radioactive elements can be detected, the tagged molecule, such as a **protein**, nucleic acid, or sugar, can then be detected with great accuracy and sensitivity, especially if only a small amount of the molecule is present.

amino acid a building block of protein

nucleotide the building block of RNA or DNA

In a type of experiment called a pulse-chase, a radionuclide-tagged **amino acid** or **nucleotide** is incorporated into a protein or nucleic acid, and the fate of the protein or nucleic acid is monitored over time. For instance, cells are fed a nutrient mixture (the "pulse") containing a radioactively tagged amino acid such as methionine, containing sulfur 35. After a few minutes, the cells have incorporated the tagged amino acid into most of the proteins synthesized during exposure to the tagged amino acid. The tagged amino acid mixture is then removed and replaced with untagged amino acids ("the chase") that are then incorporated into all newly synthesized proteins from that point on. As time passes, the radioactivity incorporated into each protein will disappear due to degradation of the protein by the cell. This is a measure of protein longevity and will vary from protein to protein.

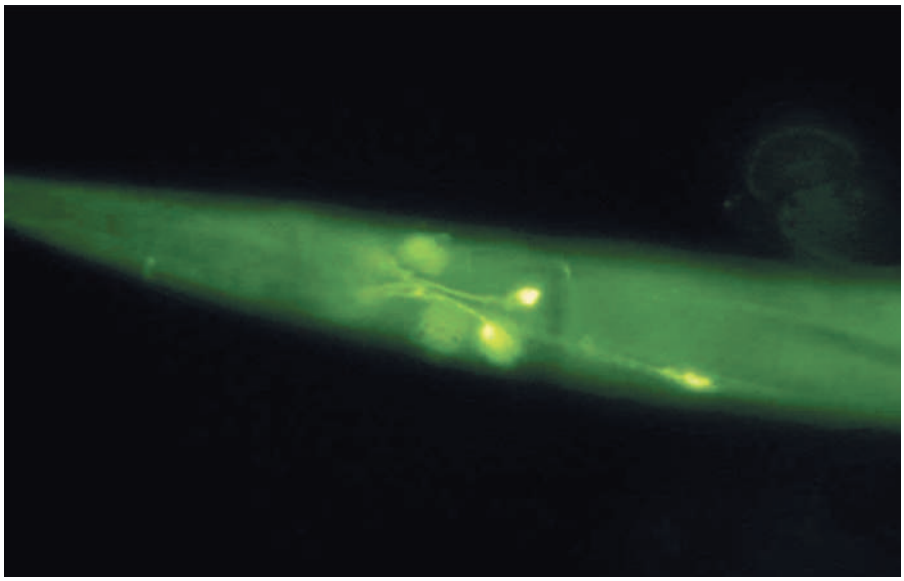
Radionuclides can also be used to monitor the metabolic fate of a nutrient. For instance, radionuclide-tagged sugars can be fed to cells or to a live animal and samples of the cells or waste products from the animal analyzed over time. The radionuclide tag will appear in new compounds as time passes. The first products to appear are the initial metabolic breakdown products of the sugar. Later, other radioactive compounds will appear representing intermediates in the complete breakdown of the sugar. This procedure can be used to identify the metabolic pathway used to break down the sugar and derive energy. For instance, the carbon in C-14-tagged **glucose** will eventually be found in carbon dioxide, the final breakdown product. SEE ALSO KREBS CYCLE; METABOLISM, CELLULAR; PHOTOSYNTHESIS; PROTEIN SYNTHESIS; REPLICATION

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

Stephen A. Adam

Recombinant DNA

Recombinant deoxyribonucleic acid (DNA) technology allows the creation and manipulation of DNA sequences that come from different sources, even different species. The development of recombinant DNA technology in the 1970s was hailed as the most exciting invention since the development of transistors some twenty to thirty years earlier. The transistor changed people's lives forever by creating the microelectronics revolution and enabling



Recombinant DNA technology helps highlight the brain of *C. elegans.* To photograph its brain, a fluorescent protein was linked to the fax-1 protein in the brain; the glowing neurons reveal the cells in which fax-1 functions.

the development of portable radios, tape and compact disc players, cellular phones, and computers, all leading to fabulous wealth in the developed world. Recombinant DNA technology is likely to also have profound effects on society, including better health through improved disease diagnosis, much better understanding of human **gene** variation, improved drug and pharmaceutical production, vastly more sensitive and specific crime scene **forensics**, and production of genetically modified organisms that significantly improve yields and nutritional value of crops while decreasing reliance on pesticides and artificial fertilizers. Recombinant DNA and the **transgenic** technology that it spawned have already entered everyday lives to a degree, as evidenced by the completion of a draft of the human **genome** sequence, criminal trials relying on DNA evidence, and controversy over the use of genetically modified corn and other organisms.

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

forensic related to legal proceedings

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

genome total genetic material in a cell or organism

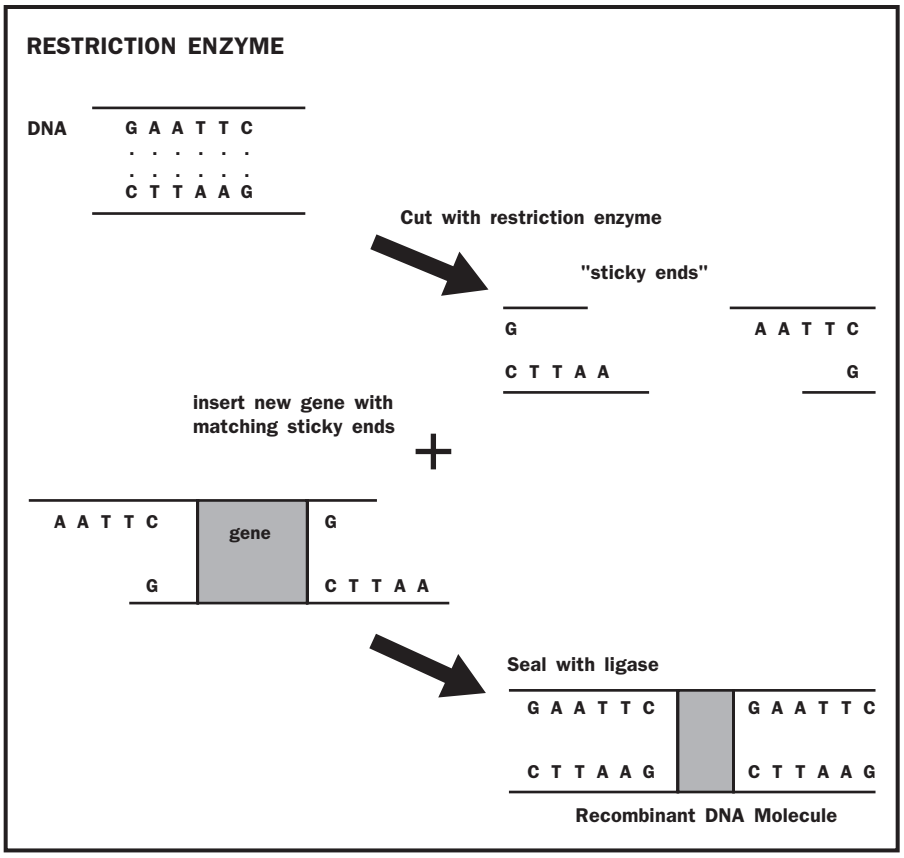
Recombinant DNA technology has had to create its place instead of entering an existing market. As a result, recombinant DNA technology has probably consumed more finances than it has yet generated, although this discounts the long-term value of increasing knowledge. Where recombinant DNA technology has made the biggest economic impact is in the pharmaceutical industry, allowing the production of single human **proteins** for therapeutic use or to generate specific antibodies. Harvesting human insulin created in bacterial cells is far easier than isolating it from pig or human cadaver pituitary glands, for instance. The financial base for recombinant DNA technology should continue to improve as genetically modified organisms are becoming widely used in agriculture; more than half the U.S. soybean crop now consists of a strain genetically modified to reduce the amount of herbicides necessary to bring in a good yield.

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

Gene Cloning

A clone is a collection of organisms that are genetically identical, and a recombinant DNA clone is a collection of genetically identical organisms (most often bacteria) that each carry a specific foreign (from another source) DNA molecule. "Clone" also refers to the foreign DNA itself after being

The process of DNA cloning has two components: one is the use of restriction enzymes *in vitro* to cut DNA into a unique set of fragments; the other is the use of vectors to ensure that the host organism carries and replicates the foreign DNA.



placed in the target organism. Thus, scientists would speak of the "cloned DNA." Typically, a specific DNA molecule is inserted into a **vector** DNA molecule that can carry foreign DNA, and the resulting recombinant DNA is introduced into a host organism (often the common bacterium *Escherichia coli* or the yeast *Saccharomyces cerevisiae*). Large numbers of genetically identical host organisms, each carrying the same specific foreign DNA molecule, can be produced, allowing the DNA or its protein product to be produced in large quantities.

vector carrier

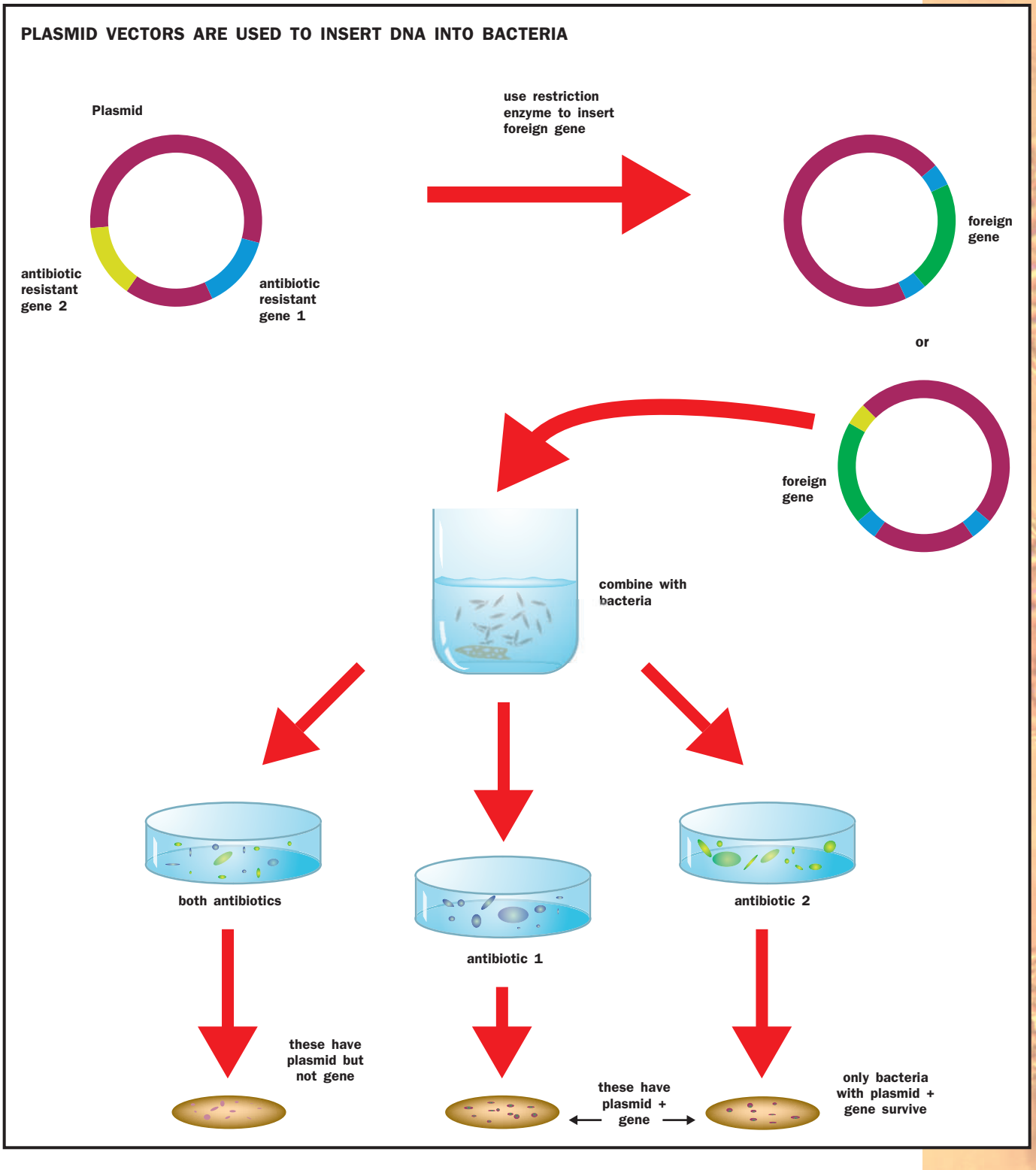
The process of DNA cloning has two components. One is the use of **restriction enzymes** *in vitro* to cut DNA into a unique set of fragments. Restriction enzymes are endonucleases that bacteria naturally use to defend against DNA viruses by cleaving DNA at specific sites. The **enzyme** EcoRI, for example, from *E. coli*, cleaves every site with the six-nucleotide sequence of GAATTC, found on average every 4,100 **nucleotides** in DNA. (A companion methylase enzyme modifies the bacterium's own GAATTC sites so they are not targets of EcoRI.) Researchers have isolated many different restriction enzymes from bacterial species. The enzymes differ in the sequences of the target sites that they cut, in the locations of the cleavage sites, and by whether modified target sites are cleaved (in some cases modification is required for cleavage). The collection of restriction enzymes with these different properties provides an invaluable toolbox for cutting and joining DNA molecules from different sources.

restriction enzyme enzyme that cuts DNA at a particular sequence

enzyme protein that controls a reaction in a cell

nucleotide the building block of RNA or DNA

The other component of DNA cloning technology is the use of vectors to ensure that the host organism carries and replicates the foreign DNA.



A plasmid carrying antibiotic resistant genes provides both a vector for introducing a foreign gene into a bacterium, and a method for testing the success of the introduction.

Most often bacteria are used as the host organism, because of their fast growth and the ready availability of techniques for manipulating and growing bacteria in small- and large-scale cultures. Vectors are DNA molecules that contain an origin of replication that functions in the host organism (to allow the vector to be copied), and a gene that confers some survival advantage on host

cells that contain the vector DNA. Typically the vector carries a gene that confers resistance to a particular drug, such as an antibiotic.

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

plasmid small ring of DNA found in many bacteria

The original vectors used were based on naturally occurring small, circular DNA molecules distinct from the bacterial **chromosome**, called **plasmids**. The most widely used vector of the late 1970s to early 1980s was the plasmid pBR322, which contained an origin of replication, a gene that confers resistance to the antibiotic ampicillin, and a second gene that confers resistance to the antibiotic tetracycline. Each of these antibiotic resistance genes contains the recognition sequence for a restriction endonuclease. Opening the vector at one of those sites by restriction digestion *in vitro* and ligating (splicing) the foreign DNA into that site destroys the resistance encoded by that gene but leaves the other resistance factor intact. Plasmid DNA can then be put back into bacterial host cells (by transfection) where it can replicate up to several hundred copies per bacterium. The bacteria are then grown in media containing one or the other antibiotic. This facilitates selection and identification of bacteria receiving the ligation product. The cloned DNA then replicates along with the rest of the plasmid DNA to which it is joined.

inducible able to be switched on

promoter DNA sequence to which RNA polymerase binds to begin transcription

transcribe creation of an RNA copy of a DNA gene

Later improved editions of plasmid vectors incorporated such features as polylinker sequences that consist of several unique restriction sites close together to form a specific cloning site and **inducible promoter** sequences adjacent to the polylinker used to **transcribe** into RNA, or "express," the cloned DNA as desired.

cDNAs and Gene Analysis

reverse transcriptase enzyme that copies RNA into DNA

gene expression use of a gene to create the corresponding protein

Plasmid vectors are limited in the size of the cloned DNA that can be incorporated and successfully reintroduced into the bacterium, typically holding a maximum of about 15 kb (kilobases [1 kb equals 1,000 bases]) of foreign DNA. One common use for plasmid vectors is to make cDNA (complementary DNA) libraries; cDNA molecules are DNA copies of messenger ribonucleic acid (mRNA) molecules, produced *in vitro* by action of the enzyme **reverse transcriptase**. Because cDNAs represent only the portions of eukaryotic genes that are transcribed into the mRNA, cDNA clones are particularly useful for analysis of **gene expression** and cell specialization. The existence of a cDNA is also evidence that the gene is active, or transcribed, in the cells or tissues from which the mRNA was isolated. Such information can be used to compare gene activities in healthy versus diseased cells, for instance.

Frequently the simpler sequence of a cDNA is easier to analyze than the corresponding genomic sequence since it will not contain noncoding, or intervening, sequences (introns). Another advantage of cDNA is that generally the sequence does not include enhancers or regulatory sequences to direct their transcription. As a result, they can be combined with other regulatory systems in the clone to direct their expression.

Genome sequencing projects typically generate sequence information from many different cDNA clones. The cDNA cloned sequence is termed an "expressed sequence tag" (EST), and, when correlated with the whole genomic DNA sequence, EST information can help determine the locations and sizes of genes.

In order to obtain the cDNA for a specific gene, it is first necessary to construct a cDNA "library." This is a collection of bacteria that contain all the cDNAs from the cell or tissue type of interest. To make a library, the thousands of different mRNAs are first harvested from the cell of interest, and cDNA is made using reverse transcriptase. The cDNA is then cloned into plasmids, and introduced into bacteria. Under the right conditions, each bacterium will take up only one cDNA. The bacteria are then grown in Petri dishes on a solid medium. A library therefore consists of a mixed population of bacteria, each carrying one type of cDNA. To find the bacterium containing a particular type of cDNA, one can either search for the gene itself with a nucleotide probe or for its protein product with an **antibody**.

antibody immune system protein that binds to foreign molecules

Screening a library depends either on having a probe bearing part of the nucleotide sequence or an antibody or other way of recognizing the protein coded by the gene. Screening by nucleotide probes (labeled with radioactive or chemical tags for detection) depends on **base pair** complementarity between the single-stranded target DNA and the probe DNA; this allows the label to mark the cell with the desired cDNA. Screening by labeled antibody depends on binding of the antibody to the protein encoded by the gene. Literally thousands of cloned genes have been isolated this way from libraries of many different species. One of the most powerful observations in biology is that the same or similar gene sequences can be isolated from different species, ranging from bacteria to humans.

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

Human insulin was the first medicine to be created through recombinant DNA technology. Insulin is a protein **hormone** produced by the pancreas that is vital for regulation of blood sugar. In the disease insulin-dependent diabetes mellitus (IDDM), the immune system attacks and destroys the insulin-producing cells. A person with IDDM requires daily injections of insulin to control blood sugar. Before 1980, insulin was isolated from pigs or other animals. Animal insulin has a slightly different **amino acid** sequence from the human form. In the early 1980s, recombinant DNA technology was used to splice the human insulin gene into bacteria, which were grown in vats to make large amounts of the human protein. Recombinant human insulin was the first recombinant drug approved for human use. Since then more than two dozen other drugs have been created in this way, including growth hormone, blood clotting factors, and tissue plasminogen activator, used to break up blood clots following a stroke. Gene sequence similarities indicate that all living organisms have descended from shared common ancestors, back to the beginning of life.

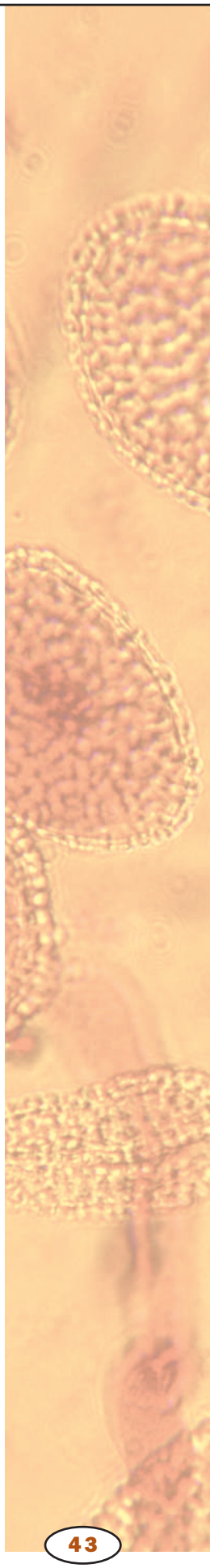
hormone molecule released by one cell to influence another

amino acid a building block of protein

Transgenic Organisms

Cloned DNA can also be incorporated into the genomes of multicellular organisms to create a transgenic organism. This makes possible a new approach to designing genotypes by adding genes (gene-coded functions) to species where those genes (functions) do not exist. Genetically modified organisms (GMOs) created by modifying a gene or adding one from another species frequently offer the most direct way to improve the way people use organisms for food or chemistry.

One example of a GMO is the development of "golden rice," designed to reduce blindness caused by vitamin A deficiency in rice-consuming areas



endosperm nutritive tissue within a seed

of the world. A polished rice grain, which is the portion of the seed that provides nourishment (the **endosperm**) does not contain beta-carotene, the substance the human body converts into vitamin A, yet many plants with yellow/orange colored leaves or flowers produce it in abundance. To convert rice endosperm into a beta-carotene-rich food, a transgene was constructed with the genes required for beta-carotene production and inserted into rice cells. The transgene consists of a cDNA for phytoene synthase, from a daffodil flower library, plus other sequences. Rice with these extra genes show a rich "golden" color from the beta-carotene that accumulates in the rice grain. If golden rice can be bred into commercial strains and enough can be provided into the diet to reduce the incidence of vitamin A–related blindness, current agitation against GMO crops may evolve into enthusiasm for their application.

Genome Libraries: Sequencing Genomes

intron untranslated portion of a gene that interrupts coding regions

Recall that cDNAs do not contain **introns**. Comparing a cDNA sequence with its corresponding DNA sequence on a chromosome (the genomic sequence) reveals the locations of introns in the genomic sequences. Genomic DNA libraries, in which the cloned DNA originates from fragments of the chromosomal DNA, carry intronic sequences, as well as the DNA between genes. In the more complex eukaryotes the same genomic region may correspond to several different cDNAs. This reveals the existence of alternative splicing, in which different sets of exons are used to make separate mRNA transcripts from one gene region. This expands the diversity of the protein, encoded by a single gene to include slightly different protein forms, called isoforms. Tissue-specific regulation of splicing indicates that these isoforms contribute important nuances to creating developmental differences between tissues.

Genomic DNA libraries have also proved invaluable for isolating genes that are poorly expressed (that is, make little mRNA) and for mapping disease-causing genes to specific chromosomal sites. The vectors used in genomic libraries are designed to incorporate greater lengths of cloned DNA than plasmids can carry. The first of these vectors was the lambda bacterial virus, which could hold an insert of 15 kb, followed by the cosmid, a **hybrid** between a plasmid and a phage (a virus that infects bacteria) with a DNA insert size of 45 kb. Development of linear yeast artificial chromosomes (YACs), which include a yeast **centromere**, origin of replication, and ends (telomeres), which successfully grow in the yeast *Saccharomyces cerevisiae*, carry clones of 200 kb to more than 2,000 kb. Subsequent development of bacterial artificial chromosomes (BACs) that contain 100 kb of insert DNA and are relatively easy to culture has put genomic cloning within reach of almost every molecular biology laboratory. (Clones are harder to work with as they get larger.)

hybrid combination of two different types

centromere region of the chromosome linking chromatids

BACs provided one route to sequencing the human genome, where their large capacity was critical. All the different genome sequencing projects start with a large number of BAC clones for that species, subclone 1 kb fragments of the DNA from each BAC into plasmids, and determine their sequence using high-speed machines. Computer-based comparisons of the results then assemble the nucleotide sequences into a coherent order by aligning the regions where they overlap.

A library of genomic DNA contains many clones with inserts that partially overlap each other because random breakage of chromosomal DNA is used to produce fragments for cloning. The order of fragments in the original chromosome can be determined by "chromosome walking." In this technique, a portion (subclone) from one clone is used as a probe to identify another clone that also carries that sequence. The two clones are then compared, and the nonoverlapping end of the second clone is subcloned for use as the next probe. In this way, a "walk" is carried out over many steps to identify adjacent DNA on the same chromosome, allowing the fragments to be placed in sequence. A series of sequential, partially overlapping clones is termed a "contig" (for **contiguous** sequence); the goal of genome mapping is to make a separate contig for all the DNA clones from one chromosome (a continuous covalent molecule). Contigs made large genome sequencing feasible since a minimum number of BACs could be chosen from their order in the map.

contiguous adjacent to or touching

Finding Disease Genes

Locating a human disease gene on a chromosome map is now equivalent to locating the gene (approximately) on a contig and the DNA sequence map. This speeds gene identification through cloning the gene and determining what protein the gene encodes. The positional approach is important for single-gene (Mendelian) disease traits that are well known clinically but not at a biochemical level.

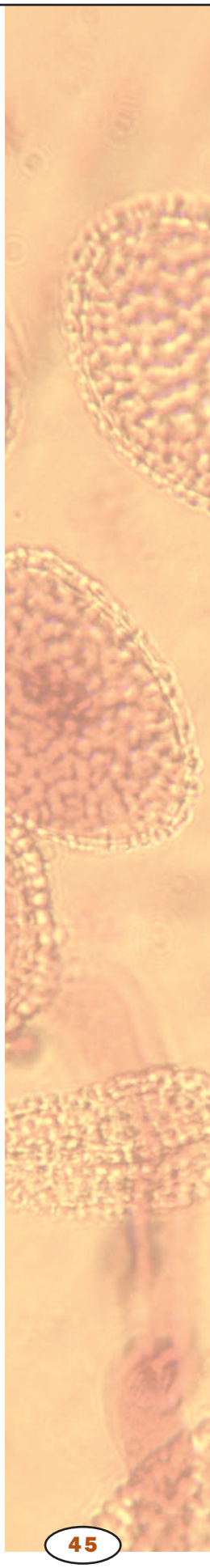
Cystic fibrosis (CF) was one such disease. It is the most common severe autosomal recessive disorder among European populations and their descendants in the New World. Patients suffer from mucus accumulation and frequent bacterial infections in their lungs. In the United States, CF patients are the single largest group receiving transplants to replace damaged lungs. However, the clinical studies failed to determine which gene product is defective in the patients. Extensive studies on families with CF led to identification of the causative gene on chromosome 7.

Initially recombination studies placed the gene within a small region of the chromosome of approximately one million base pairs. Starting at DNA clones from both ends of this region, the researchers used chromosome walking to clone all of the interval; several candidate genes were identified within the region but rejected as the cause of CF. Finally, one gene was identified within these clones that had the right properties: It was normally expressed in the lungs but not the brain, and it encoded a protein that made sense for the cause of the disease. In addition, patients with CF had specific mutations in this gene. The functional CF gene encodes a chloride channel transmembrane regulatory protein (CFTR) that controls transport of certain **ions** in and out of epithelial (surface) cells. The most common mutation encodes a CFTR protein that is missing one amino acid and cannot reach its site of function in the cell membrane. As a result, ions become too concentrated inside the cell, and water moves in. The result is dried **secretions**, such as very sticky mucus.

ion an electrically charged particle

secretion material released from the cell

Gene therapy to add a functional copy of the CFTR to lung cells has not been successful, in part because the patients develop an immune response to reject the vector, and, in some cases, the normal protein. Mild improvements have been short-lived, or affect only small patches of cells in



the respiratory tract. Alternative approaches to better understanding the physiology of the disease to direct drug design seem more viable. To this end, a mouse model with an inactivated CFTR gene is used to test potential drugs. SEE ALSO BACTERIAL GENETICS; BIOINFORMATICS; CLONE; DNA SEQUENCING; FORENSIC DNA ANALYSIS; GENE THERAPY; GENETIC DISEASES; GENOME; GENOMICS; HUMAN GENOME PROJECT; RADIATION HYBRID MAPPING; REVERSE TRANSCRIPTASE; TRANSGENIC TECHNIQUES

John Merriam

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Remote Sensing

At its simplest definition, remote sensing is obtaining information about an object by a device that is not in contact with the object. In ecology remote sensing usually involves sensors on satellite platforms or airplanes. Most devices have a series of sensors that record the intensity of **electromagnetic radiation** in particular segments of the spectrum for each point, or pixel, in an image. These sensors are designed to collect data in the visible wavelength as well as in other portions of the electromagnetic spectrum (such as the infrared region) that are needed to examine specific aspects of the physical world.

electromagnetic radiation light, X rays, and other forms of radiant energy

In addition to collecting data from a large part of the electromagnetic spectrum, remote sensing systems collect data over large areas. For instance, the U.S. *Landsat* satellites record continuous data over an area 71.4 square miles (185 square kilometers) wide. Since some satellites have been in orbit since the mid-1970s scientists can effectively "collect data" from this time period. Therefore, remote sensing offers scientists a wide spectral, spatial, and temporal data range.

For remote sensing to be of use to ecologists the spectral data must be related to some ground-based measurement such as land cover type or vegetation characteristics (biomass or net primary production, **evapotranspiration** rates, water stress, vegetation structure). Most work in ecology is done at the scale of a small plot, or piece of a field or forest. It can be difficult to extrapolate these small-scale measurements to larger, **heterogeneous** areas. Because sensors record continuous data over large areas, remote sensing can be used to "scale-up" plot-based measurements to examine landscape or even regional patterns. For example, ecologists have used remote sensing data to determine the rate at which rainforest in Brazil is being converted to agricultural land. In North America, scientists using satellite data have determined that one of the most endangered **ecosystems**, the tallgrass prairie, is being replaced by woody vegetation at an alarming rate.

evapotranspiration loss of water from a plant by evaporation within the leaf

heterogeneous composed of or containing different parts or types

ecosystem an ecological community and its environment

Another set of questions that can be addressed with remote sensing data involves landscape heterogeneity. In these analyses, any of a number of spatial statistics can be applied to the original spectral data. Also, the original bands can be recombined to create indices. The most common of these is the Normalized Difference Vegetation Index, a ratio of red to near infrared bands, which has been useful in quantifying vegetation in numerous locations around the world.

Spectral data can be analyzed directly (total infrared reflected) or a classification can be performed on the data. With this method, the spectral data are analyzed and each pixel is assigned to a land cover type: forest, grassland, or urban. For instance, forests reflect less infrared than grasslands. These land cover data can then be incorporated into a Geographical Information System (GIS) for further analysis. A GIS is a computer-based system that can deal with virtually any type of information that can be referenced by geographical location.

Once the land cover types are identified and GIS coverage is generated, additional data such as soil type, elevation, and land use history can be entered into the GIS. Ecologists can then ask questions about landscape-level patterns such as the average patch size of a certain land cover type or its dispersion across the landscape. This information can then be related to some ecological process such as the movement or dispersal of animals. SEE ALSO ECOLOGY; ECOSYSTEM; GRASSLAND; LANDSCAPE ECOLOGY

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Replication

There is no more critical issue in the origin of life than a method for the faithful and timely replication of genetic information. Genes are encoded in deoxyribonucleic acid (DNA), which is made of four types of **nucleotides**, distinguished by the bases adenine (A), guanine (G), cytosine (C), and thymine (T). When James Watson and Francis Crick discovered the double helical structure of deoxyribonucleic acid (DNA), they also recognized that DNA replication could occur by opening the double helix into single strands, and from those **templates** creating new **complementary** strands by the principle of **base pairing**. As an overview, their proposal was correct. The details of the chemistry, of the **enzymes** involved, and of the structure on which replication occurs tell a fascinating story that is far more complex than Watson and Crick anticipated.

nucleotide the building block of RNA or DNA

template master copy

complementary matching opposite

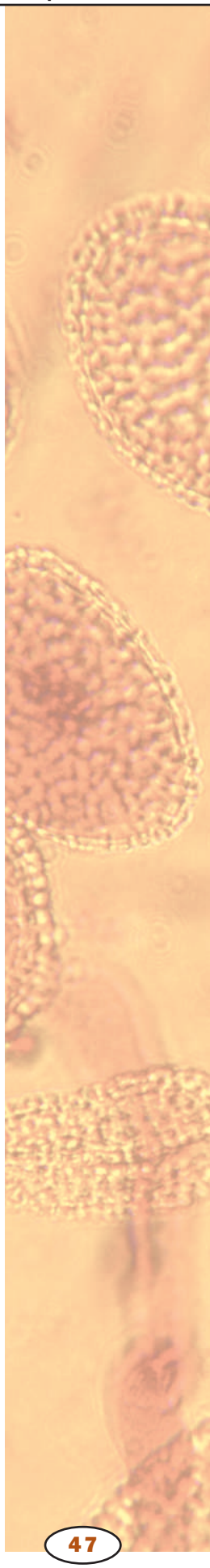
base pair two nucleotides (either DNA or RNA) linked by weak bonds

enzyme protein that controls a reaction in a cell

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

Semiconservative Replication

Chromosomes are the extended molecules of DNA that carry genes in both bacteria and eukaryotes. Bacterial **chromosomes** are usually circular, with



the double helix looping around to make a complete circle. Eukaryotic chromosomes are linear, with the double helix sealing up at the two distant ends. In both cases, the result of replication is that one double helix with its two complementary strands of nucleotides becomes two identical double helices with the same sequence of nucleotides. In this way, the genetic material of a cell is passed along unchanged through all the descendants of the original cell (except for replication errors or other mutations).

Each new helix includes one original side and one new side, and so the replication process is said to be "semiconservative." Semiconservative replication was discovered by Matthew Meselson and Frank Stahl, who grew bacteria with radioactive nucleotides. Fully radioactive chromosomes became half as radioactive after one round of replication, indicating that half the original chromosome was preserved in each new copy.

Replication Forks and Accessory Enzymes

Replication is a huge task, whether in bacteria or in eukaryotes. There are several physical and biochemical challenges the cell must overcome. First, the site or sites at which to begin replication must be located and the proper enzymes collected there. Second, the double helix must be unwound to expose the two strands. This imposes twisting strain on the portions of the helix farther away from the unwinding site, much like untangling a twisted phone cord does, and those forces must be relieved to prevent breakage of the DNA strands. Complementary nucleotides must be put in place and linked to form a new strand, and errors must be checked and corrected.

The orientation of the two strands poses an additional challenge. Because of the way the deoxyribose sugar is structured, the sugar, and hence the whole DNA strand, has a direction, an up versus down, so to speak. The two sides are oriented with up and down directions opposite, in a so-called antiparallel fashion. In biochemical terms, one direction is 5′-3′ ("five-prime to three-prime"), while the other side is oriented 3′-5′. The consequence of this arises because the enzymes that perform replication only function in one direction. The solution to this problem is discussed below.

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

Much of the understanding of DNA replication has come from studying the bacterium *Escherichia coli*. In bacterial chromosomes one site, called the origin of replication, has a sequence of base pairs to which an initiator **protein** binds. The initiator protein attracts enzymes called helicases that interrupt base pairing in a way that separates the double helix into a short region of two single strands. Other binding proteins then attach to maintain the single strand separation on the double-stranded region. Adjacent to the single-stranded region, an enzyme called gyrase cleaves and reforms the sugar-phosphate backbones in the double strand helix, which relieves the strain that the single strand separation causes. Separating the double-stranded helix into a region of two single strands creates a "replication bubble" initially of a few hundred nucleotides. Within the replication bubble, each strand serves as the template for a new chain; these chains grow in opposite directions because the templates have opposite 5′to 3′polarity. As the chains elongate, the replication bubble expands in both directions, and the ends become known as replication forks. As replication occurs, the helicase molecules are pushed toward the fork where the double strand separates into

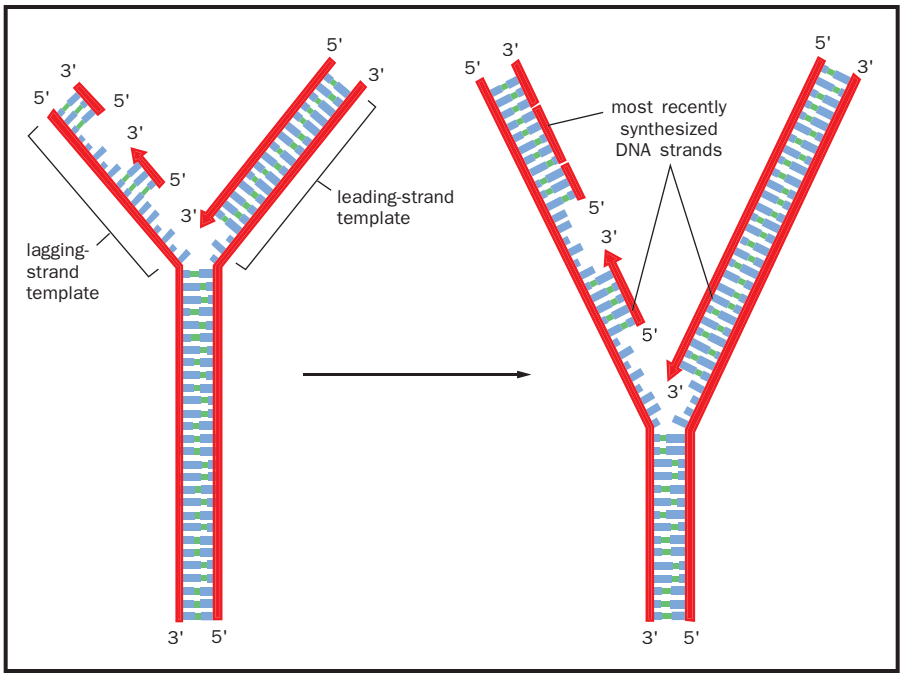


Figure 1. Replication adds a free nucleotide to the 3′ OH group of the last nucleotide in the growing chain of DNA.

single strands, thus moving the fork and extending the region of single strands.

Priming and Elongation

E. coli use three enzymes for replications, called *pol I*, *pol II*, and *pol III*. Early work with *pol I* showed that replication adds a free nucleotide to the 3′OH group of the last nucleotide in the growing chain (see Figure 1). Each nucleotide-added hydrogen bonds to the complementary nucleotide in the template single strand. The 3′OH of the last nucleotide attacks the high-energy triphosphate group at the 5′position of the free nucleotide, splitting off two phosphates and forming a covalent bond to the innermost phosphate. This binds the new nucleotide to the existing chain.

Some anticancer and antiviral drugs are nucleotides missing the 3′ OH. Such "dideoxy" nucleotides shut down replication after being incorporated into the strand. Fast-replicating DNA in cancer cells or viruses is inactivated by these drugs.

polymerase enzyme complex that synthesizes DNA or RNA from individual nucleotides

To begin elongation, DNA **polymerases** require an existing chain with a 3′ OH end. This posed the problem of how replication could ever begin, since the needed 3′ OH is on the newly replicated strand. The key to understanding the initiation of replication came with the discovery of ribonucleic acid (RNA) priming, which does not require an existing 3′ OH to start the process. In priming, an enzyme called primase places a short sequence of RNA nucleotides into position at the origin of replication. This sequence is complementary to the 3′end of the single-stranded portion of the template at that point. DNA polymerase then adds nucleotides to the RNA's 3′OH, continuing replication, until they reach the end of the complementary template.

Since polymerase only elongates in a 5′to 3′direction, at each replication fork only one chain is elongating in a smooth, unbroken fashion. The

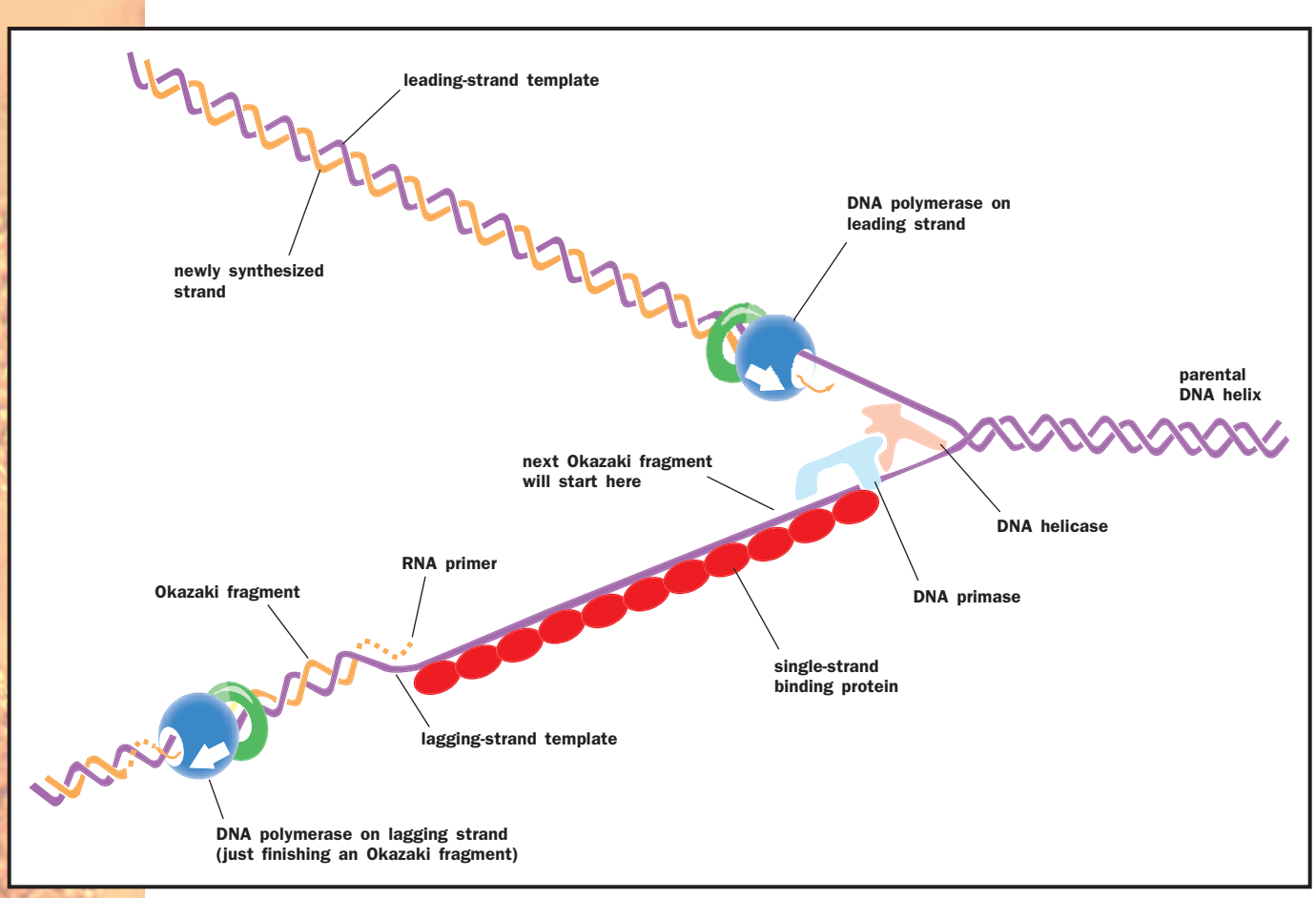


Figure 2. The proteins at a DNA replication fork.

primer short nucleotide sequence that helps begin DNA replication

catalyze aid in the reaction of

continuous elongation product is termed the "leading strand," while the discontinuous product is the "lagging strand." For every new section on the lagging strand, primase creates a new RNA **primer** and 3′OH end to start DNA chain elongation. Called Okazaki fragments after their discoverer, each short fragment lasts only a brief period before the primer ribonucleotides are digested and replaced with DNA nucleotides, which are then ligated ("tied") to the adjacent nucleotides by DNA ligase. Ligation of the Okazaki fragments into long chains completes synthesis of the lagging strand (see Figure 2). The *pol III* enzyme is a large complex of subunits that **catalyzes** both leading-strand and lagging-strand elongation and has roles in proofreading and replacing mismatched nucleotides. The *pol I* enzyme digests the RNA nucleotides and replaces them with DNA nucleotides; it also proofreads and replaces incorrect with correct nucleotides. It is thought that *pol II* mostly repairs replication errors.

Replication in the *E. coli* chromosome is bidirectional and continues in opposite directions until the two replication forks meet about halfway around the circular chromosome. Replication is then complete.

Special Features of Eukaryotic Replication

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

Replication of eukaryotic chromosomes is more complex inasmuch as they are linear (versus circular) and usually much larger than bacterial chromosomes. DNA replication is restricted to the S, or synthesis, phase during the **cell cycle**, between mitotic divisions. As a result of replication, each chro-

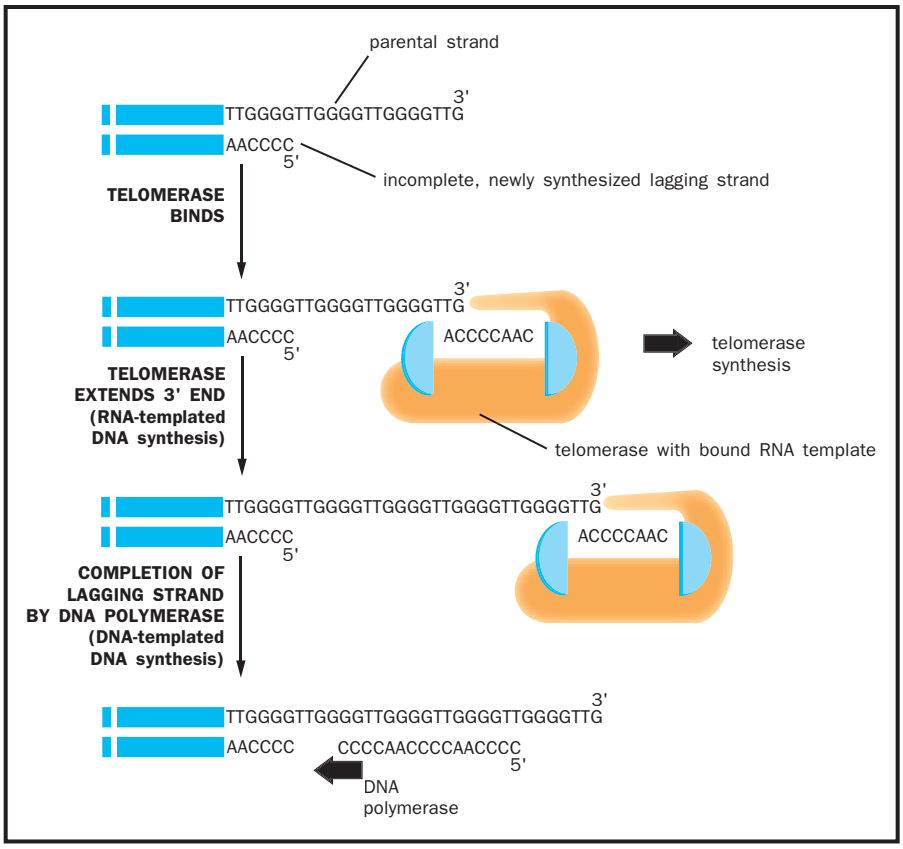


Figure 3. Telomerase is a hybrid protein-RNA molecule; the RNA sequence is complementary to several repeat lengths of the telomeric DNA. The telomerase uses the RNA sequence to bind to the template end of telomeric DNA, and uses the overhang protein portion to add DNA nucleotides to the template, extending it beyond its normal length.

mosome consists of two identical **chromatids** joined together, which are then separated into daughter cells by mitotic division.

chromatid a replicated chromosome before separation from its copy

Instead of a single origin of replication, as in bacteria, eukaryotic chromosomes have many origins for each chromosome in keeping with their much larger size. Replication proceeds bidirectionally from each origin until it meets the replication fork from the adjacent origin. A replicon refers to the interval replicated from one origin. This concept is shaky, however, since there is evidence that origins of replication are somewhat specific to the stage and tissue the cells are in, rather than being a permanent physical property. For example, nuclei in the *Drosophila* embryo divide every nine minutes initially. This requires the fastest replication of chromosomes known and utilizes many origins. Later stages use fewer origins.

Eukaryotes have five polymerases, termed alpha, beta, gamma, delta, and epsilon. Replication of nuclear DNA utilizes the alpha and delta polymerases. Alpha polymerase is a complex of several subunits, one of which has primase activity when it is in the complex. The alpha polymerase is thought to carry out synthesis of the lagging strand, whereas the delta polymerase, also a complex of subunits but lacking primase activity, carries out synthesis of the leading strand. As in the **prokaryotes**, helicase and gyrase are required to unwind the double helix ahead of the replication fork. The alpha and delta polymerases function in proofreading and correction as well. The beta and epsilon polymerases are thought to carry out nuclear DNA repair. The gamma polymerase replicates the **mitochondrial genome**. It lacks the error correction mechanism of the other polymerases, with the re-

prokaryote single-celled organism without a nucleus

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

genome total genetic material in a cell or organism

sult that the mutation rate in mitochondrial replication is substantially higher than it is in replication of nuclear DNA.

Telomeres and Telomerase

Because eukaryotic chromosomes are linear and have ends, another enzyme, called telomerase, is necessary but is not found in the prokaryotes. The problem with chromosome ends, called telomeres, is that the 3′template for the lagging strand cannot be primed at the last nucleotides because there is no further DNA on which to build. By itself, this would reduce the length of the lagging strand and the chromosome would get shorter at each replication. Telomeric DNAs, which are repeats of a specific sequence of six nucleotides, are normally present at the ends of chromosomal DNA and avoid this problem. Telomerase is a **hybrid** protein-RNA molecule; the RNA sequence is complementary to several repeat lengths of the telomeric DNA. The telomerase uses the RNA sequence to bind to the template end of telomeric DNA and uses the overhang protein portion to add DNA nucleotides to the template, extending it beyond its normal length. With several movements of the enzyme outward and reiterations of this process, the template 3′end is extended sufficiently to allow DNA polymerase to complete synthesis of a normal length lagging strand. In multicellular organisms, **somatic** cells usually cease mitotic division during development and lack telomerase activity thereafter. Cancer cells abnormally turn their telomerase back on, which enables the cell to divide continually. Telomerase is a target of drug research for the combat of cancer. SEE ALSO BACTERIAL CELL; CELL CYCLE; CHROMOSOME, EUKARYOTIC; DNA; NUCLEOTIDES; RNA; TRANSCRIPTION

hybrid combination of two different types

somatic nonreproductive; not an egg or sperm

John Merriam

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Reproduction in Plants

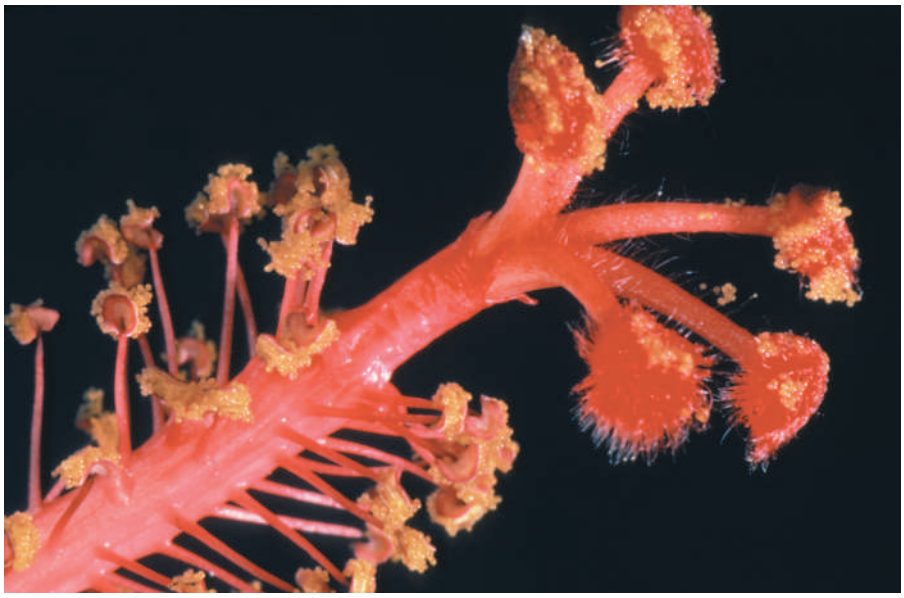
Plant reproduction is the process by which plants generate new individuals, or offspring. Reproduction is either sexual or asexual. Sexual reproduction is the formation of offspring by the fusion of **gametes**. Asexual reproduction is the formation of offspring without the fusion of gametes. Sexual reproduction results in offspring genetically different from the parents. Asexual offspring are genetically identical except for mutation. In higher plants, offspring are packaged in a protective seed, which can be long lived and can disperse the offspring some distance from the parents. In flowering plants (angiosperms), the seed itself is contained inside a fruit, which may protect the developing seeds and aid in their dispersal.

gamete reproductive cell, such as sperm or egg

Sexual Reproduction in Angiosperms: Ovule Formation

All plants have a life cycle that consists of two distinct forms that differ in size and the number of **chromosomes** per cell. In flowering plants, the

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



A hibiscus flower, showing anthers, five stigmas, and pollen.

large, familiar form that consists of roots, shoots, leaves, and reproductive structures (flowers and fruit) is **diploid** and is called the sporophyte. The sporophyte produces **haploid** microscopic **gametophytes** that are dependent on tissues produced by the flower. The reproductive cycle of a flowering plant is the regular, usually seasonal, cycling back and forth from sporophyte to gametophyte.

diploid having pairs of chromosomes in the nucleus

haploid having single, nonpaired chromosomes in the nucleus

gametophyte a haploid plant that makes gametes by mitosis

The flower produces two kinds of gametophytes, male and female. The female gametophyte arises from a cell within the **ovule**, a small structure within the ovary of the flower. The ovary is a larger structure within the flower that contains and protects usually many ovules. Flowering plants are unique in that their ovules are entirely enclosed in the ovary. The ovary itself is part of a larger structure called the carpel, which consists of the stigma, style, and ovary. Each ovule is attached to ovary tissue by a stalk called the funicle. The point of attachment of the funicle to the ovary is called the placenta.

ovule multicellular structure that develops into a seed after fertilization

As the flower develops from a bud, a cell within an ovule called the archespore enlarges to form an embryo-sac mother cell (EMC). The EMC divides by **meiosis** to produce four megaspores. In this process the number of chromosomes is reduced from two sets in the EMC to one set in the megaspores, making the megaspores haploid. Three of the four megaspores degenerate and disappear, while the fourth divides mitotically three times to produce eight haploid cells. These cells together constitute the female gametophyte, called the embryo sac.

meiosis cell division that forms eggs or sperm

The eight embryo sac cells differentiate into two synergids, three antipodal cells, two fused **endosperm** nuclei, and an egg cell. The mature embryo sac is situated at the outer opening (micropyle) of the ovule, ready to receive the sperm cells delivered by the male gametophyte.

endosperm nutritive tissue within a seed

Pollen

The male gametophyte is the mature pollen grain. Pollen is produced in the anthers, which are attached at the **distal** end of filaments. The filament and

distal away from

anther together constitute the stamen, the male sex organ. Flowers usually produce many stamens just inside of the petals. As the flower matures, cells in the anther divide mitotically to produce pollen mother cells (PMC). The PMCs divide by meiosis to produce haploid microspores in groups of four called tetrads. The microspores are housed within a single layer of cells called the tapetum, which provides nutrition to the developing pollen grains.

Each microspore develops a hard, opaque outer layer called the exine, which is constructed from a **lipoprotein** called sporopollenin. The exine has characteristic pores, ridges, or projections that can often be used to identify a species, even in fossil pollen. The microspore divides mitotically once or twice to produce two or three haploid nuclei inside the mature pollen grain. Two of the nuclei function as sperm nuclei that can eventually fuse with the egg and endosperm nuclei of the embryo sac, producing an embryo and endosperm, respectively.

lipoprotein combination of protein and lipid, or fatlike molecule

For sexual fusion to take place, however, the pollen grain must be transported to the stigma, which is a receptive platform on the top of the style, an elongated extension on top of the carpel(s). Here the moist surface or chemicals cause the pollen grain to germinate. Germination is the growth of a tube from the surface of a pollen grain. The tube is a sheath of **pectin**, inside of which is a solution of water, **solutes**, and the two or three nuclei, which lack any cell walls. Proper growth of the pollen tube requires an **aqueous** solution of appropriate solute concentration, as well as nutrients such as boron, which may aid in its synthesis of pectin.

pectin carbohydrate in plants that forms crosslinks to stabilize cell walls

solute dissolved substance

aqueous watery or water-based

At the apex of the tube are active ribosomes and **endoplasmic reticulum** (types of cell **organelles**) involved in **protein** synthesis. Pectinase and a glucanase (both **enzymes** that break down **carbohydrates**) probably maintain flexibility of the growing tube and aid in penetration. The pollen tube apex also releases ribonucleic acid (RNA) and ribosomes into the tissues of the style. The tube grows to eventually reach the ovary, where it may travel along intercellular spaces until it reaches a placenta. Through chemical recognition, the pollen tube changes its direction of growth and penetrates through the placenta to the ovule. Here the tube reaches the embryo sac lying close to the micropyle, and sexual fertilization takes place.

endoplasmic reticulum network of membranes within the cell

organelle membrane-bound cell compartment

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

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

Double Fertilization

Fertilization in flowering plants is unique among all known organisms, in that not one but two cells are fertilized, in a process called double fertilization. One sperm **nucleus** in the pollen tube fuses with the egg cell in the embryo sac, and the other sperm nucleus fuses with the diploid endosperm nucleus. The fertilized egg cell is a **zygote** that develops into the diploid embryo of the sporophyte. The fertilized endosperm nucleus develops into the **triploid** endosperm, a nutritive tissue that sustains the embryo and seedling. The only other known plant group exhibiting double fertilization is the Gnetales in the genus *Ephedra*, a nonflowering seed plant. However, in this case the second fertilization product degenerates and does not develop into endosperm.

nucleus membrane-bound portion of cell containing the chromosomes

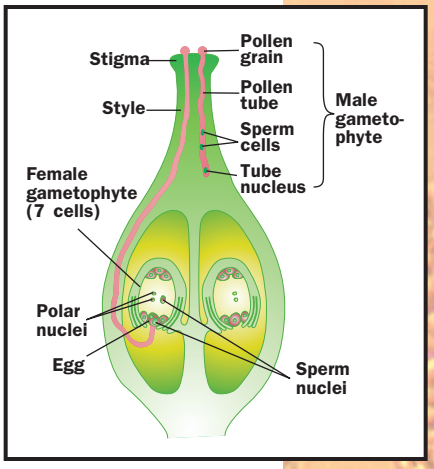
zygote fertilized egg

triploid possessing three sets of chromosomes

Double fertilization begins when the pollen tube grows into one of the two synergid cells in the embryo sac, possibly as a result of chemical attraction to calcium. After penetrating the synergid, the apex of the pollen tube breaks open, releasing the two sperm nuclei and other contents into

the synergid. As the synergid degenerates, it envelops the egg and endosperm cells, holding the two sperm nuclei close and the other expelled contents of the pollen tube. The egg cell then opens and engulfs the sperm cell, whose membrane breaks apart and allows the nucleus to move near the egg nucleus. The **nuclear envelopes** then disintegrate, and the two nuclei combine to form the single diploid nucleus of the zygote. The other sperm cell fuses with the two endosperm nuclei, forming a single triploid cell, the primary endosperm cell, which divides mitotically into the endosperm tissue.

Double fertilization and the production of endosperm may have contributed to the great ecological success of flowering plants by accelerating the growth of seedlings and improving survival at this vulnerable stage. Faster seedling development may have given flowering plants the upper hand in competition with gymnosperm seedlings in some habitats, leading to the abundance of flowering plants in most temperate and tropical regions. **Gymnosperms** nevertheless are still dominant at higher elevations and latitudes, and at low elevations in the Pacific Northwest coniferous forests, such as the coastal redwoods. The reasons for these patterns are still controversial.



Anatomy of the reproductive organs in angiosperms.

The Seed

The seed is the mature, fertilized ovule. After fertilization, the haploid cells of the embryo sac disintegrate. The maternally derived diploid cells of the ovule develop into the hard, water-resistant outer covering of the seed, called the testa, or seed coat. The diploid zygote develops into the embryo, and the triploid endosperm cells multiply and provide nutrition. The testa usually shows a scar called the hilum where the ovule was originally attached to the funicle. In some seeds a ridge along the testa called the raphe shows where the funicle originally was pressed against the ovule. The micropyle of the ovule usually survives as a small pore in the seed coat that allows passage of water during germination of the seed.

nuclear envelope double membrane surrounding the cell nucleus

gymnosperms "naked seed" plants, including conifers

In some species, the funicle develops into a larger structure on the seed called an aril, which is often brightly colored, juicy, and contains sugars that are consumed by animals that may also disperse the seed (as in nutmeg, arrowroot, oxalis, and castor bean). This is distinct from the fruit, which forms from the ovary itself.

The embryo consists of the **cotyledon(s)**, epicotyl, and hypocotyl. The cotyledons resemble small leaves, and are usually the first photosynthetic organs of the plant. The portion of the embryo above the cotyledons is the epicotyl, and the portion below is the hypocotyl. The epicotyl is an **apical meristem** that produces the shoot of the growing plant and the first true leaves after germination. The hypocotyl develops into the root. Often the tip of the hypocotyl, the radicle, is the first indication of germination as it breaks out of the seed. Flowering plants are classified as monocotyledons or dicotyledons (most are now called **eudicots**) based on the number of cotyledons produced in the embryo. Common monocotyledons include grasses, sedges, lilies, irises, and orchids; common dicotyledons include sunflowers, roses, legumes, snapdragons, and all nonconiferous trees.

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

apical meristem growing tip from which all plant tissues arise

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

The endosperm may be consumed by the embryo, as in many legumes, which use the cotyledons as a food source during germination. In other species the endosperm persists until germination, when it is used as a food

reserve. In grains such as corn and wheat, the outer layer of the endosperm consists of thick-walled cells called aleurone, which are high in protein.

The Fruit

The fruit of a flowering plant is the mature ovary. As seeds mature, the surrounding ovary wall forms a protective structure that may aid in dispersal. The surrounding ovary tissue is called the pericarp and consists of three layers. From the outside to inside, these layers are the exocarp, mesocarp, and endocarp. The exocarp is usually tough and skinlike. The mesocarp is often thick, succulent, and sweet. The endocarp, which surrounds the seeds, may be hard and stony, as in most species with fleshy fruit, such as apricots.

aggregate clump together

inflorescence characteristic arrangement of flowers on a stalk

A fruit is termed simple if it is produced by a single ripened ovary in a single flower (apples, oranges, apricots). An **aggregated** fruit is a cluster of mature ovaries produced by a single flower (blackberries, raspberries, strawberries). A multiple fruit is a cluster of many ripened ovaries on separate flowers growing together in the same **inflorescence** (pineapple, mulberry, fig). A simple fruit may be fleshy or dry. A fleshy simple fruit is classified as a berry (grape, tomato, papaya), pepo (cucumber, watermelon, pumpkin), hesperidium (orange), drupe (apricot), or pome (apple).

Dry simple fruits have a dry pericarp at maturity. They may or may not dehisce, or split, along a seam to release the seeds. A dehiscent dry fruit is classified as legume or pod (pea, bean), silique or silicle (mustard), capsule (poppy, lily), or follicle (milkweed, larkspur, columbine). An indehiscent dry fruit that does not split to release seeds is classified as an achene (sunflower, buttercup, sycamore), grain or caryopsis (grasses such as corn, wheat, rice, barley), schizocarp (carrot, celery, fennel), winged samara (maple, ash, elm), nut (acorn, chestnut, hazelnut), or utricle (duckweed family). Some fruiting bodies contain non-ovary tissue and are sometimes called pseudocarps. The sweet flesh of apples and pears, for example, is composed not of the pericarp but the receptacle, or upper portion, of the flowering shoot to which petals and other floral organs are attached.

Fruiting bodies of all kinds function to protect and disperse the seeds they contain. Protection can be physical (hard coverings) or chemical (repellents of seed predators). Sweet, fleshy fruits are attractive food for birds and mammals that consume seeds along with the fruit and pass the seeds intact in their fecal matter, which can act as a fertilizer. Dry fruits are usually adapted for wind dispersal of seeds, as for example with the assistance of winglike structures or a fluffy pappus that provides buoyancy. The diversity of fruiting bodies reflects in part the diversity of dispersal agents in the environment, which select for different fruit size, shape, and chemistry.

Pollination and Pollinators

Pollination is the movement of pollen from the stamens to the stigma, where germination and growth of the pollen tube occur. Most (approximately 96 percent) of all flowering plant species are hermaphroditic (possess both sexual functions within a plant, usually within every flower), and thus an individual can be pollinated by its own pollen or by pollen from another individual. Seed produced through self-pollination ("selfed" seed) is often inferior in growth, survival, and **fecundity** to seed produced through **outcross** pollination ("outcrossed" seed). As a result, in most species there is

fecundity ability to reproduce

outcross fertilization between two different plants

strong natural selection to maximize the proportion of outcrossed seed (the "outcrossing rate").

Flowering plants are unusual among seed plants in their superlative exploitation of animals (primarily insects) as agents of outcross pollination. The outcross pollination efficiency of insects, birds, and mammals (primarily bats) may have contributed to both the abundance and diversity of flowering plants. Abundance may have increased because of less wastage of energy and resources on unsuccessful pollen and ovules. Diversity may have increased for two reasons. First, insects undoubtedly have selected for a wide variety of floral forms that provide different rewards (pollen and nectar) and are attractive in appearance (color juxtaposition, size, shape) and scent (sweet, skunky) in different ways to different pollinators. Second, faithfulness of pollinators to particular familiar flowers may have reduced hybridization and speeded evolutionary divergence and the production of new species.

Some insect groups, such as bees, originated after flowering plants, their members developing mouthpart structures and behavior specialized for pollination.

Although flowering plants first appeared after most of the major groups of insects had already evolved, flowering plants probably caused the evolution of many new species within these groups. Some new insect groups, such as bees and butterflies, originated after flowering plants, their members developing mouthpart structures and behavior specialized for pollination. In extreme cases, a plant is completely dependent on one insect species for pollination, and the insect is completely dependent on one plant species for food. Such tight interdependency occurs rarely but is well documented in yuccas/yucca moths, senita cacti/senita moths, and fig trees/some fig wasps. In all three insects, females lay eggs in the flowers, and their young hatch later to feed on the mature fruit and its contents. Females ensure that the fruit develops by gathering pollen from another plant and transporting it to the stigma of the flower holding their eggs. Plants benefit greatly in outcrossed seed produced, at the small cost of some consumed fruit and seeds, and the insects benefit greatly from the food supply for developing larvae at the small cost of transporting pollen the short distances between plants.

Pollinating agents, whether **biotic** or **abiotic**, have exerted strong selection on all aspects of the flower, resulting in the evolution of tremendous floral diversity. This diversity has been distilled into a small number of characteristic pollination syndromes.

biotic living

abiotic nonliving

Pollination by beetles selects usually for white color, a strong fruity scent, and a shallow, bowl-shaped flower. Bees select for yellow or blue/purple colorings, a landing platform with color patterns that guide the bee to nectar (often reflecting in the ultraviolet range of the spectrum), bilateral symmetry, and a sweet scent. Butterflies select for many colors other than yellow, a corolla (petal) tube with nectar at the base, and the absence of any scent. Moths in contrast select for **nocturnally** opening flowers with a strong scent and drab or white color, and also a tube with nectar at the base. Bats select also for nocturnally opening flowers, but with a strong musky scent and copious nectar, positioned well outside the foliage for easy access, and drab or white color. Hummingbirds select for red or orange flowers with no scent, copious nectar production, and a corolla tube with nectar at the base. Other pollinating birds that do not hover while feeding select for strong perches and flowers capable of containing copious nectar (tubes, funnels, cup shapes).

nocturnally at night

Wind as a pollinating agent selects for lack of color, scent, and nectar; small corolla; a large stigmatic surface area (usually feathery); abundantly produced, buoyant pollen; and usually erect styles and limp, hanging stamens. In addition there is great floral diversity within any of these syndromes, arising from the diverse evolutionary histories of the member plant species.

Selfing and Outcrossing

Most flowering plant species reproduce primarily by outcrossing, including the great majority of trees, shrubs, and perennial herbs. Adaptations that prevent self-fertilization include self-incompatibility (genetic recognition and blocking of self-pollen) and dioecy (separate male and female individuals). Adaptations that reduce the chances of self-pollination in **hermaphrodites** include separation of the anthers and stigma in space (herkogamy) or time (dichogamy). In many species, both self-incompatibility and spatiotemporal separation of the sex organs occur.

hermaphrodite organism possessing both male and female reproductive structures

The ability to produce seeds by selfing, however, is advantageous in situations where outcrossing pollination is difficult or impossible. These include harsh environments where pollinators are rare or unpredictable, and regularly disturbed ground where survivors often end up isolated from each other. Selfing is also cheaper than outcrossing, because selfers can become pollinated without assistance from animals and therefore need not produce large, attractive flowers with abundant nectar and pollen rewards.

Most primarily selfing species are small annuals in variable or disturbed habitats, with small, drab flowers. Most desert annuals and roadside weeds, for example, are selfers. The evolutionary transition from outcrossing to near-complete selfing has occurred many times in flowering plants.

Outcrossing and selfing species differ in their evolutionary potential. Outcrossers are generally more genetically diverse and produce **lineages** that persist over long periods of evolutionary time, during which many new species are formed. Selfers, however, are less genetically diverse and tend to accumulate harmful mutations. They typically go extinct before they have an opportunity to evolve new species.

lineage ancestral line

Asexual Reproduction

The ability to produce new individuals asexually is common in plants. Under appropriate experimental conditions, nearly every cell of a flowering plant is capable of regenerating the entire plant. In nature, new plants may be regenerated from leaves, stems, or roots that receive an appropriate stimulus and become separated from the parent plant. In most cases, these new plants arise from undifferentiated parenchyma cells, which develop into buds that produce roots and shoots before or after separating from the parent.

New plants can be produced from aboveground or belowground horizontal runners (stolons of strawberries, rhizomes of many grasses), tubers (potato, Jerusalem artichoke, dahlia), bulbs (onion, garlic), corms (crocus, gladiola), bulbils on the shoot (lily, many grasses), parenchyma cells in the leaves (Kalanchoe, African violet, jade plant) and inflorescence (arrowhead). Vegetative propagation is an economically important means of replicating valuable agricultural plants, through cuttings, layering, and **grafting**. Veg-

grafting attachment and fusing of parts from different plants

etative reproduction is especially common in aquatic vascular plants (for example, surfgrass and eelgrass), from which fragments can break off, disperse in the current, and develop into new whole plants.

A minority of flowering plants can produce seeds without the fusion of egg and sperm (known as parthenocarpy or agamospermy). This occurs when meiosis in the ovule is interrupted, and a diploid egg cell is produced, which functions as a zygote without fertilization. Familiar examples include citrus, dandelion, hawkweed, buttercup, blackberry/raspberry, and sorbus. Agamospermous species are more common at high elevations and at high latitudes, and nearly all have experienced a doubling of their chromosome number (tetraploidy) in their recent evolutionary history. These species experience evolutionary advantages and disadvantages similar to those of selfers.

Evolutionary Significance of Plant Reproduction Strategies

The attractive, colorful, and unique features of the most abundant and diverse group of land plants—the flowering plants—are believed to have evolved primarily to maximize the efficiency and speed of outcross reproduction. Each major burst of angiosperm evolution was a coevolutionary episode with associated animals, primarily insects, which were exploited to disperse pollen and seeds in ever more efficient and diverse ways.

The first major burst of flowering plant evolution was the appearance of the closed carpel together with showy flowers that were **radially symmetrical**. The closed carpel prevented self-fertilization through recognition and blocking of self pollen within the specialized conducting tissue of the style. Insects attracted to the showy flowers carried pollen between plants less wastefully than wind, and the radial symmetry accommodated insects of many sizes and shapes.

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

The second major burst was the appearance of **bilaterally symmetrical** flowers, which happened independently in many groups of plants at the same time that bees evolved. Bilateral symmetry forced bees to enter and exit flowers more precisely, promoting even more efficient outcross pollen transfer.

bilaterally symmetric symmetric, or similar, across a central line

The third major burst of flowering plant evolution was the appearance of nutritious, fleshy fruits and seeds, coincident with a diversification of birds and rodents. The exploitation of vertebrates for fruit and seed dispersal resulted in less haphazard transport of offspring to neighboring populations of the same species (also visited as a food source), thereby reducing the chances that **progeny** inbreed with their siblings and parents and providing more assurance than wind currents that they find good habitat and unrelated mating partners of the same species. SEE ALSO ALTERNATION OF GENERATIONS; FLOWERS; FRUITS; PLANT NUTRITION; SEEDS

progeny offspring

Stewart T. Schultz

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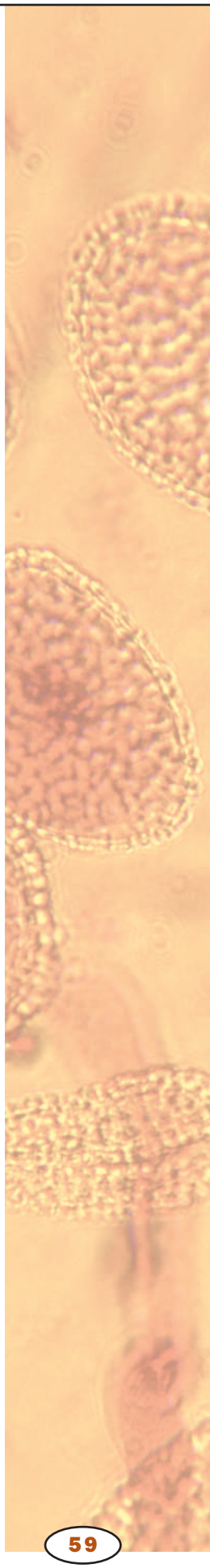

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Reproductive Technology

Reproductive technologies are medical procedures designed to help infertile people have children. These procedures include artificial insemination, *in vitro* **fertilization**, embryo adoption, and surrogate mothers.

fertilization union of sperm and egg

Artificial Insemination

In artificial insemination (AI), sperm are collected from a man and placed into the female's uterus by a reproductive specialist. AI is often used for men with low sperm counts, men with genetic disorders, and women who wish to become pregnant without a male partner. Sperm used in AI may come from a known donor or an anonymous sperm bank.

In Vitro Fertilization

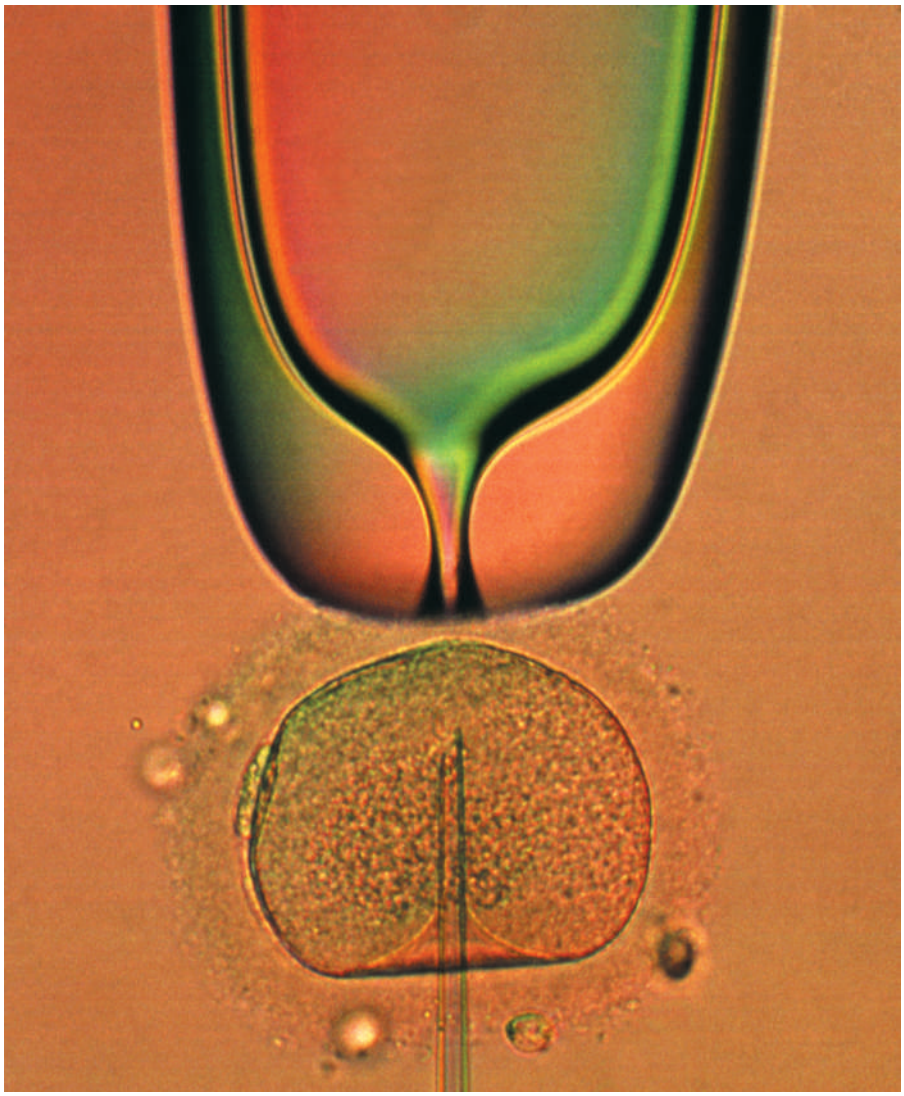
The first "test tube" baby, Louise Brown, was born in England in 1978. Since then, hundreds of thousands of babies have been born using *in vitro* fertilization and related techniques. *In vitro* (which means "in glass") fertilization (IVF) is often used for women with blocked or malfunctioning **fallopian tubes**, severe **endometriosis**, or unexplained infertility. Prior to IVF, a woman is given synthetic **hormones** that stimulate the maturation and release of a large number of eggs. The eggs are removed from the ovaries using an ultrasound-guided needle and combined with sperm in a laboratory dish. To increase the chances of pregnancy, four to six embryos are typically implanted into the woman's uterus when they are about three days old. Extra embryos may be frozen for later use.

fallopian tubes tubes through which eggs pass to the uterus

endometriosis disorder of the endometrium, the lining of the uterus

hormone molecule released by one cell to influence another

Since multiple embryos are implanted, there is an increased chance of multiple births and the associated risks to both mother and children. "Selective reduction," or abortion of one or more fetuses, may be used to reduce the number of multiples. IVF is expensive ($8,000 to $10,000 per trial) and the likelihood of producing a child using IVF decreases with increased maternal age. In addition, the success rate is typically less than 20 percent, although it varies by clinic and is improving as the procedure becomes more common.



In vitro fertilization: a needle injecting sperm DNA into a human egg.

Gamete Intrafallopian Transfer. **Gamete** intrafallopian transfer (GIFT) is similar to IVF except that eggs and sperm are mixed and placed immediately into the woman's fallopian tubes using **laparoscopic surgery**. In **zygote** intrafallopian transfer (ZIFT), eggs and sperm are fertilized in the laboratory, but the resulting zygotes are not incubated and are placed in the woman's fallopian tubes rather than her uterus. Although more complicated, GIFT and ZIFT are thought to more closely simulate natural events and have a higher (5 to 10 percent higher) success rate than IVF. Unfortunately, women with severely diseased fallopian tubes cannot use them.

Intracytoplasmic Sperm Injection. In intracytoplasmic sperm injection (ICSI), a single sperm is injected directly into an egg using a tiny glass needle to create an embryo prior to *in vitro* fertilization. ICSI therapy can be used when sperm are scarce, have poor motility, or are otherwise unable to fertilize an egg. Because the procedure has only been in effect since the early 1990s, the side effects of ICSI are not well known but may include genetic or chromosomal abnormalities, major birth defects, and infertility (particularly in males).

gamete reproductive cell, such as sperm or egg

laparoscopic surgery surgery in which an instrument is inserted through a very small incision, usually guided by some type of imaging technique

zygote fertilized egg

Embryo Adoption

Embryo adoption is a procedure in which an embryo created from the egg of a woman and the sperm of a man is transferred into the uterus of another woman to be raised by her and her partner. Embryos for "pre-birth adoption" may be surplus frozen embryos from IVF donated by the genetic parents or embryos created specifically from egg and sperm donors. In both cases, the embryo has no genetic relationship to its parents.

Surrogate Mothers

A surrogate mother is a woman who signs a contract with a man to be artificially inseminated with his sperm, give birth to the child, then turn the child over to the man and his partner at birth. The man and his partner usually legally adopt the child. Alternately, embryos created through IVF can be implanted into a surrogate mother if the female partner is unable or unwilling to go through a pregnancy herself. Surrogate mothers are paid for their expenses and receive an additional fee. Agencies and/or lawyers are often involved in the process.

The use of reproductive technologies by single people, postmenopausal women, homosexual couples, and others is increasing since the technologies give people more choices about when and how to become a parent as well as some control over the genetic quality and even the sex of the offspring. However, reproductive technologies also bring with them complex social, psychological, and ethical considerations, and the multi-billion-dollar industry has little regulation. Egg, sperm, and embryo donors may worry about anonymity or being sued for child support. Children may want the right to know their medical history and perhaps their biological parents and siblings. Genetic or surrogate parents may want to claim the children they have helped produce. Couples may argue about custody of frozen embryos or disposal of extra or inferior embryos. Others may question the ethics of selling eggs, sperm, and "womb space." SEE ALSO Birth Control; Chromosome Aberrations; Clone; Female Reproductive System; Sexual Reproduction

Lynnette Danzl-Tauer

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Reptile

The class Reptilia is composed of about 5,100 species, organized in three very closely interrelated groups: the lizards (order Lacertilia), composed of about 3,165 species; the amphisbaenians (order Amphisbaenia), which con-

sist of about 135 species; and the snakes (order Serpentes), which contain about 1,800 species. According to most experts, lizards appeared in the fossil record in the middle Jurassic, about 165 million years ago (although some authorities place the earliest known fossil lizards in the late Permian, about 250 million years ago). Fossil amphisbaenians have been recorded as early as the late Cretaceous, over 65 million years ago. Snakes are known from the early Cretaceous, about 135 million years ago.

Research has shown that the separation of lizards and snakes into distinct orders is an unnatural artifact of outmoded scientific methodologies and does not reflect the evolutionary history of these animals; significant changes in the classification of the class Reptilia can be expected in the future. Members of the class Reptilia all share numerous characteristics (called synapomorphies) of physiology, behavior, and functional **morphology** that readily set them apart from amphibians, mammals, turtles, tuataras, and birds. One of the most striking of these is the presence in males of well-developed, paired copulatory organs called hemipenes (all other classes of terrestrial vertebrates have a single penis).

morphology related to shape and form

Two of the orders exhibit a combination of characteristics that generally permit ready identification: Lizards generally possess four limbs, ear openings, and eyelids, and snakes lack functional limbs, ear openings, and eyelids. Amphisbaenians differ substantially from lizards and snakes in many ways, most notably by their very short tails, distinctly annulated (ringed) bodies, and the reduction of the right lung (instead of the left lung, as in snakes and limbless lizards).

From small lizards such as geckos, with a snout-vent length sometimes as small as 1.5 centimeters (.59 inches), to the reticulated python of southeastern Asia that reaches 10 meters (32.8 feet) in total length, reptiles display an amazing diversity of size, shape, color, and pattern. Their beauty and comparative ease to maintain as pets has created an entirely new venture, distinct and separate from the science of herpetology, known as herpetoculture. Herpetoculturists worldwide are devoted to the husbandry of many reptiles (mostly snakes), breeding, trading, and selling captive reptiles for fun and profit. SEE ALSO AMPHIBIAN; CROCODILIANS; TUATARA; TURTLE;

Joseph T. Collins

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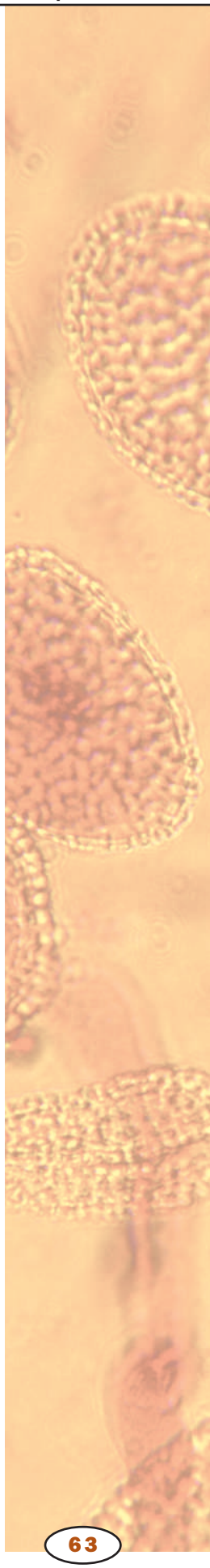
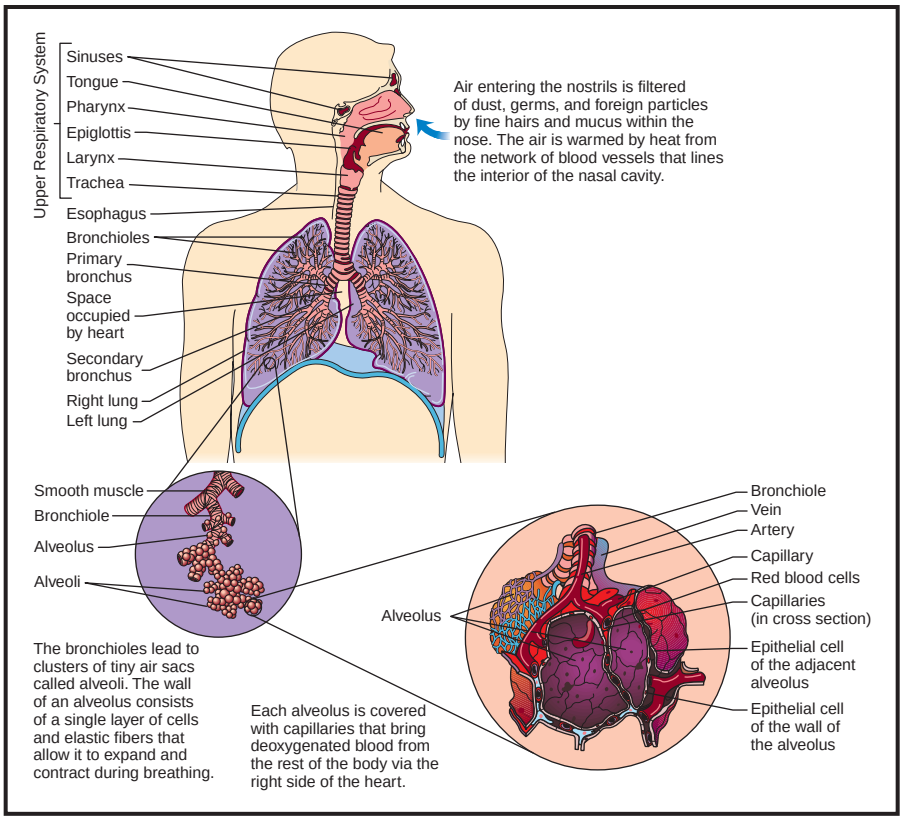
Respiration

Respiration refers to the mechanisms for obtaining oxygen from the air and delivering it to the tissues, while eliminating carbon dioxide from the body. It is related to cellular respiration, the biochemical processes that consume this oxygen and generate the carbon dioxide in the course of making adenosine triphosphate (**ATP**). Respiration in the former sense involves four processes: (1) breathing, or ventilation of the lungs; (2) gas exchange be-

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



The human respiratory system.



tween air and blood in the lungs; (3) gas transport in the blood; and (4) gas exchange between the blood and target tissues.

Respiratory Anatomy

pharynx throat

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

The respiratory system consists of: (1) the nasal cavity, which warms, cleans, and humidifies inhaled air; (2) the **pharynx**, where the respiratory and digestive systems meet and then diverge again; (3) the **larynx**, or voice box, which contains the vocal cords; (4) the trachea, or windpipe, a tube about 12 centimeters (4.7 inches) long and 2.5 centimeters (just less than an inch) wide that passes behind the heart and branches like a Y at its lower end; (5) bronchi and bronchioles, air tubes that begin at the fork of the trachea and divide into smaller and smaller divisions within each lung; and (6) alveoli, millions of tiny air sacs in the lung.

Except in the walls of the bronchi and bronchioles, the lungs have no muscle; they do not pump air in and out of themselves like the heart pumping blood, but are passively ventilated as the chest expands and contracts. The muscles that drive pulmonary ventilation are the diaphragm, a sheet of muscle between the thoracic and abdominal cavities; the intercostal muscles between the ribs; and other muscles of the abdomen and thorax that aid the primary respiratory muscles.

Pulmonary Ventilation

neuron nerve cell

Ventilation is a rhythmic process, like the heartbeat, but its pacemakers are in the brainstem rather than in the chest. The medulla oblongata of the brainstem contains an inspiratory center composed of **neurons** that send

signals to the diaphragm and external intercostal muscles. When these muscles are stimulated, they contract and enlarge the thoracic cavity. This creates a partial vacuum in the lungs. With the atmospheric pressure outside the body now greater than the pressure in the lungs, air flows "downstream" into the lungs and inflates them.

Usually no muscular effort is needed to exhale. When these muscles stop contracting, the elasticity of the thoracic cage (ribs, cartilages, diaphragm, and ligaments) causes it to spring back by itself, squeezing air out of the lungs. When one needs to exhale more deeply, however, the expiratory center of the medulla sends signals to the internal intercostal muscles, which pull the ribs downward and produce an extra degree of chest compression. The abdominal muscles also aid by increasing pressure in the abdominal cavity, pushing up on the diaphragm. These muscles are important in public speaking, singing, shouting, playing wind instruments, and blowing out candles, for example.

In normal, relaxed breathing, most adults inhale a tidal volume averaging 500 milliliters (16.9 fluid ounces) of air in each respiratory cycle. With maximum effort, however, one can inhale a greater amount called the vital capacity, averaging about 4,700 milliliters (almost 159 fluid ounces) in adults.

Pulmonary Gas Exchange

About 70 percent of the air a person inhales fills the millions of alveoli in the lungs. Each alveolus is surrounded by a basketlike mesh of blood capillaries. The wall separating the inhaled air from the blood is only 0.5 micrometer thick—only one-fifteenth the diameter of a single red blood cell—so it presents very little barrier to gas diffusion between the air and blood.

Oxygen has a concentration (partial pressure) of 104 mmHg in the alveolar air and 40 mmHg in the arriving capillary blood. Thus, it diffuses down its concentration **gradient** from the air, through the alveolar wall, into the blood. About 98.5 percent of this oxygen binds to the pigment **hemoglobin** in the red blood cells, and the other 1.5 percent dissolves in the blood plasma.

gradient difference in concentration between two places

hemoglobin oxygen-carrying protein complex in red blood cells

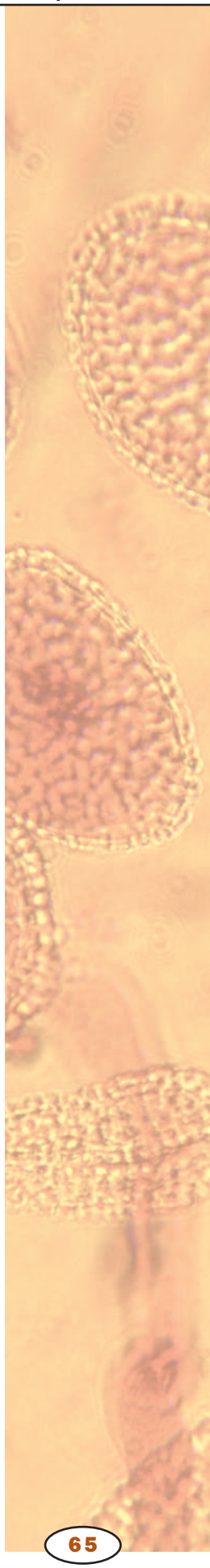
Carbon dioxide (CO_2), has a partial pressure of 46 mmHg in the arriving blood and 40 mmHg in the alveolar air, so its concentration gradient dictates that it diffuses the other way, from blood to air, and is then exhaled. About 70 percent of this CO_2 comes from the breakdown of carbonic acid in the blood; 23 percent from CO_2 bound to hemoglobin, albumin, and other blood **proteins**; and 7 percent from gas dissolved in the blood plasma.

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

Gas Transport

Blood leaving the lungs is therefore relatively high in O_2 (oxygen in its diatomic form) and low in CO_2. It travels via the pulmonary veins to the left side of the heart, which pumps it out into the **systemic** circulation. This division of the circulatory system delivers it to every organ of the body.

systemic throughout the body



Systemic Gas Exchange

When the blood reaches the systemic blood capillaries, gases undergo processes that are essentially the reverse of what occurs in the pulmonary alveoli. The blood unloads O_2, which diffuses into the tissue fluid and thus reaches the cells around the blood capillaries. At the same time, the CO_2 generated by the **metabolism** of those cells diffuses into the blood to be carried away to the lungs for disposal.

metabolism chemical reactions within a cell

Blood typically contains 95 mmHg O_2 upon arrival at the systemic capillaries and 40 mmHg O_2 upon leaving. Conversely, the blood has 40 mmHg of CO_2 on arrival at the systemic capillaries and typically 46 mmHg CO_2 when it leaves. The blood does not, however, unload the same amount of O_2 to all tissues or pick up the same amount of CO_2. The more active a tissue is, the warmer it is, the lower its O_2 level is, and the lower its **pH** is (because it generates more CO_2 and CO_2 reduces the pH of body fluids). Heat, low O_2, low pH, and other factors enhance O_2 unloading and CO_2 loading, so tissues that need the most oxygen and waste removal get more than less active tissues do. The biochemistry of hemoglobin is mainly responsible for this elegant adjustment of gas exchange to the individual needs of different tissues. SEE ALSO BLOOD; BLOOD VESSELS; BRAIN; GAS EXCHANGE; HEART AND CIRCULATION; OXIDATIVE PHOSPHORYLATION

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

Kenneth S. Saladin

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Retrovirus

Retroviruses are a unique class of single-stranded ribonucleic acid (RNA) containing viruses, which replicate their **genome** through a double-stranded viral deoxyribonucleic acid (DNA) intermediate in the **nucleus** of the host cell. This is in contrast to all other RNA-containing viruses that replicate their genomes through double-stranded RNA intermediates almost always in the **cytoplasm** of host cells. Most retroviruses contain an RNA genome of 9 to 10 **kilobases** in length, which encodes a minimum of three genes required for replication. These are referred to as *gag* (structural **proteins** of the virus), *pol* (enzymes involved in replication), and *env* (envelope glycoproteins required for the virus to attach to a receptor of a new host cell). Human immunodeficiency virus (HIV), which causes acquired immunodeficiency syndrome (AIDS), belongs to a subclass of retroviruses, the lentiviruses, which encode additional viral genes that permit the virus to grow in nondividing cells, such as white blood cells.

genome total genetic material in a cell or organism

nucleus membrane-bound portion of cell containing the chromosomes

cytoplasm material in a cell, excluding the nucleus

kilobase one thousand DNA bases; a measure of size of a piece of DNA

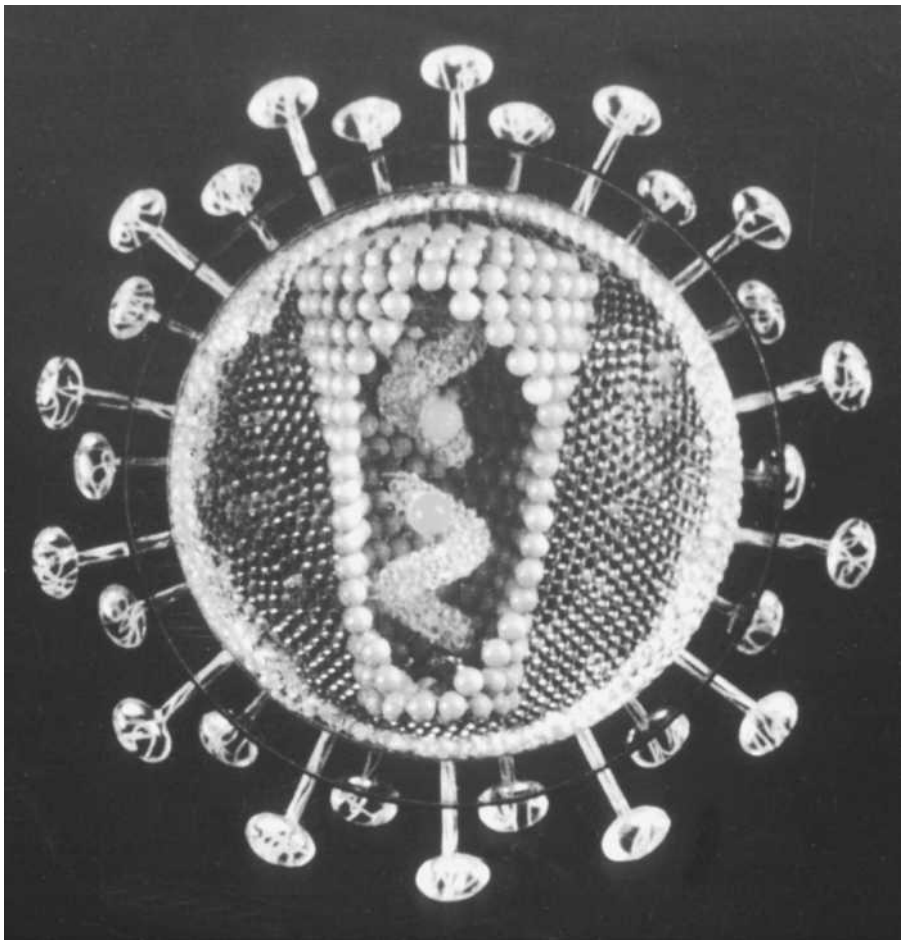
protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

enzyme protein that controls a reaction in a cell

reverse transcriptase enzyme that copies RNA into DNA

catalyze aid in the reaction of

The remarkable replication pathway of retroviruses requires that once the virus enters the host cell, a viral *pol* gene–encoded **enzyme** called **reverse transcriptase** (RT), which is packaged in virus particles, reverse transcribes the single-stranded RNA genome into a double-stranded DNA. This DNA intermediate migrates to the nucleus of the cell where it is integrated into the host cell genome. This process is **catalyzed** by another viral en-



Model of the human immunodeficiency virus (HIV). RNA is enclosed within proteins, surrounded by membrane and glycoproteins.

zyme called integrase (IN). Since there is no matching sequence between the viral DNA and the host genomic DNA, sites of insertion are mostly randomly distributed. Because the viral DNA is now part of the cellular **chromosome**, it is duplicated whenever the cell's own DNA is replicated.

Transcription of the viral sequence from the integrated DNA to make messenger RNA (mRNA) requires cellular enzymes. Full-length viral mRNA is transported to the cytoplasm where it is either packaged into **progeny** virus or translated on non-membrane-bound (free) **ribosomes** to yield viral Gag and Gag-Pol polyproteins (assemblies of many similar proteins). These polyproteins in turn migrate to the cell membrane where they assemble into virus particles, containing RNA, which bud from the cell surface. Concomitantly, viral glycoproteins are translated as polyproteins from a smaller-sized, spliced viral mRNA on membrane-bound ribosomes. These polyproteins are processed in the **endoplasmic reticulum**, where they also go through an additional modification known as glycosylation, in which sugar groups are added to the protein. When virus particles bud from the cell, they pinch off a portion of the cell membrane, containing the viral glycoproteins. This membrane becomes an outer coating of the virus particle.

The Gag and Gag-Pol polyproteins are cleaved into the mature-sized proteins during or immediately after the budding process by a third viral-encoded enzyme called protease (PR). Once the protein-cleaving proteolytic processing is complete, an infectious virus results, which can infect new cells.

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

progeny offspring

ribosome protein-RNA complex in cells that synthesizes protein

endoplasmic reticulum network of membranes within the cell

During an active infection process, approximately 1 percent of a cell's resources are diverted to synthesis of virus genomes and proteins. Infected cells are therefore not killed. Most retroviruses activate expression of a cancer-causing gene, called an "oncogene," which transforms host cells so that they become immortalized, providing a long-term home for the retrovirus. Lentiviruses, including HIV, do not transform cells. Instead they cause cell death in some of the cell types in which they replicate. When these cells are important components of the immune system, an infected person loses the ability to mount an effective immune response, resulting in AIDS. This leaves the person susceptible to almost any **opportunistic** infection. Patients with HIV infection are treated with drugs that inhibit either RT or PR to slow the spread of virus. As of May 2001, the treatment of choice for HIV patients included two RT inhibitors and one PR inhibitor, and is known therefore as "triple therapy." These drugs do not cure AIDS because the viral genome is integrated into the host chromosome. Also, virus-containing drug-resistant enzymes can be rapidly selected in a treated patient, necessitating the need for multidrug clinical strategies. Thus the only sure defense against AIDS is not to become infected by the virus. SEE ALSO AIDS; Oncogenes and Cancer Cells; Protein Synthesis; Replication; Reverse Transcriptase; Transcription; Transposon; Virus

Jonathan Leis

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

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Reverse Transcriptase

Reverse transcriptase **catalyzes** the formation of double-stranded deoxyribonucleic acid (DNA) from a single-stranded ribonucleic acid (RNA) **genome**. It is called "reverse" transcriptase because it reverses the usual direction of information flow, from DNA to RNA. Reverse transcriptase is characteristic of retroviruses, including HIV (human immunodeficiency virus), the virus responsible for AIDS (acquired immunodeficiency syndrome).

catalyze aid in the reaction of

genome total genetic material in a cell or organism

All retroviruses encode a polymerase **enzyme** in their *pol* gene that is both necessary and sufficient for the replication of their RNA genomes. The enzyme was first detected in virus particles in 1970 by Howard Temin and David Baltimore. These investigators permeablized the virus membrane with non-ionic detergents, which allowed them to introduce deoxynucleotides. They detected the synthesis of DNA that was dependent upon the RNA genome. This was a novel reaction because, at this time, polymerases were only known to use DNA for the synthesis of RNA in a process known as **transcription**. Thus this new process of using RNA as a **template**/primer for the synthesis of DNA was named reverse transcription. For their discovery, Temin and Baltimore shared the Nobel Prize.

enzyme protein that controls a reaction in a cell

transcription messenger RNA formation from a DNA sequence

template master copy

Reverse transcriptase (RT) has several **enzymatic** activities, including an RNA-dependent DNA polymerase, DNA-dependent DNA poly-

enzymatic related to function of an enzyme

merase, RNase H (a ribonuclease that degrades RNA in RNA-DNA **hybrid** structure), and the ability to unwind DNA-DNA and RNA-DNA duplexes. Each of these activities is required during the process of reverse transcription to convert the single-stranded RNA genome into a double DNA copy, which in turn becomes integrated into the host **chromosome** of the infected cell catalyzed by a second *pol* gene-encoded enzyme, called integrase.

hybrid combination of two different types

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

Purified RT has become a very useful as a tool for modern molecular biology, especially coupled to polymerase chain reaction (PCR) techniques. It provides the ability to reverse transcribe any RNA with the appropriate **complementary primer** into a DNA copy that can then be amplified many times by a thermal stable DNA polymerase during the PCR reaction. The combination of the two techniques has allowed scientists to clone actively expressed genes in cells from their mRNAs (messenger RNAs). SEE ALSO AIDS; CLONE; RETROVIRUS

complementary matching opposite

primer short nucleotide sequence that helps begin DNA replication

Jonathan Leis

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Rhythms of Plant Life

Plants exhibit regular, cyclic physiological changes of many sorts. For example, leaflets of wood sorrel, *Oxalis*, fold downward to a vertical position at night and return to their normal horizontal orientation during the day. Because this rhythm takes place over a period of approximately twenty-four hours, it is called a **circadian** rhythm.

circadian related to a day or daylength

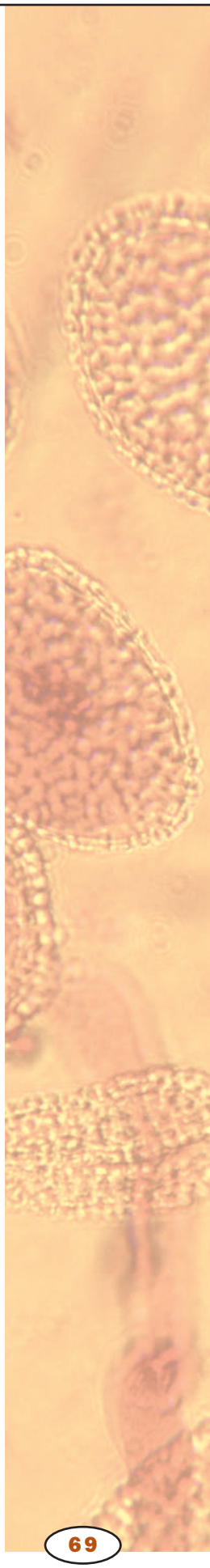
Forces within the plant control the movements of wood sorrel and many other circadian rhythms. This is easily demonstrated by placing wood sorrel in total darkness for several days. In the absence of external light stimuli, the movements continue in an approximate circadian rhythm, but the period tends to lengthen slightly to approximately twenty-six hours. A rhythm that is controlled by an internal timing mechanism, the so-called "biological clock," is an **endogenous** rhythm.

endogenous caused by factors inside the organism

Environment can affect endogenous rhythms. By changing the photoperiod scientists can alter the period of a circadian rhythm as long as the imposed photoperiod does not differ significantly from the normal circadian rhythm. Altering circadian rhythms by varying one or more environmental parameters is called entrainment. Phytochrome, an important plant pigment, and blue light receptors regulate entrainment.

Why should a plant like wood sorrel fold its leaves at night? German botanist Erwin Bünning suggests that the folding of leaves at night hides them from moonlight, which could disrupt the plant's ability to measure night length accurately. Thus, wood sorrel can use its internal biological clock to anticipate the middle of the night, when a moon might be full.

Circadian rhythms are advantageous to *Gnetum gnemon*, a plant found in tropical rainforests, which secretes nectar in the evening, the most active time for the moths that carry its pollen. Other endogenous circadian



An old-growth forest with an understory of wood sorrel in Mt. Hood National Forest in Oregon. Plants exhibit regular, cyclic physiological changes of many sorts.

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

rhythms of plants include opening and closing of **stomata**, growth rate of stems and roots, opening and closing of flowers, production of floral scent, and carbon dioxide uptake. SEE ALSO HORMONES, PLANT; PHOTOPERIODISM

George H. Wittler

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Ribosome

The ribosome is the molecular machine inside the cell that makes **proteins** from **amino acids** in the process called **translation**. It binds to a messenger ribonucleic acid (mRNA) and reads the information contained in the **nucleotide** sequence of the mRNA. Transfer RNAs (tRNAs) containing amino acids enter the ribosome in a special pocket, or binding site, called the acceptor site (A site). Once correctly bound, the ribosome can add the amino acid on the tRNA to the growing protein chain.

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

amino acid a building block of protein

translation synthesis of protein using mRNA code

nucleotide the building block of RNA or DNA

Structure

The ribosome is made up of two parts, called subunits. The larger of the two subunits is where the amino acids get added to the growing protein chain. The small subunit is where the mRNA binds and is decoded. Each of the subunits is made up of both protein and ribonucleic acid (RNA) components.

The small ribosomal subunit is made up of one ribosomal RNA (rRNA) and approximately twenty-one proteins in **prokaryotes** (bacteria) and approximately thirty-three proteins in **eukaryotes** (mammals). In prokaryotes, the large ribosomal subunit contains two rRNAs—one large one and one small one—and approximately thirty-one proteins. In eukaryotes, the large subunit is composed of three rRNAs—one large one and two different small ones—and approximately forty-nine proteins. In eukaryotic cells, ribosomal subunits are synthesized in the nucleolus and then exported to the **cytoplasm** before use.

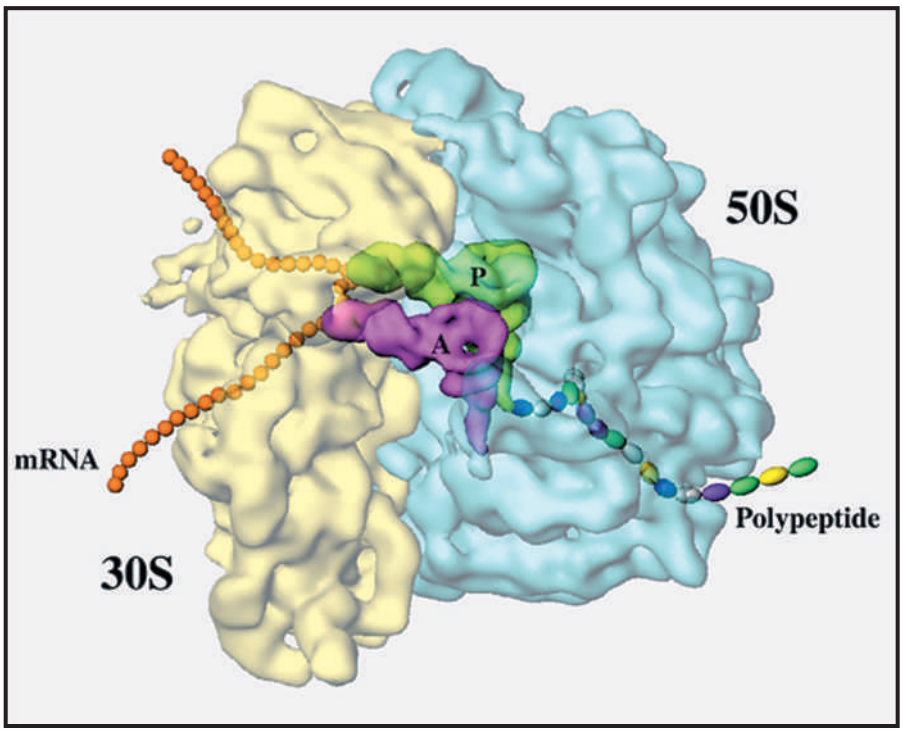
prokaryote single-celled organism without a nucleus

eukaryote an organism whose cells have nuclei

cytoplasm material in a cell, excluding the nucleus

The rRNAs have many regions of self-complementarity, that is, regions within the rRNA that can form **base pairs** with other regions of the same rRNA, linking them together. This self-complementarity produces highly

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



A color-coded cryo-EM map of an *E. coli* ribosome showing the interface between the small (30S) and large (50S) ribosomal subunits.

structured RNA molecules that serve as the core of the ribosome. In fact, rRNAs make up most of the mass of the ribosome. The proteins bind to various parts of the rRNAs to fill in the ribosome's structure.

Researchers have worked for many years to try to determine what the ribosome's structure is at the atomic level. How are all the atoms that make up the ribosome arranged in three-dimensional space? On a gross level, the ribosome looks something like an oyster with one of its shells somewhat smaller than the other. The two subunits are joined to each other by interactions between the rRNAs in one subunit and proteins in the other subunit. There may also be interactions between an RNA on one subunit and an RNA on the other subunit and between proteins on the two subunits.

RNA Movements

tRNAs move through the ribosome during the course of protein synthesis. A tunnel runs through the ribosome, right at the interface between the two subunits, and the tRNAs enter one side of this tunnel and are propelled along it during each step of protein synthesis. The three tRNA binding sites of the ribosome—A (acceptor), P (peptidyl), and E (exit)—appear to be intermediate spots in this tunnel. The mRNA binds to a groove at the bottom of the tRNA tunnel. After each amino acid is added to the growing protein, the tRNAs must be moved from one site to the next, and the mRNA must also be moved over one **codon** (three bases) so that the next amino acid coded for by the mRNA can be added to the protein.

codon sequence of three mRNA nucleotides coding for one amino acid

These movements of the tRNAs and mRNA are made possible by a protein factor, called EF-G in prokaryotes or EF-2 in eukaryotes, which binds to the ribosome and uses the energy stored in the triphosphate group of guanosine triphosphate (GTP) to help propel the tRNAs and mRNA along. It also appears that parts of the ribosome move as the tRNAs and mRNA move. In fact, it is possible that EF-G produces movement of these parts of the ribosome and that these movements in turn produce movement of the tRNAs and mRNAs. Certain antibiotics (drugs that kill bacteria) are known to work by preventing some of the movements of bacterial ribosomes, thus stopping protein synthesis.

The poison ricin, from castor bean seeds, cleaves part of the RNA in the large subunit.

Intriguingly, there are certain mutations of the ribosome (changes to the structure of the rRNA or proteins) that affect its movements during translation and appear to cause a decrease in the accuracy of protein synthesis (for example, the wrong amino acids get put into the protein with increased frequency). Thus, the movements themselves may be directly tied to the mechanism by which the ribosome makes sure that the correct amino acid is being added to the protein at each point along the mRNA.

The growing protein chain exits the ribosome through a second tunnel, this one at the top of the large subunit. When protein synthesis ends, the binding of proteins called release factors is thought to induce the ribosome to release the finished protein into the cytoplasm. Exactly how the ribosome does this is unclear.

For many years it was thought that the rRNAs in the ribosome served merely as a scaffold on which to hang the ribosomal proteins. It was proposed that the proteins did all of the important work in the ribosome, such as catalyzing the formation of **peptide bonds** and moving the tRNAs and

peptide bond bond between two amino acids

mRNA along during protein synthesis. However, it is now clear that the rRNAs play an active role in protein synthesis and are not merely the frame on which the ribosome is built. As more detailed information about the three-dimensional structure of the ribosome becomes available and as researchers do more experiments to probe the inner workings of this fascinating machine, we will have a better understanding of what the rRNAs do and how they do it. SEE ALSO NUCLEOLUS; PROTEIN SYNTHESIS; RNA; TRANSFER RNA

Jon Lorsch

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Rivers and Streams

On the continents, aquatic **ecosystems** are of two kinds: lotic ecosystems, in which the water is free-flowing (streams and rivers), and lentic ecosystems, in which the water is relatively stationary. The scientists who specialize in aquatic ecosystems are limnologists.

ecosystem an ecological community and its environment

Physical Features

The limiting factors that govern what organisms can live in lotic ecosystems include current, light intensity, temperature, **pH**, dissolved oxygen, salinity, and nutrient availability—variables routinely measured by limnologists to develop a profile of the environment. These conditions differ greatly between small headwater streams and the mouths of such great rivers such as the Mississippi and the Amazon. Living occupants of streams and rivers show corresponding differences along the way.

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

Small headwater streams, where water first collects by runoff from the land or emerges from springs, are called first-order streams. When two first-order streams meet, they form a second-order stream; two of these converge to form a third-order stream, and so on, until the water may flow into bodies as large as twelfth-order rivers (for example, the Columbia and the Mississippi). Bodies of the first to third order are usually considered streams, and those of the fourth order and larger are considered rivers.

Streams provide diverse habitats including relatively swift rapids and quiet pools. They often have hard **substrates** of stones, rubble, or bedrock to which animals can cling. Flat rocks and rubble typically harbor the greatest species diversity of stream animals. Stream animals often have flat, streamlined bodies that are not easily swept away by currents, and hooks, suckers, or sticky undersides for clinging to substrates. They tend to face into a current and swim against it, behavior called rheotaxis. Lake animals,

substrate the molecule acted on by an enzyme

Farmland on the banks of the Nile River near Luxor, Egypt.

by contrast, are unaccustomed to resisting currents and allow themselves to be passively washed away if placed in flowing water.

Food Chains and Ecosystem Structure

The bank of a stream or river is called the riparian zone, a place where overhanging foliage provides shade and the tree roots of undercut banks provide shelter. The deep shade produced by riparian foliage limits photosynthesis and primary production of **organic** nutrients. Much or most of the organic matter that nourishes the stream habitat originates as foliage that falls into the water, ranging from leaves, twigs, and seeds to fallen trees. Aquatic food chains in first-order streams thus begin with coarse particulate organic matter. This matter enters the food chain by way of aquatic bacteria and fungi that decompose it, and animals classified as shredders that tear it into finer particles. Shredders produce nutrient-rich feces that, in turn, are eaten by collectors. Farther downstream where there is more light, algae grow on rocks and other submerged surfaces and support a small community of animal grazers. Most shredders, collectors, and grazers are aquatic insects, but snails, bivalves, and crustaceans also play a part. The total pop-

organic composed of carbon, or derived from living organisms

ulation of these invertebrates is relatively small, however, so there are few predators in headwater streams; there is not enough for them to eat.

Rivers, being wider, have more surface exposed to sunlight, so their primary productivity (photosynthesis) is greater. This is aided by **inorganic** nutrients such as nitrogen and phosphorus flowing down from the smaller-order streams. Fourth- to sixth-order rivers provide ideal conditions for algae and rooted aquatic plants because of their softer substrates and ample light. Shredders become less abundant, grazers increase, and the relative populations of collectors and predators remain about the same. Species diversity increases in these mid-order rivers, with fish and burrowing animals such as clams and worms becoming more common. High-altitude, cold, oxygen-rich midsized rivers are an ideal haven for trout, which feed on the insect community. The organisms in midsized rivers, where there is more photosynthesis, produce more organic matter than they consume, and the excess nourishes the larger rivers downstream.

inorganic not bonded to carbon

Large rivers (seventh to twelfth order) are relatively deep and wide. They are rich in organic matter but also contain a lot of inorganic sediment produced by erosion and runoff into the upland waters. Thus, the water is more turbid (muddy), and there is insufficient light to support as much photosynthesis as in smaller rivers. Collectors and predators dominate the consumer community, and consumption exceeds primary production. Fish species such as sturgeon and catfish, which feed on sediments, are more common here than predatory fish.

All **lotic** organisms must adapt to drift, the incessant flow of water toward the sea, carrying nutrients and the organisms themselves downstream. Drift is particularly significant when spring snowmelts and heavy summer rains increase the current. River valleys offer especially rich farmland because of the great quantities of nutrients deposited by periodic flooding. Nutrient loss by drift is compensated for by the continual addition of riparian organic matter to the lower-order upland streams, while animals compensate for drift by their rheotaxis and other means. Many aquatic insects fly upstream to lay their eggs, and fish such as trout and salmon are well known for their upstream spawning runs. The immature animals drift downstream as they grow and typically reach maturity at lower altitudes, only to repeat the process and deposit their offspring back in the headwaters. SEE ALSO Ecosystem; Lakes and Ponds; Limnologist

lotic of, relating to, or living in actively moving water

Kenneth S. Saladin

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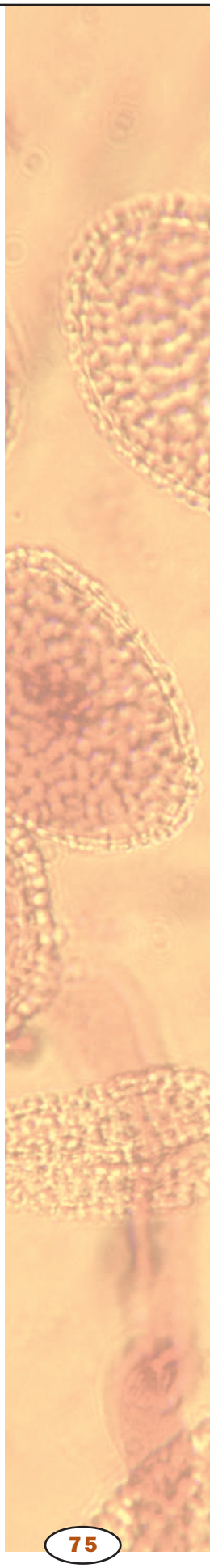
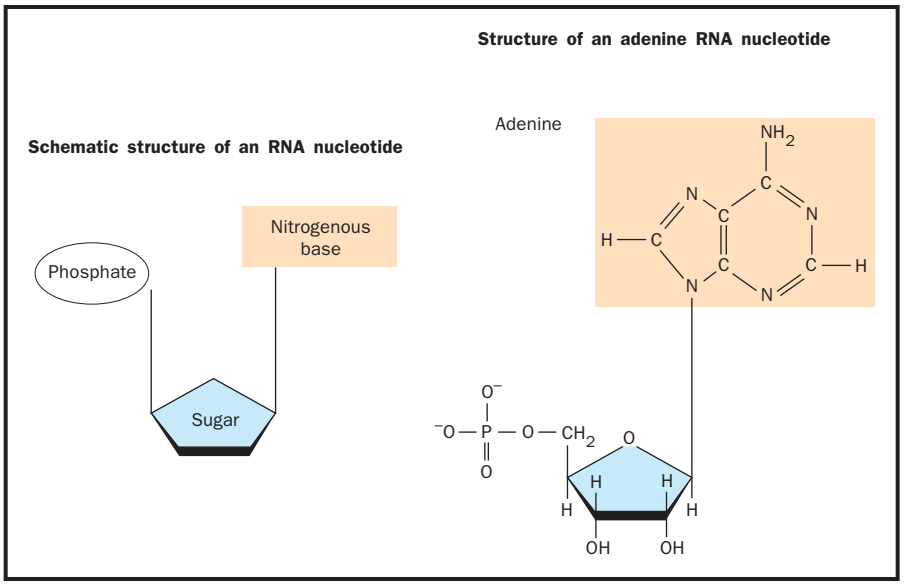
RNA

Ribonucleic acid (RNA), like deoxyribonucleic acid (DNA), is a polymer made up of **nucleotides**. A nucleotide is composed of a pentose (5-carbon)

nucleotide the building block of RNA or DNA



RNA chains are composed of simpler units called nucleotides. Four different bases are used in RNA; adenine is shown.



sugar, a nitrogen-containing base, and phosphate. The pentose sugar found in RNA nucleotides is ribose, whereas that in DNA is 2′ (2-prime) deoxyribose. The bases commonly found in RNA nucleotides are adenine (A), guanine (G), cytosine (C), and uracil (U). Bases found in DNA are A, G, C, and thymine (T instead of U). As in DNA, the individual nucleotides in the polymer are joined together by **phosphodiester** bonds. Unlike DNA, RNA is single-stranded; however, many RNA molecules fold into complex three-dimensional structures.

phosphodiester the link between two nucleotides in DNA or RNA

During **transcription** the DNA code is read and copied into RNA. The sequence of nucleotides in an RNA is therefore determined by the sequence of nucleotides in the **gene** from which it was transcribed. Following transcription, RNA may be processed before it becomes functional.

transcription messenger RNA formation from a DNA sequence

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

There are three main classes of RNA: messenger RNA (mRNA), transfer RNA (tRNA), and ribosomal RNA (rRNA). Each of the classes is important in some aspect of **protein** synthesis. The nucleotide sequence of a messenger RNA specifies the order of **amino acids** in the protein which it encodes. A cell contains many different mRNA molecules, each being the blueprint for a different protein. Although mRNAs are the least abundant class of RNA, they are the most **heterogeneous**. **Ribosomes** play an important role in protein synthesis, and ribosomal RNA (rRNA), is an important structural component of ribosomes. rRNA is the most abundant type of RNA. tRNAs act as adaptors in protein synthesis, in that they read the sequence of nucleotides in the mRNA and deliver the correct amino acid to the growing **polypeptide** chain.

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

amino acid a building block of protein

heterogeneous composed of or containing different parts or types

ribosome protein-RNA complex in cells that synthesizes protein

polypeptide chain of amino acids

Most scientists believe that life has evolved from what was essentially an "RNA world." In today's world, most organisms store their genetic information in DNA and use proteins (encoded by DNA) to **catalyze** biologically important chemical reactions. RNA molecules, however, are believed to have been the first biological catalysts. Through evolution, some of these RNA molecules gained the ability to replicate themselves, and through many rounds of replication, the RNA molecules gained new capa-

catalyze aid in the reaction of

bilities, such as the ability to code for and synthesize proteins. Eventually, the RNA **genome** was replaced with DNA.

Scientists have uncovered a number of **enzymatic** RNA molecules, called ribozymes, believed to be typical of those in the RNA world. RNA **enzymes** can make phosphodiester bonds, suggesting that early RNA molecules could reproduce their genetic material. In fact, it is now known that RNA in the ribosome catalyzes the formation of **peptide bonds** during protein synthesis, supporting the idea that RNA molecules were able to synthesize proteins. Even in the twenty-first century, not all genomes are composed of DNA: some very important viruses, such as the one that causes AIDS (acquired immunodeficiency syndrome), has RNA as its genetic material. However, the so-called RNA viruses express their genome only after they have turned it into DNA. SEE ALSO RIBOSOME; RNA PROCESSING; TRANSFER RNA

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genome total genetic material in a cell or organism

enzymatic related to function of an enzyme

enzyme protein that controls a reaction in a cell

peptide bond bond between two amino acids

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RNA Processing

In the appropriate cell type and at the correct developmental stage, ribonucleic acid (RNA) polymerase **transcribes** an RNA copy of a gene, the primary transcript. However, the primary transcript may contain many more **nucleotides** than are needed to create the intended protein. In addition, the primary transcript is vulnerable to breakdown by RNA-degrading enzymes.

transcribe create an RNA copy of a DNA gene

nucleotide the building block of RNA or DNA

Before the primary transcript can be used to guide protein synthesis, it must be processed into a mature transcript, called messenger RNA (mRNA). This is especially true in **eukaryotic cells**. Processing events include protection of both ends of the transcript and removal of intervening nonprotein-coding regions.

eukaryotic cell a cell with a nucleus

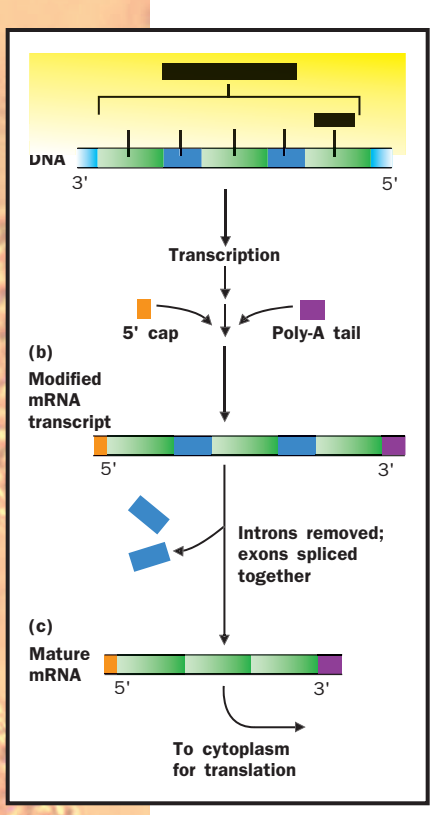
On an RNA molecule, the end formed earliest is known as the 5′ (5-prime) end, whereas the trailing end is the 3′ end. The ends of the primary transcript are particularly susceptible to a class of degradative enzymes called exonucleases. During processing, the 5′ end of the primary transcript is protected against the effects of these enzymes by the addition of a CAP. The CAP uses an unusual linkage between nucleotides. Exonucleases do not recognize this unusual structure and therefore cannot remove the CAP. Since exonucleases work only from an end, if the CAP nucleotide cannot be removed, the entire 5′ end of the mRNA is protected. The 5′ CAP also aids in transport out of the **nucleus** and helps bind the mRNA to the **ribosome**.

β-thalassemia, a hemoglobin disease, can be caused by an intron mutation that prevents recognition of a splice site.

nucleus membrane-bound portion of cell containing the chromosomes

ribosome protein-RNA complex in cells that synthesizes protein

To protect the 3′ end against degradative exonucleases, a poly-A tail is added by poly-A polymerase. Poly-A is a chain of adenine nucleotides, one hundred to two hundred units long. The poly-A tail has typical bonds that are susceptible to degradation by exonucleases, but it does not have any protein coding function so it does not particularly matter if some of the A



Stages in the processing of an mRNA transcribed from a gene of a eukaryote. (a) Genetic data are transcribed into an RNA copy. (b) The copy is modified with a cap at the 5′ end and a poly-A tail at the 3′ end. (c) The exons are spliced together. The mature mRNA then passes to the cytoplasm, where it is translated into protein.

residues are degraded. It actually takes quite some time for the poly-A tail to be completely lost, and during this time the protein coding portion of the mRNA remains intact. Without the poly-A tail, however, the exonucleases would rapidly degrade into the protein coding portion of the mRNA. An exception to the poly-A strategy is seen in the mRNA for histones, proteins that wrap deoxyribonucleic acid (DNA) into chromosomes. Instead of poly-A, histone mRNA uses a much smaller structure that is regulated by factors present during DNA synthesis.

The most striking event in RNA processing occurs because the protein coding region in eukaryotic genes is not continuous. A typical eukaryotic gene is composed of a number of protein coding regions, called exons, that are separated by noncoding regions called introns. In fact, the number of nucleotides in the introns can be much larger than the number of nucleotides in the combined exons. The DNA gene contains the code for both the exons and the introns, as does the primary RNA transcript, but the noncoding intron sequences must be removed to form the mRNA before protein synthesis.

The process by which introns are removed and exons are joined to one another is called RNA splicing, and it is **catalyzed** by complexes of proteins and RNA called SNuRPs (small nuclear **ribonucleoprotein** particles). These complexes locate special RNA sequences that flank the exon/intron junctions, bind to them, and catalyze the splicing reactions. Some primary transcripts can be spliced in a few different ways. Such "alternate splicing" yields a range of related proteins.

After addition of the CAP to the 5′ end, the poly-A tail to the 3′ end, and splicing of the introns, the processing is complete and the mRNA is transported through nuclear pores to the **cytoplasm** of the eukaryotic cell where translation (protein synthesis) will occur. SEE ALSO GENE; NUCLEAR TRANSPORT; PROTEIN SYNTHESIS; RNA; TRANSFER RNA; TRANSCRIPTION

James E. Blankenship

catalyze aid in the reaction of

ribonucleoprotein combination of RNA and protein

cytoplasm material in a cell, excluding the nucleus

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RNA Virus

See Retrovirus

Roots

Plants are autotrophic and make their own food via photosynthesis. However, they must acquire the molecular building blocks for the production of food from the environment. Carbon dioxide (CO_2), water, and a variety of **minerals** are needed for photosynthesis to occur. While CO_2 comes from the air, all plants get the majority of their water and minerals from the soil via their roots. In addition, roots provide structural support for the plant. Moreover, roots can serve as storage houses for the food produced by the plant. Roots also act as the gatekeepers for the plant by actively regulating the entry of substances into the plant body.

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

The root system of a plant.

Root Anatomy

Examining the anatomy of a root reveals a highly organized set of cell types that reflect the main functions of roots previously mentioned. The exterior of the root is called the epidermis and is composed of dermal tissue, made up of epidermal cells. Some of these epidermal cells have long membranous extensions called root hairs. Root hairs increase the surface area of the root, maximizing water and mineral absorption. Immediately interior to the epidermis lies the root cortex. The parenchyma cells store nutrients and are also involved in mineral uptake. In roots that are designed for storage, these cells are numerous and are filled with the carbohydrate products of photosynthesis (starch).

The innermost layer of the cortex, surrounding the vascular tissue (stele), is the endodermis. A waxy material called the Casparian strip surrounds each individual endodermal cell. This structure acts as a gasket, creating a seal to limit diffusion of water and minerals into the vascular tissue of the root. Due to the presence of the Casparian strip, all water and minerals must pass through endodermal cells, not around them, before entering the vascular

tissue of the plant. This allows the endodermal cells to regulate the entry of nutrients and other substances into the plant.

xylem water-transporting system in plants

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

Finally, **xylem** and **phloem** occupy the central region of the root. The xylem transports the water and minerals absorbed by the root up to the stems, leaves, and flowers. The phloem transports the sugars and other nutrients made by the leaves down to the root for immediate use or for storage during periods of dormancy.

Root Symbioses

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

Most root systems have microorganisms that are living in or near them in **symbiosis**. These microorganisms help the root absorb and process nutrients that are needed by the plant, while the root delivers food made by the plant to the microorganism.

Nitrogen-Fixing Bacteria. Many of the minerals needed by the plant are readily available in the soil in forms that the plant can use (including calcium, sulfur, sodium, chloride, and potassium). However, nitrogen in the environment is in the form of nitrogen gas. Plants cannot convert nitrogen gas into ammonia or nitrate (nitrogen forms they can use to build **proteins**). However, many microorganisms that live in the soil (and some that live in the root cells of some plants) have the proper **enzymes** to convert nitrogen into ammonia or nitrate. These bacteria are called "nitrogen-fixing" because they capture atmospheric nitrogen and convert it into a usable form. Some plants, notably the legumes such as soybeans, house specific nitrogen-fixing bacteria with their roots in specialized structures called nodules.

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

Mycorrhizae. In addition to their symbiotic relationships with bacteria in the soil, roots have symbiotic relationships with fungi. Particular types of fungi can infect the root epidermis and provide the plant with phosphate that it cannot acquire on its own. Roots that have these beneficial fungal infections are called mycorrhizae.

Types of Roots

As there are many different types of plants, there are many different types of root systems. Each system is structured to serve the needs of the plant body, based on the metabolic demands of the plant and the environment in which it lives.

Taproots. Taproots are roots that are specialized for reaching water deep in the ground or for storing the nutrients produced by the plant. Many **eudicots** such as sugar beets and carrots have taproot systems that are specialized for storage. In fact, the most familiar part of the carrot (the orange, edible portion) is a taproot. In addition, conifers (evergreens) that live in climates with harsh winters have taproot systems. During the winter months the water in the upper layers of the soil is frozen and inaccessible to the plant. The taproot system in these plants can grow to access available water sources in deep layers of the soil.

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

Fibrous Roots. Fibrous root systems consist of an elaborate network of small roots that spread throughout the upper layers of soil. Most monocots, such as grasses, have fibrous root systems. These roots allow the plant to access a large area of soil water and minerals. The mat-like formation of fi-

brous roots provides a strong anchor for the plant and also preserves the integrity of the top layer of soil by preventing erosion.

Adventitious Roots. Both taproots and fibrous roots are root systems that arise at the base of the plant shoot during germination. However, it is not uncommon for roots to develop from plant structures such as stems or leaves that are aboveground. These roots are called **adventitious** roots and mainly serve both support and conductive roles. SEE ALSO MYCORRHIZAE; NITROGEN FIXATION; PLANT DEVELOPMENT; PLANT NUTRITION; SOIL; WATER MOVEMENT IN PLANTS

adventitious growing from a nonstandard location

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Scaling

Scaling can be defined as the structural and functional consequences of a change in size and scale among similarly organized animals. To examine what "consequences of a change in size" means, consider what would happen if one scaled up a cockroach simply by expanding it by a factor of 100 in each of its three dimensions. Its mass, which depends on volume, would increase by a factor of 1 million (100 x 100 x 100). The ability of its legs to support that mass, however, depends on the cross-sectional area of the leg, which has only increased by a factor of ten thousand (100 x 100). Similarly, its ability to take in oxygen through its outer surface will also grow only by ten thousand, since this too is a function of surface area. This disparity between the rapid growth in volume and the slower growth in surface area means the super-sized cockroach would be completely unable to support its weight or acquire enough oxygen for its greater body mass.

The consequences of body size on the physiology, ecology, and even behavior of animals, can be appreciated if one examines in more detail differences in function between organisms of widely different sizes. For example, consider that a 4-ton elephant weighs about 1 million times more than a 4-gram shrew, and further consider that the shrew consumes enough food daily to equal about 50 percent of its body weight. Imagine then what the daily food consumption of 1 million shrews would be (2 tons of food), and realize that the elephant is probably consuming instead only about 100 pounds of food. From this example it is obvious that daily food requirements do *not* scale directly with body mass. In fact, most body processes scale to some proportion of body mass, rarely exactly 1.0.

Allometric Analysis

How can one determine the relationship of body processes to body mass? The best technique for uncovering the relationship is to plot one variable (for example, food requirements or metabolic rate) against body mass for groups of similar animals (for example, all mammals, or even more specifically, carnivorous mammals). Such a plot is called an X-Y regression. Using a statistical technique called least-squares regression gives an equation

metabolism chemical reactions within a cell

that best fits the data. The equation for scaling of any variable to body mass is $Y = aW^b$, where Y is the variable to be determined, W is the animal body mass (or weight), and a and b are empirically derived constants from the regression. The exponent b is of particular interest, since it gives the scaling relationship one is looking for in nonlinear relations, such as that of **metabolism** and body mass. This mathematical technique is called allometric analysis. Allometric analysis can be used to predict the capacity or requirements of an unstudied animal, one that might be too rare to collect or too difficult to maintain in captivity for study.

Metabolism

Using this technique, several interesting relationships between animal structure and function have been uncovered. Among the most well studied is the relationship between animal metabolism and body mass, introduced above, in which M (metabolism) scales to the 0.75 power of body weight ($M = aW^{0.75}$). This means that while the total energy needs per day of a large animal are greater than that of a small animal, the energy requirement *per gram* of animal (mass-specific metabolism) is much greater for a small animal than for a large animal. Why should this be the case? For birds and mammals that maintain a constant body temperature by producing heat, the increased mass-specific metabolism of smaller animals was once thought to be a product of their greater heat loss from their proportionately larger surface area-to-volume ratio. However, the same mathematical relationship between metabolism and body mass has been found to hold for all animals studied, and even unicellular organisms as well. Therefore, the relationship of metabolism to body size seems to represent a general biological rule, whose basis eludes scientific explanation at this time.

Allometric analysis has shown that different body processes, involving different organs, scale with different exponents of body mass. For example, blood volume, heart weight, and lung volume all scale almost directly with body mass (exponent = 0.99–1.02). Thus, the oxygen delivery system (heart and lungs) is directly proportional to body mass, even though the metabolism, and thus oxygen requirements, of the body scale with body mass to the 0.75 power. If the hearts are proportionately the same size for large and small animals, but mass-specific oxygen requirements are higher for small animals, then this implies that hearts in small animals must pump faster to deliver the greater quantity of oxygenated blood. Similarly, lung ventilation rates of smaller animals must be higher than those of larger animals. Both predictions have been borne out by measurements that support this conclusion from the allometric analysis.

Locomotion

The energy requirement for locomotion also scales with body size, in much the same way that metabolism does. But here another factor comes into play: the type of locomotion. It is obvious that locomotion is much more energetically expensive than sitting still, but are some types of locomotion more expensive than others? Let's compare running, swimming, and flying. In plotting the cost of running versus body mass, one notes that metabolic cost increases directly as a function of mass. What about swimming and flying?

Again, cost increases with mass, but the regression lines for these allometric analyses exhibit different slopes than the one for runners. As might be expected the cost (per kilometer per gram of animal) is lowest for swimmers, where the body mass is supported by buoyancy; next highest for flyers, where body mass is partially supported by air mass; and highest for runners, who lose energy to friction with the ground. While water is more **viscous** to move through than air, swimmers (especially fish) have streamlined bodies that reduce frictional drag and reduce cost.

viscous thick

Allometric analysis helps explain why animals can only get so large or so small. Limits placed on structural support, amount of gut surface area required to process the required energy per day, and cost of locomotion become limiting factors for large animals. High surface area-to-volume ratios, high metabolic costs of existence, and limits on the speed of diffusion and cell surface area become limiting factors for small animals. Thus, animal structural design has functional implications that determine physiological processes and ultimately the ability to exist under specific ecological constraints. SEE ALSO CIRCULATORY SYSTEMS; FLIGHT; GAS EXCHANGE; PHYSIOLOGICAL ECOLOGY; TEMPERATURE REGULATION

Susan Chaplin

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Science Writer

In 1999, gene therapy researchers accidentally killed a healthy nineteen-year-old boy and then covered up the evidence. Only the work of two newspaper reporters—one a science writer—brought the story to light. The science writer's work showed that the scientists had continued risky experiments on humans for months.

A science writer is a person who writes about science for newspapers, magazines, television shows, or university public information offices. Anyone with a talent for writing can become a science writer. Most science writers have at least a college degree. Some have no training in science and learn what they need to know on the job by talking to scientists. Others have at least a B.A. in a science such as biology or chemistry.

To become a science writer, you can just start writing articles and try to get them published, perhaps in a college newspaper. Once you have "clips" from your volunteer work, you can show them to an editor and find paying work. Many students enter a graduate program in science writing, then launch their careers by taking an internship or job at a newspaper, radio station, or magazine.

Jennie Dusheck

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Secondary Metabolites in Plants

Secondary metabolites are chemicals produced by plants for which no role has yet been found in growth, photosynthesis, reproduction, or other "primary" functions. These chemicals are extremely diverse; many thousands have been identified in several major classes. Each plant family, genus, and species produces a characteristic mix of these chemicals, and they can sometimes be used as taxonomic characters in classifying plants. Humans use some of these compounds as medicines, flavorings, or recreational drugs.

Secondary metabolites can be classified on the basis of chemical structure (for example, having rings, containing a sugar), composition (containing nitrogen or not), their solubility in various solvents, or the pathway by which they are synthesized (e.g., phenylpropanoid, which produces tannins). A simple classification includes three main groups: the terpenes (made from mevalonic acid, composed almost entirely of carbon and hydrogen), phenolics (made from simple sugars, containing benzene rings, hydrogen, and oxygen), and nitrogen-containing compounds (extremely diverse, may also contain sulfur).

The apparent lack of primary function in the plant, combined with the observation that many secondary metabolites have specific negative impacts on other organisms such as herbivores and **pathogens**, leads to the hypothesis that they have evolved because of their protective value. Many secondary metabolites are toxic or repellant to herbivores and microbes and help defend plants producing them. Production increases when a plant is attacked by herbivores or pathogens. Some compounds are released into the air when plants are attacked by insects; these compounds attract **parasites** and predators that kill the herbivores. Recent research is identifying more and more primary roles for these chemicals in plants as signals, **antioxidants**, and other functions, so "secondary" may not be an accurate description in the future.

pathogen disease-causing organism

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

antioxidant substance that prevents damage from oxidation

Consuming some secondary metabolites can have severe consequences. Alkaloids can block **ion** channels, inhibit **enzymes**, or interfere with neurotransmission, producing **hallucinations**, loss of coordination, convulsions, vomiting, and death. Some phenolics interfere with digestion, slow growth, block enzyme activity and cell division, or just taste awful.

ion an electrically charged particle

enzyme protein that controls a reaction in a cell

hallucination altered sensory experience

Most herbivores and plant pathogens possess mechanisms that ameliorate the impacts of plant metabolites, leading to evolutionary associations between particular groups of pests and plants. Some herbivores (for example, the monarch butterfly) can store (sequester) plant toxins and gain protection against their enemies. Secondary metabolites may also inhibit the growth of competitor plants (allelopathy). Pigments (such as terpenoid carotenes, phenolics, and flavonoids) color flowers and, together with terpene and phenolic odors, attract pollinators.

Secondary chemicals are important in plant use by humans. Most pharmaceuticals are based on plant chemical structures, and secondary metabolites are widely used for recreation and stimulation (the alkaloids nicotine and cocaine; the terpene cannabinol). The study of such plant use is called ethnopharmacology. Psychoactive plant chemicals are central to some religions, and flavors of secondary compounds shape our food preferences. The characteristic flavors and aroma of cabbage and relatives are caused by

Class	Example Compounds	Example Sources	Some Effects and Uses
NITROGEN-CONTAINING			
Alkaloids	nicotine cocaine theobromine	tobacco coca plant chocolate (cocao)	interfere with neurotransmission, block enzyme action
NITROGEN- AND SULFUR-CONTAINING			
Glucosinolates	sinigrin	cabbage, relatives	
TERPENOIDS			
Monoterpenes	menthol linalool	mint and relatives, many plants	interfere with neurotransmission, block ion transport, anesthetic
Sesquiterpenes	parthenolid	Parthenium and relatives (*Asteraceae*)	contact dermatitis
Diterpenes	gossypol	cotton	block phosphorylation; toxic
Triterpenes, cardiac glycosides	digitogenin	Digitalis (foxglove)	stimulate heart muscle, alter ion transport
Tetraterpenoids	carotene	many plants	antioxidant; orange coloring
Terpene polymers	rubber	Hevea (rubber) trees, dandelion	gum up insects; airplane tires
Sterols	spinasterol	spinach	interfere with animal hormone action
PHENOLICS			
Phenolic acids	caffeic, chlorogenic	all plants	cause oxidative damage, browning in fruits and wine
Coumarins	umbelliferone	carrots, parsnip	cross-link DNA, block cell division
Lignans	podophyllin urushiol	mayapple poison ivy	cathartic, vomiting, allergic dermatitis
Flavonoids	anthocyanin, catechin	almost all plants	flower, leaf color; inhibit enzymes, anti- and pro-oxidants, estrogenic
Tannins	gallotannin, condensed tannin	oak, hemlock trees, birdsfoot trefoil, legumes	bind to proteins, enzymes, block digestion, antioxidants
Lignin	lignin	all land plants	structure, toughness, fiber

nitrogen- and sulfur-containing chemicals, glucosinolates, which protect these plants from many enemies. The astringency of wine and chocolate derives from tannins. The use of spices and other seasonings developed from their combined uses as preservatives (since they are antibiotic) and flavorings. SEE ALSO FLOWERS; HERBIVORY AND PLANT DEFENSES; METABOLISM, CELLULAR; POISONS

Jack Schultz

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A kidney bean sprouting into a seedling.

Seed Germination and Dormancy

The embryo, contained within the seed, is the next generation of plant. Thus successful seed germination is vital for a species to perpetuate itself. By definition, germination commences when the dry seed, shed from its parent plant, takes up water (imbibition), and is completed when the embryonic root visibly emerges through the outer structures of the seed (usually the seed or fruit coat). Thereafter, there is seedling establishment, utilizing reserves stored within the seed, followed by vegetative and reproductive growth of the plant, supported by photosynthesis.

Quiescence and Germination

The seed is metabolically inactive (quiescent) in the mature, dry state and can withstand extremes of drought and cold. For example, dry seeds can be stored over liquid nitrogen at -150 degrees Celsius (-238 degrees Fahrenheit) for many years without harm. Upon hydration of a seed, **metabolism** commences as water enters its cells, using **enzymes** and structural components present when the seed was dry. Respiration to provide energy has been observed within minutes of water uptake. **Mitochondria** that were stored in the dry seed are involved, although initially they are somewhat inefficient because of damage sustained during drying and rehydration. During germination they are repaired and also new **organelles** are synthesized. **Protein** synthesis also commences rapidly in the imbibing seed.

Early during germination, stored messenger ribonucleic acids (mRNAs) are used as **templates** for protein synthesis, but later in germination these are replaced with newly **transcribed** messages, some of which code for a different set of proteins. Although the pattern of seed protein synthesis changes during germination, no proteins have been identified as being essential for this event to be completed.

Elongation of cells of the radicle (embryonic root) is responsible for its emergence from the seed. This is a **turgor**-driven process and is achieved through increased elasticity of the radicle cell walls, by a process which is not known. Cell division and deoxyribonucleic acid (DNA) replication occur after germination, as the radicle grows, and reserves of protein, carbohydrate, and oil, stored in the dry seed, are used to support seedling growth.

Dormancy

Mature seeds of some species are incapable of germinating, even under ideal conditions of temperature and hydration, unless they receive certain environmental stimuli; such seeds are dormant. Breaking of this dormancy may be achieved in several ways, depending upon the species. Frequently, dormancy is lost from seeds as they are stored in the dry state for several weeks

metabolism chemical reactions within a cell

enzyme protein that controls a reaction in a cell

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

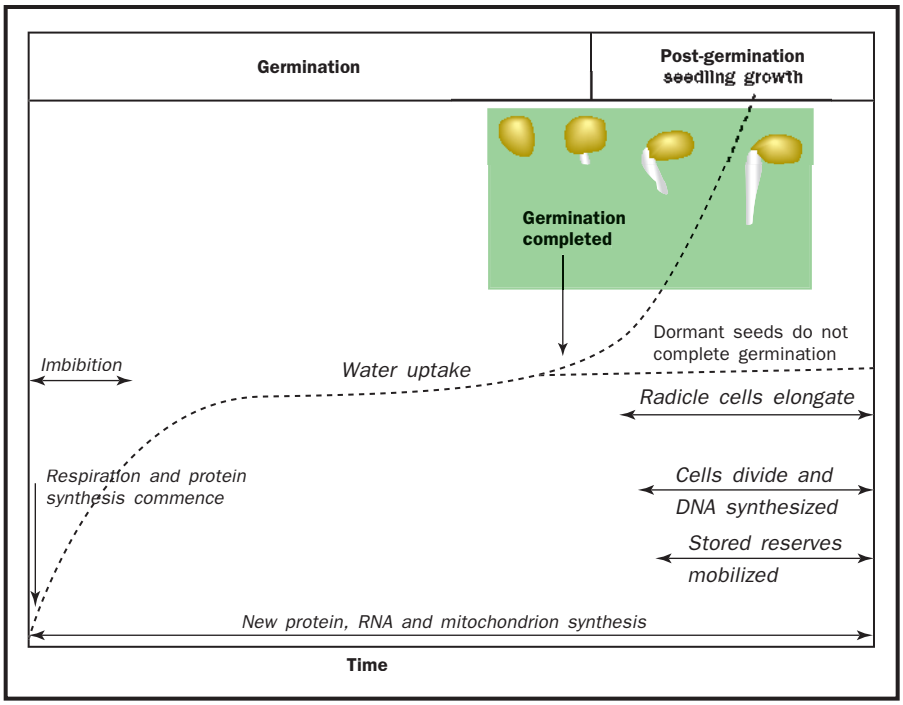
organelle membrane-bound cell compartment

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

template master copy

transcribe create an RNA copy of a DNA gene

turgor internal pressure



The stages of germination and early growth.

to years, a phenomenon called dry after-ripening. But many seeds remain dormant in a fully imbibed state; they are as metabolically active as non-dormant seeds, but yet fail to complete germination. Dormancy of these seeds may be broken by one or more of the following: (1) light, sunlight being the most effective; (2) low temperatures (1 to 5 degrees Celsius [33.8 to 41 degrees Fahrenheit]) for several weeks; (3) day/night fluctuating temperatures of 1 to 10 degrees Celsius (41 to 50 degrees Fahrenheit); (4) chemicals, such as nitrate in the soil, or applied **hormones** (gibberellins) in the laboratory; and (5) fire.

hormone molecule released by one cell to influence another

Dormancy mechanism operate to control the germination of seeds in their natural environment and to optimize the conditions under which the resultant seedling can become established. Dormant seeds that require light will not germinate unless they are close to the soil surface; hence germinated seeds will not expend their stored reserves before they can reach the surface and become photosynthetically independent seedlings. This is particularly important for small, wind-dispersed weed seeds. The light-perception mechanism in light-requiring seeds involves a receptor protein, phytochrome, which is activated by red wavelengths of light and inactivated by far-red (near-infrared). Far-red light from sunlight penetrates farther into soil than does red, but also light penetrating through a leaf canopy is richer in far-red than red, since the latter is absorbed by photosynthetic pigments in the leaf. Hence, germination of light-sensitive seeds is advantageously inhibited under a leaf canopy and helps explain why germination and subsequent plant growth is so profuse in forest clearings.

Seeds that need a period of low temperature cannot germinate immediately after dispersal in the summer or early autumn but will do so after being subjected to the cold of winter, conditions that may cause the parent plant to die, and thus remove competition for space in the spring. The requirement for alternating temperatures will prevent germination of seeds

beneath dense vegetation because the latter dampens the day/night temperature fluctuations; these seeds will germinate only when there is little vegetation cover, again reducing competition with established plants.

Seed dormancy is also important in relation to agricultural and horticultural crops. Its presence causes delayed and sporadic germination, which is undesirable. On the other hand, the absence of dormancy from cereals, for example, can result in germination of the seed on the ear, causing spoilage of the crop. Thus having mild dormancy to prevent this, which is lost during storage of the seed (dry after-ripening), is desirable. SEE ALSO FIRE ECOLOGY; REPRODUCTION IN PLANTS; SEEDS

J. Derek Bewley

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Seedless Vascular Plants

xylem water-transporting system in plants

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

When one walks through a contemporary forest, all of the surrounding trees are vascular plants. Wood, which is made up primarily of **xylem**, and bark, which contains **phloem**, are the major structural elements of the trunks and stems. These trees produce seeds, whether they be formed within the cones of the pines or within fruits, such as the winged samaras of maples or the fleshy cherries of the cherry tree. In the Carboniferous period a similar hike would also place one in a forest of woody trees, many as large as 98 feet (30 meters) tall, but there would be no seeds produced. These plants were seedless vascular plants, which were propogated by spores. Ultimately they became extinct, leaving behind expansive fossil fuel deposits.

gamete reproductive cell, such as sperm or egg

zygote fertilized egg

diploid having pairs of chromosomes in the nucleus

gametophyte a haploid plant that makes gametes by mitosis

fertilization union of sperm and egg

The differences between spores and seeds are extensive. Seeds are multicellular structures that provide a protected place where the egg (n) was to be fertilized by male **gamete** nuclei (n) in pollen. The resulting cell, called a **zygote**, is **diploid** (2n), the same as the original plant that produced it. It repeatedly divides mitotically, while still within the protection of the seed coat, to form an embryo. The embryo may remain dormant for a significant time period but ultimately emerges from the seed when it germinates.

The seedless vascular plants do not have this protection. Their gametes are produced mitotically by a **gametophyte** (n) that lives independently. There are often many vase-shaped archegonia on these small plants, and the unfertilized egg is inside the base of this structure. The embryo formed following **fertilization** is not as well protected as one located within a seed. It grows and emerges from the archegonium, where it is exposed to the environment.

These embryos survive best to develop into young sporophyte individuals when they are in moist habitats, whereas seeds can endure more severe conditions and therefore can have wide habitat type distributions. The sporophyte eventually develops rhizomes, underground stems, roots, or rhizoids that serve to absorb water and nutrients and allow independent survival. In the case of the plants of the Carboniferous forests, this development was extensive.

The simplest type of spore production in living seedless vascular plants is found in the leafless whisk fern, *Psilotum*, a member of the **phylum** Psilotophyta. This sporophyte (2n) plant, really little more than a branching twig, has many sets of three-fused sporangia, which produce spores through **meiosis**. These **haploid** (n) spores grow into minute plants about the size of a small piece of macaroni. These plants have archegonia and small gametangia (which produce the male gametes) to complete sexual reproduction and make new sporophytes.

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

meiosis cell division that forms eggs or sperm

haploid having single, nonpaired chromosomes in the nucleus

Many variations on this basic spore-producing alternation of generations life cycle are found in the seedless vascular plants. The carboniferous trees, which are now recognized only through the study of their fossils, most likely had common ancestors with a variety of present-day organisms including the ferns, horsetails, and lycopods.

The modern ferns, phylum Pterophyta, have leaves of varying sizes and shapes and still occur as trees in tropical areas. The descendents in the other groups do not presently attain treelike stature. Horsetails or scouring rushes, phylum Sphenophyta, have ancestors stretching as far back as the Devonian era. A ribbed, silicon-impregnated stem has branches in many species that are whorled and give the plant the appearance of a bottle brush or animal tail.

The phylum Lycophyta includes club mosses, sometimes called ground pines, which in some cases have stems with reduced leaves (microphylls) fused together to look like the foot of an animal. The name lycopodium means "wolf foot," and most likely originated because of this morphological analogy. The selaginellas, which often **superficially** resemble mosses, are in fact very different from mosses. Their small, leafy green stems are sporophytes (2n) and have vascular tissue. In contrast, the small leaves of mosses are gametophytes (n) and no vascular tissue is present. Shifts like this, from a predominant gametophyte generation to a predominant sporophyte generation represent one of the major trends of evolutionary advance in the plant kingdom. SEE ALSO ALTERNATION OF GENERATIONS; BRYOPHYTES; EVOLUTION OF PLANTS; PLANT; PTERIDOPHYTES

superficial on the surface; not deep

Dean Cocking

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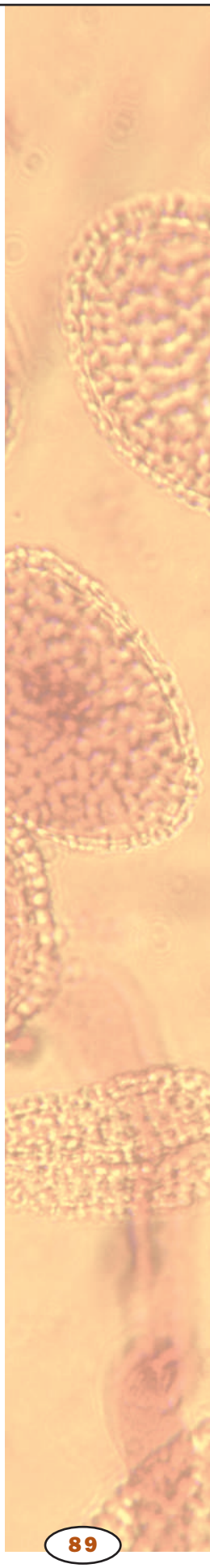
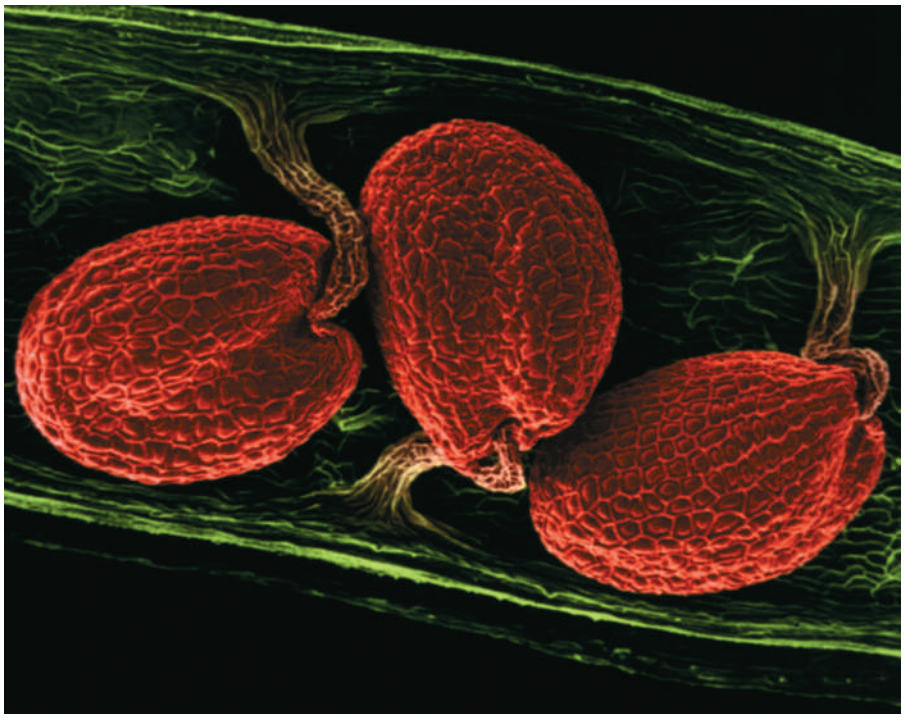
Seeds

In seed-bearing plants, a seed is the end product of sexual reproduction. It is a mature **ovule**, comprising an embryo or miniature plant along with food reserves, all within a protective seed coat. Seed plants first appeared during the Devonian period some 400 million years ago and rapidly became the dominant vegetation. Up to that point, plants relied on spores for dispersal and were heavily dependent on water for reproduction.

ovule multicellular structure that develops into a seed after fertilization





A scanning electron micrograph image of Arabidopsis seed pods.

fertilization union of sperm and egg

gymnosperms "naked seed" plants, including conifers

nucleus membrane-bound portion of cell containing the chromosomes

gamete reproductive cell, such as sperm or egg

diploid having pairs of chromosomes in the nucleus

zygote fertilized egg

triploid possessing three sets of chromosomes

endosperm nutritive tissue within a seed

intracellular within a cell

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

polysaccharide carbohydrate composed of many individual units of sugar

hydrolyze to split apart using water

Seeds develop by **fertilization** of ovules, both the exposed ovules of **gymnosperms** like the conifers and the enclosed ovules of the angiosperms (flowering plants). The seeds of gymnosperms are virtually naked and exposed to the elements, whereas those of the flowering plant develop within a protective structure: the fruit. In both groups, the egg within the ovule is fertilized by a male **nucleus** arriving via a pollen grain. From this, a miniature plant or embryo develops that will later resume development in a process termed "germination," utilizing energy stores laid down in the seed.

Flowering plants differ from gymnosperms in that seed development in angiosperms starts with double fertilization. Male and female **gametes** fuse to form the **diploid zygote**, which develops into the embryo, while a second male nucleus fuses with two other nuclei of the ovule to give rise to a **triploid endosperm**. The endosperm is a nutritive tissue that provides food material for the developing embryo. In some flowering plant seeds it remains throughout seed development, storing the reserves that the embryo will require for germination. Such endospermic seeds are produced by cereals like wheat, as well as dicotyledonous plants like castor bean.

In nonendospermic seeds the endosperm virtually disappears, all the food reserves being transferred during seed development to the embryo itself. In such seeds, the cotyledons or first seed leaves become quite large and accumulate the reserves that will be mobilized later in germination. Reserves may take the form of **intracellular** oil droplets (for example, the sunflower), **protein** bodies (beans), and starch grains (cereals), or combinations of these. Some seeds also store **polysaccharide** reserves as massively thickened cell walls (some leguminous plants and date palm) that will later be **hydrolyzed**. The exception to this general pattern is the family of flowering plants known as orchids. They produce the smallest seeds known. These dustlike seeds contain just a few cells, often not even organized into a rec-

ognizable embryo, and contain absolutely no food reserves. Their germination relies on symbiotic associations with fungi to provide the fuel for germination.

Seeds often exhibit dormancy, meaning they fail to germinate even when provided with adequate water and suitable temperature conditions. Dormancy acts to prevent germination until conditions are right. This dormancy may be broken by proper exposure to light or darkness. Alternatively, a hard seed coat may physically prevent water uptake and embryo expansion or even gas exchange, with germination only proceeding following physical damage to the seed coat. Last, chemical inhibitors present in the seed may cause dormancy, and these must first leach out into the soil before germination can take place. Seeds of crop plants can often be stored for years under cold, dry conditions, and some plants show extreme seed longevity under natural conditions (for example, the sacred lotus germinates after hundreds of years buried in lake mud). SEE ALSO ANGIOSPERMS; FLOWERS; FRUITS; GRAIN; GYMNOSPERMS; POLLINATION AND FERTILIZATION

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Senescence

Senescence refers to all of the changes that take place in a plant that will finally lead to the death of cells, tissues, and, eventually, the whole plant body. These changes can be seen to occur in some cells even in very young, vigorously growing plants. For example the contents of those cells that make up the **xylem** tissue must senesce and die very early in development. The hollow cells, their cell walls arranged in a pipeline, can then allow water to flow up the plant in a process called transpiration.

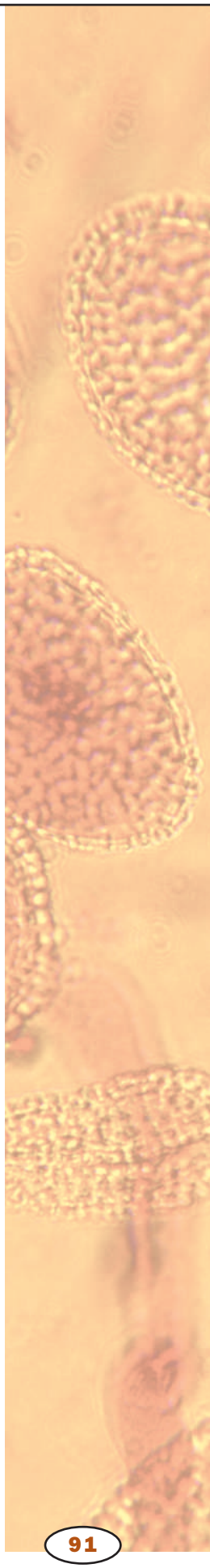
xylem water-transporting system in plants

Apart from the very precisely controlled death of specific cells during early development, senescence can also be seen in large, multicellular plant organs including leaves and fruits. Golden fields of ripening grain and the reds and yellows of the fall landscape in forests are both due to the pigment changes occurring during the early stages of senescence in millions and millions of leaves. The green chlorophyll pigments are removed, some yellow carotenes remain, and some species synthesize the red anthocyanin pigments at this time. Similar pigment changes occur in many fruits. These symptoms of organ senescence are often accompanied by changes in the levels of plant **hormones** in the cells, with shifts in the absolute amount and sensitivity towards the gaseous hormone, ethylene, playing a pivotal role.

hormone molecule released by one cell to influence another

Annual herbaceous plants live only a single growing season, with senescence occurring in all of the structures as the next generation, represented by the seeds, is shed. In perennial plants like trees, the leaves may be shed every year in a process called **abscission**, but the main part of the plant will continue to survive. Abscission in these deciduous plants is often considered as a part of their senescence, although the process of leaf abscission and the formation of a leaf scar is an active process. Some perennials are evergreen,

abscission shedding of leaves; falling off



The reds and yellows of the fall landscape are due to the pigment changes occurring during the early stages of senescence in millions and millions of leaves.

and their leaves may be retained and function in the processes of photosynthesis for several years.

Although some individual trees and some seeds can survive for many decades or even centuries, eventually disease and other environmental challenges will lead them to their death. At that time the plant body, along with those thousands of tons of plant material returned to the soil every year, will be recycled by microbes and other soil organisms and feed a new generation of living plants.

In a world increasingly dominated by global markets for fruits, vegetables, and horticultural products, including cut flowers, people's ability to

control the rate of senescence in plant tissues has become one of the most important technologies. Harvesting, transport, storage, and distribution facilities are now focused on attempts to delay the natural senescence of a huge range of living commodities. Scientists will continue to develop their understanding of the biochemistry and molecular biology of plant senescence and refine the environmental controls in storage and transport facilities so that the world's harvest can feed everyone. SEE ALSO HORMONES, PLANT; WATER MOVEMENT IN PLANTS

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Separation and Purification of Biomolecules

Cell biologists research the intricate relationship between structure and function at the molecular, subcellular, and cellular levels. However, a complex biological system such as a biochemical pathway can only be understood after each one of its components has been analyzed separately. Only if a biomolecule or cellular component is pure and biologically still active can it be characterized and its biological functions elucidated.

Fractionation procedures purify **proteins** and other cell constituents. In a series of independent steps, the various properties of the protein of interest—solubility, charge, size, polarity, and specific binding **affinity**—are utilized to fractionate it, or separate it progressively from other substances. Three key analytical and purification methods are chromatography, electrophoresis, and ultracentrifugation. Each one relies on certain physicochemical properties of biomolecules.

Test tube showing the opalescent line of purified adenovirus after centrifugation.

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

affinity attraction

ionic based on or functioning by means of ions

Chromatography

Chromatography is the separation of sample components based on differential affinity for a mobile versus a stationary phase. The mobile phase is a liquid or a gas that flows over or through the stationary phase, which consists of spherical particles packed into a column. When a mixture of proteins is introduced into the mobile phase and allowed to migrate through the column, separation occurs because proteins that have a greater attraction for the solid phase migrate more slowly than do proteins that are more attracted to the mobile phase.

Several different types of interactions between the stationary phase and the substances being separated are possible. If the retarding force is **ionic** in character, the separation technique is called ion exchange. Proteins of different ionic charges can be separated in this way. If substances absorb onto the stationary phase, this technique is called absorption chromatography. In gel filtration or molecular sieve chromatography, molecules are separated because of their differences in size and shape. Affinity chromatography exploits a protein's unique biochemical properties rather than the small dif-

ferences in physicochemical properties between different proteins. It takes advantage of the ability of proteins to bind specific molecules tightly but noncovalently and depends on some knowledge of a particular protein's properties in the design of the affinity column.

Electrophoresis

Many important biological molecules such as proteins, deoxyribonucleic acid (DNA), and ribonucleic acid (RNA) exist in solution as cations (+) or anions (-). Under the influence of an electric field, these molecules migrate at a rate that depends on their net charge, size and shape, the field strength, and the nature of the medium in which the molecules are moving.

Electrophoresis in biology uses porous gels as the media. The sample mixture is loaded into a gel, the electric field is applied, and the molecules migrate through the gel **matrix**. Thus, separation is based on both the molecular sieve effect and on the electrophoretic mobility of the molecules. This method determines the size of biomolecules. It is used to separate proteins, and especially to separate DNA for identification, sequencing, or further manipulation.

matrix a network, usually of threadlike fibers

Ultracentrifugation

Cells, **organelles**, or **macromolecules** in solution exposed to a centrifugal force will separate because they differ in mass, shape, or a combination of those factors. The instrument used for this process is a centrifuge. An ultracentrifuge generates centrifugal forces of 600,000 g and more. (G is the force of gravity on Earth.) It is an indispensable tool for the isolation of proteins, DNA, and subcellular particles. SEE ALSO ELECTROPHORESIS

Gabriele K. Wienhausen

organelle membrane-bound cell compartment

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

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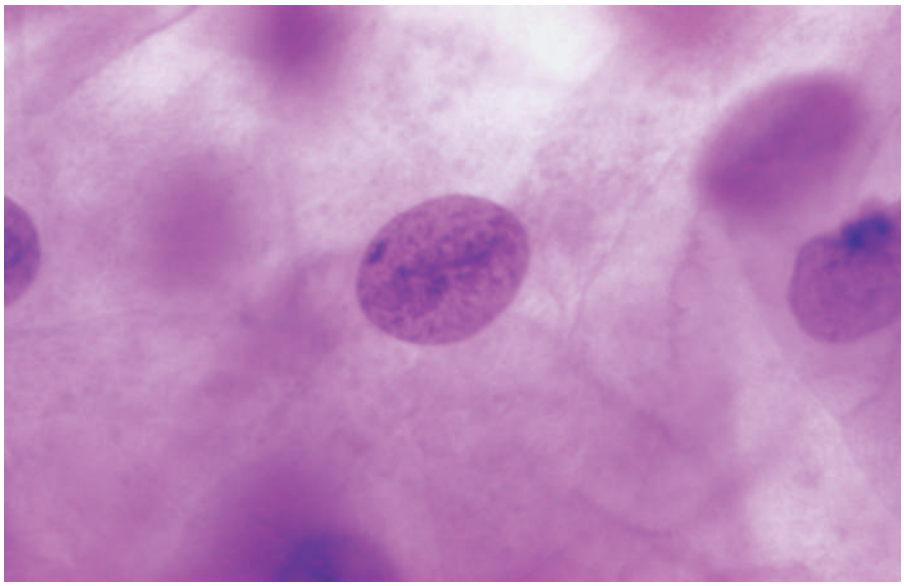
Sex Chromosomes

Sex chromosomes are particular chromosomes that are involved in determining the sex of an organism. In the cells of humans and many other organisms the sex chromosomes consist of a pair of chromosomes called the X and Y chromosomes. The X and Y chromosomes were first discovered in beetles by Nettie Stevens in 1906. She noticed that cells of female beetles had identical looking pairs of each of their several chromosomes, but that male beetles had one pair in which the chromosomes were very different in appearance from each other. She called these two chromosomes the X and the Y, and found that female beetles differed from males in containing two X chromosomes. The same situation is also found in humans where females are XX and males are XY.



A Barr body—a condensed X chromosome—in a female squamous epithelium cell at interphase.

The X and Y chromosomes in humans are also very different in appearance, with the X chromosome being considerably larger than the Y. With the exception of only about nine shared **genes**, the X and Y chromosomes do not contain the same genes, unlike the other twenty-two pairs of human chromosomes in which members of a pair share all the same genes. The Y chromosome contains the genes for determining a male pattern of development, and in the absence of a Y chromosome an embryo will follow a female pattern of development.

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

The sex of an individual is determined by which paternal sex chromosome (X or Y) is inherited at **fertilization**. Eggs and sperm, as reproductive cells, each contain only one of the two sex chromosomes as a result of having undergone **meiosis**, a form of cell division that produces daughter cells containing only one member of each chromosome pair. All eggs therefore contain an X chromosome, but half of sperm will contain an X chromosome and the other half a Y chromosome. If an egg is fertilized by a sperm carrying an X chromosome an XX or female embryo will result, while fertilization of the egg by a Y-bearing sperm will produce an XY or male embryo. In some organisms, including birds, the female contains the unlike pair of sex chromosomes. Thus, in these cases the mother determines the sex of the offspring.

fertilization union of sperm and egg

meiosis cell division that forms eggs or sperm

Since cells in a male contain a single X chromosome and cells in a female contain two X chromosomes, females contain twice as many copies of the genes on the X chromosome per cell as do males. To equalize the dosage of X chromosome genes between the two sexes, one of the two X chromosomes in each cell of all female mammals is inactivated early in embryonic development by becoming very tightly wound up or condensed. Most of the genes on the condensed X chromosome cannot be expressed. Since males carry only one copy of each X-linked gene, they are much more likely to suffer from disease if they inherit a defective gene. X-linked disorders include some forms of color blindness, Duchenne's muscular distrophy, and some types of hemophilia.

The inactivation of an X chromosome in the cells of a developing female embryo occurs randomly, so that about half of the cells express the

genes in one X chromosome and half express the genes in the other X chromosome. Once a particular X chromosome has been inactivated in a cell, it will remain inactivated in all of the descendants of that cell. If a female mammal has different forms or **alleles** of a particular gene on each of her two X chromosomes, then about half of her cells will express one of the alleles and about half the other allele. An example of such a genetic mosaic is a calico cat, carrying an allele for orange fur color on one X chromosome and an allele for black fur color on the other X chromosome. The result is a characteristic coat of mottled orange and black patches of fur. Since this type of genetic mosaicism requires the presence of two X chromosomes, calico cats are normally always female.

allele a particular form of a gene

Chromosomes are ordinarily visible under a microscope only when the cell is dividing. However, when nondividing cells are treated with stains that bind to chromosomes, a darkly staining body is visible in the nuclei of cells from females but not in cells from normal males. This body is actually the condensed X chromosome, and it is called a "Barr body" after its discoverer, Murray Barr. In 1961 Mary Lyon proposed that the **condensation** of the X chromosome into a Barr body was a mechanism for inactivating the genes on the chromosome. This is called "The Lyon Hypothesis," in her honor. The presence or absence of a Barr body in cells is used in medical and criminal **forensics** to determine and legally define the sex of an individual. SEE ALSO CHROMOSOME, EUKARYOTIC; CONTROL OF GENE EXPRESSION; GENE; SEX DETERMINATION

condensation compaction of chromosome strands into a tight structure

forensic related to legal proceedings

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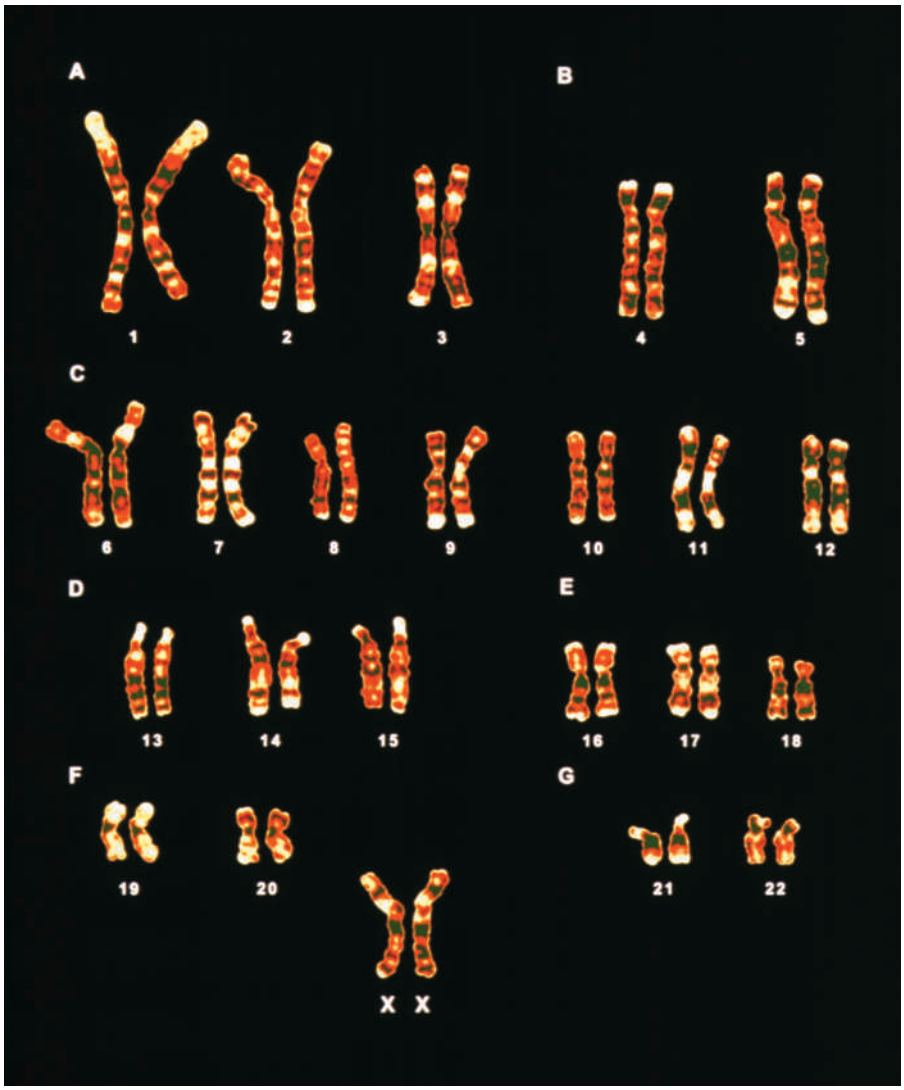
Sex Determination

Sex determination refers to the hormonal, environmental, and especially genetic mechanisms that make an organism male or female.

Chromosomal Sex Determination

It is widely known that people who inherit sex chromosome X from the mother and Y from the father are genetically male, while people who inherit X from both parents are genetically female. Thus, the sex of an offspring is determined entirely by which of the male's sperm (one carrying X or Y) fertilizes the egg (which always carries X). This fact was not realized until the twentieth century, however. Before that, women were often held accountable for not producing a male heir, and in some cases even murdered for it (as in the case of Anne Boleyn, second wife of King Henry VIII).

In actuality, it is merely the presence of a Y chromosome that makes a person male and its absence that makes a person female. Through accidents of chromosomal sorting (meiosis) during sperm and egg production, some people inherit an XXY combination, but are still male (with Klinefelter syndrome). Others inherit only one X, and are thus denoted XO; they are genetically female (with Turner syndrome). Such people are often, but not



Normal human female chromosomes (XX) in karyotype (their ordered set). The stained banding reveals variations in the DNA sequence composition.

always, sterile. (The YO condition is fatal, because the X carries many genes that are indispensible for survival.)

The biological law that XX results in a female and XY results in a male is true not only in humans, but in all mammals. In birds and most reptiles, however, it is the opposite: XX individuals are male and XY individuals are female. In fruit flies (*Drosophila*), XX is female and XY is male, but the Y is inert and the sex is determined by whether there are two X chromosomes or only one. (Thus, XO is female in humans but male in *Drosophila*.)

Not all animals have sex chromosomes. In ants, wasps, and bees (insect order Hymenoptera), sex is determined by whether or not the egg is fertilized. If it is not, it remains **haploid** (n) and produces a male; if fertilized, in becomes **diploid** (2n) and produces a female. This is true in some other invertebrates as well, such as rotifers. In whip-tailed lizards of northern Mexico and the southwestern United States, males are nonexistent. Every egg remains unfertilized and produces a female, yet females have to simulate copulation with each other to induce the eggs to develop.

haploid having single, nonpaired chromosomes in the nucleus

diploid having pairs of chromosomes in the nucleus

STEVENS, NETTIE MARIA (1861–1912)

American biologist who first showed, in 1906, that sex is determined by the presence or absence of X and Y chromosomes, thus confirming the new theory that chromosomes carry the genes and are the instruments of heredity.

Hormonal Sex Determination

Genes are not enough to make a male or female. To produce a human male requires not only the XY chromosome pair but also an adequate level of testosterone exposure during fetal development. If testosterone or the cellular receptors for it are lacking, as in androgen-insensitivity syndrome (AIS), an XY human may be born with female **genitalia** and misidentified as a baby girl. Conversely, if an XX fetus is exposed to a testosterone excess (from the adrenal glands), the labia may fuse into a scrotumlike sac, the clitoris may grow to resemble a penis, and the baby may be misidentified as a boy; this is called adrenogenital syndrome (AGS). The mistaken identity often comes to light only at puberty, when the individual fails to develop as he or she normally would for the mistakenly assumed sex. Such belated discovery of the child's genetic sex creates some difficult issues of gender identity.

genitalia reproductive organs

Environmental Sex Determination

In some fish and reptiles, sex is determined by the temperature at which the eggs are incubated. In lizards and alligators, warm incubation temperatures cause all eggs to produce males, while temperatures only 1 or 2 degrees Celsius (34 or 35 degrees Fahrenheit) cooler produce females. The opposite is true of most turtles. Thus, a sea turtle might have all daughters if she lays her eggs on a beach site with full sun, but all sons if she lays them in the shade of vegetation in the dunes. Conservationists who rescue sea turtle eggs from predators and hatch them in the laboratory quickly learned that they had to vary the incubation temperature if they were to produce a mixture of sexes.

The sex of an animal is not always fixed for life. Many fish change sex at some point. In some coral reef fish, a male controls a harem of females, and the females have a dominance hierarchy among themselves. If the male dies or disappears, the top-ranking female changes into a male within a few days. Her ovaries regress, testes develop, and she/he soon produces sperm and takes over control of the harem. SEE ALSO CROCODILIANS; FEMALE REPRODUCTIVE SYSTEM; MALE REPRODUCTIVE SYSTEM; REPTILE; SEX CHROMOSOMES; SEXUAL REPRODUCTION; TURTLE

Kenneth S. Saladin

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Sexual Reproduction

Sexual reproduction is a method for producing a new individual organism while combining **genes** from two parents. A single sperm and egg fuse during **fertilization**, and their **genomes** combine in the new **zygote**. Sperm are small and contain little more than the father's genes. Eggs are large and contain the mother's genes and all cellular components necessary for the

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

fertilization union of sperm and egg

genome total genetic material in a cell or organism

zygote fertilized egg

Common frogs in amplexus. Sexually reproducing individuals spend a considerable amount of time and energy locating mates, exchanging genetic material, and often caring for young.

early development and nutrition of the embryo. The sexual dimorphism in **gamete** size is echoed in many other traits of adults and has resulted in the evolution of different male and female reproductive strategies. Sexual reproduction is widespread in almost all groups of multicellular organisms, but the reasons for its evolution and prevalence are not well known.

gamete reproductive cell, such as sperm or egg

Fertilization

Much scientific knowledge about the steps of fertilization comes from observations on sea urchins and other marine invertebrates. In these animals, sperm cells that contact the jelly coat surrounding the egg react with large **carbohydrates** in the jelly. These carbohydrates cause the sperm to release **protein**-digesting **enzymes** that erode a path through the jelly coat and stimulate the sperm to burrow into the egg. Once the sperm reaches the egg surface, a protein called bindin on the sperm membrane attaches to a receptor molecule on the egg membrane. Following this attachment, the egg and sperm membranes fuse and fertilization is complete.

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

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

enzyme protein that controls a reaction in a cell

Fertilization usually must involve only one egg and one sperm. Fusion of additional sperm is prevented by a change in the electrical voltage of the egg cell membrane within a second or two of the first sperm fusing with it. The change in voltage results from sodium **ions** moving into the egg **cytoplasm**, but how it prevents additional sperm from fusing is not well known. Multiple fertilizations are further prevented by chemical reactions that change the receptivity of the egg's outer layers.

ion an electrically charged particle

cytoplasm material in a cell, excluding the nucleus

Successful fertilization must involve gametes (sperm and egg) from the same species. In many animals with internal fertilization, courtship behaviors and reproductive anatomy prevent fertilization between species. In some animals with external fertilization (like marine invertebrates that release their gametes into the water around them), fertilization involves species-specific chemical interactions. For example, in many sea urchins the

JUST, ERNEST E. (1883–1941)

American biologist who first described how fertilization sets the stage for development. Just found that the place on an egg where a sperm enters determines which side of the embryo will be the dorsal (back) side and which the ventral (belly) side.

sperm-activating carbohydrates in the jelly and the bindin and bindin-receptor proteins are very species-specific, thereby ensuring conspecific fertilizations.

Male and Female Sexual Strategies

Because their gametes are rare and energetically costly to produce, females suffer a greater consequence of mating with the wrong species or with a low-quality mate than do males. This disparity between the sexes imposes different selective pressures on males and females. Females usually increase their evolutionary fitness (number of surviving offspring) by mating with high-quality males. Males usually increase their fitness by mating frequently to increase the chances that their sperm will encounter a rare egg. Consequently, females have often evolved mechanisms for choosing the fathers of their children, while males have often evolved mechanisms for gaining access to females and their eggs.

Males may gain access to females by competing with other males. The enormous size of bull elephant seals and the head-slamming contests of mountain goat rams are familiar examples of attributes that increase an individual male's access to females. More cryptically, competition for access to eggs rather than to females can occur among sperm even after mating has occurred. For example, boars and some promiscuous monkeys produce copious amounts of semen to displace the sperm left in the female's vagina by other males. A male damselfly will remove a previous male's sperm from a female before depositing his own. Male snakes insert a plug into the female's reproductive tract after mating to prevent insemination by subsequent males. Many rodents have evolved penises with hooks and spines to dislodge the plug left by a previous male. And mammalian semen contains **prostaglandins** that stimulate the uterus to contract, thereby pumping the semen toward the egg and hastening fertilization.

prostaglandins hormone-like molecules released by one cell that affect nearby cells, including smooth muscle

Females can choose mates on the basis of material offerings or particular male traits. Female hangingflies mate with males that present them with large prey items, while peahens choose peacocks with showy tails, and female frogs choose males with energetic calls. As with sperm competition in males, females may also exercise cryptic choice in deciding which males will fertilize their eggs even after mating with them. Examples include beetles in which the female contracts muscles in her reproductive tract to prevent males from inserting their sexual organs completely, lionesses that delay ovulation after their pride is taken over by new males, zebras that eject semen from their vaginas, and female spiders that transport more or less sperm from a given male down their reproductive tracts depending on the vigor of his courtship.

Evolution of Sexual Reproduction

Many organisms reproduce asexually; that is, they produce genetically identical clones. All of an asexual individual's offspring can also produce offspring, but for a sexual female that produces both daughters and sons, only the daughters can bear young. If an asexual individual and a sexual female each produce the same total number of offspring in an unchanging environment, then the asexual individual will have twice as many grandchildren as will the sexual female (since only half of the sexual female's children will

bear young), four times as many great-grandchildren, and so on. In this sense, sex is evolutionarily very costly; that is, it appears to have a lower fitness than a strictly asexual strategy. Sex also carries other costs such as energy expenditures associated with finding and competing for mates and the risk of exposure to sexually transmitted diseases. So why has sex evolved and why does it persist?

Most explanations for sex are based on the fact that sexual reproduction results in genetically variable offspring, whereas asexual reproduction does not. Genetic variation among offspring is valuable, particularly when environments change over time. If the environment changes for the worse, an asexual mother may lose all of her offspring, while a sexual mother is likely to have at least some of her offspring survive the new conditions. Environments usually do change, particularly in terms of the adaptations of other organisms with which a species interacts. In such uncertain environments sexual reproduction should be favored by natural selection. But as in much of biology, there is no single widely accepted answer for the evolution and persistence of sex in all organisms. SEE ALSO EVOLUTION; FEMALE REPRODUCTIVE SYSTEM; FETAL DEVELOPMENT, HUMAN; MALE REPRODUCTIVE SYSTEM; MATING SYSTEMS; MEIOSIS; SEX DETERMINATION; SEXUAL REPRODUCTION, EVOLUTION OF; SEXUAL SELECTION

Tim Watkins

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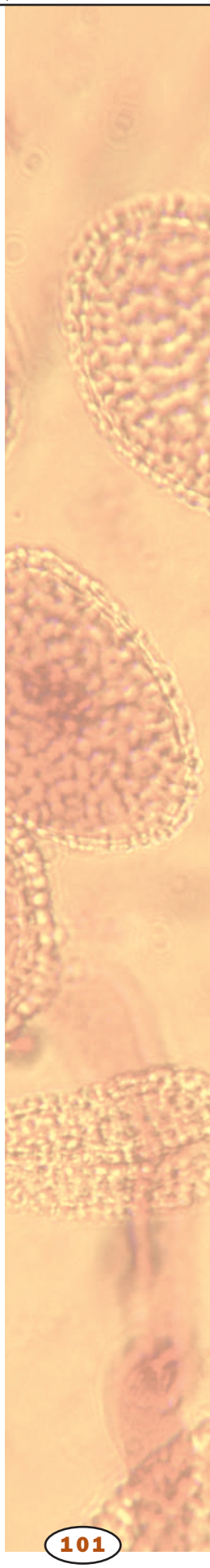
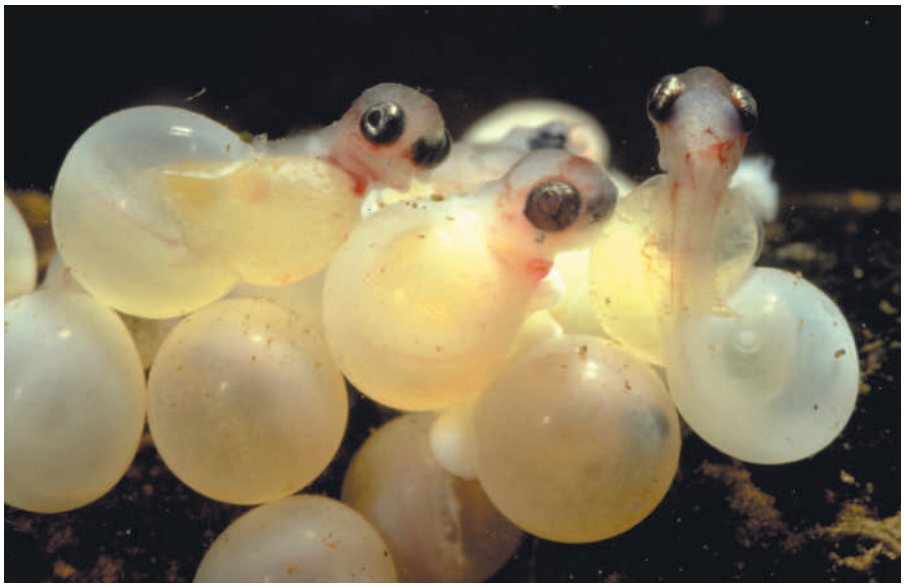
Sexual Reproduction, Evolution of

The most basic way to reproduce is to make more copies of one's self, a process called asexual reproduction. In contrast, sexual reproduction involves the union of specialized sex cells (eggs and sperm) from two parents to produce genetically unique offspring.

Asexual Reproduction

A variety of ways exist by which organisms can reproduce asexually. Many protozoans, such as Euglena or Amoeba, undergo binary fission, whereby a single-celled organism divides evenly into two identical cells. Others, such as Trypanosoma (which causes African sleeping sickness), undergo multiple fission, involving repeated nuclear division before splitting into many daughter cells. Some organisms divide in a different way, with a single parent forming an outgrowth, or bud. Many yeasts, hydroids, and freshwater sponges reproduce by budding, typically in combination with sexual reproduction. A wide variety of organisms are capable of regenerating whole individuals from a fragment. Flatworms, sea anemones, green algae, and some





Rainbow trout hatchlings emerging from their eggs. Organisms producing many unique individuals in an unpredictable environment have a greater chance that at least some their offspring will survive.

plants can reproduce asexually by fragmentation if injured, and some sea stars can actually split their own body into pieces to form multiple individuals.

Parthenogenesis is another unique form of asexual reproduction in which female organisms are able to produce offspring from unfertilized eggs. Several species of **nematodes**, crustaceans, insects, and desert lizards are able to reproduce parthenogenetically. Many plants are capable of reproducing both asexually and sexually. Asexual reproduction occurs in a variety of ways, including production of rhizomes (horizontal underground stems), runners (aboveground stems that run along the ground), and suckers (vertical stems that arise from the base of stumps or existing stems).

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

Because asexually reproducing organisms produce identical copies of themselves, they pass on the maximum quantity of their own genetic material to each offspring: 100 percent. This kind of reproduction is typically very rapid.

Sexual Reproduction

In contrast, sexually reproducing individuals spend a considerable amount of time and energy locating mates, exchanging genetic material, and often caring for young. Sexual reproduction begins with production of sex cells via **meiosis**, a process that halves the genetic material of each parent in preparation for combination with another sex cell. Consequently, a sexually reproducing parent transfers only 50 percent of its genetic material to each offspring. This loss in genetic contribution to each offspring is known as the cost of meiosis. In addition to this cost, males produce enough sperm to fertilize the eggs of many females, yet many males in some species never even fertilize one egg, resulting in many wasted sperm. In light of all of these disadvantages, why did sexual reproduction evolve?

meiosis cell division that forms eggs or sperm

For some plants, spore-forming protozoans, and invertebrates, sexual reproduction may yield seeds or eggs that are resistant to harsh environments and are capable of being dispersed. However, scientists agree that

the most important advantage of sexual reproduction is the variation produced by the continual recombination of sex cells to create unique individuals. In 1930, Ronald A. Fisher noted in *The Genetical Theory of Natural Selection* that this variation allowed evolution to occur at a faster rate. This idea led to two theories explaining how increased genetic variation might benefit individuals.

Importance of Genetic Variation

George Williams compared reproduction to a raffle in which one can either have many tickets with different numbers (sexual reproduction) or many tickets with the same number (asexual reproduction). If one doesn't know which number will be drawn in a raffle, it is better to have many different tickets. Similarly, organisms producing many unique individuals in an unpredictable environment have a greater chance that at least some their offspring will survive. Thus, Williams proposed that sexual reproduction evolved because of the benefits gained by organisms in fluctuating physical environments. This is often called the "bet-hedging" or "tangled bank" hypothesis.

Others argue that sexual reproduction evolved because of advantages gained in the face of changes in other organisms. Predators, prey, and **parasites** constantly improve their efficiency at capturing prey, evading predators, and extracting nutrients from hosts. Genetically variable offspring offer more opportunities for each to increase its efficiency. This is called the "Red Queen" hypothesis after the popular book, *Alice in Wonderland*, in which the queen tells Alice, "Now *here*, you see, it takes all the running you can do, to keep in the same place."

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

Scientists have collected data in support of each of these hypotheses. The bet-hedging or tangled bank hypothesis predicts that sexual reproduction should predominate in unpredictable environments, while asexual reproduction should be found more frequently in stable environments. In support of this prediction, scientists have found that when species alternate between sexual and asexual reproduction, they often reproduce asexually in the spring and summer but sexually in the fall and winter when the environment is harsher.

The Red Queen hypothesis, on the other hand, predicts that sexual reproduction should increase in frequency as rates of parasitism or predation increase. Curt Lively studied a species of snail that lives in lakes and streams in New Zealand. He found more parasites infecting the snails living in the lakes than the snails living in the streams. As predicted by the Red Queen hypothesis, the snails in the lakes were more likely to reproduce sexually than those living in the streams. Furthermore, the number of males in a population (an indicator of the frequency of sexual reproduction) increased as rates of parasitism increased. Scientists continue to seek support for each of these hypotheses, and it appears likely that each applies to at least some situations; both environmental and **biotic** fluctuations make sexual reproduction advantageous.

biotic living

Michelle J. Solensky

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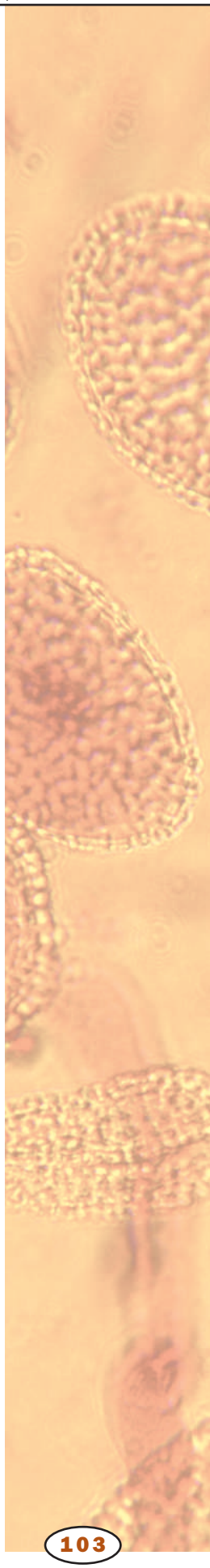

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Sexual Selection

English naturalist Charles Darwin revolutionized scientific thinking when he proposed that species evolve over time to become adapted to their environments by means of natural selection in his *On the Origin of Species* (1859). He was initially puzzled, though, by the seemingly useless exaggerated characters often found in animals, particularly males. The long and colorful tail of the peacock, for example, seemed to hinder rather than help its bearer survive. In his later work, *The Descent of Man, and Selection in Relation to Sex* (1871), Darwin proposed that some characters do not increase survival, but instead increase reproductive success. He called this sexual selection, which refers to the process that produces traits that affect an individual's reproductive success as a result of competition over mates.

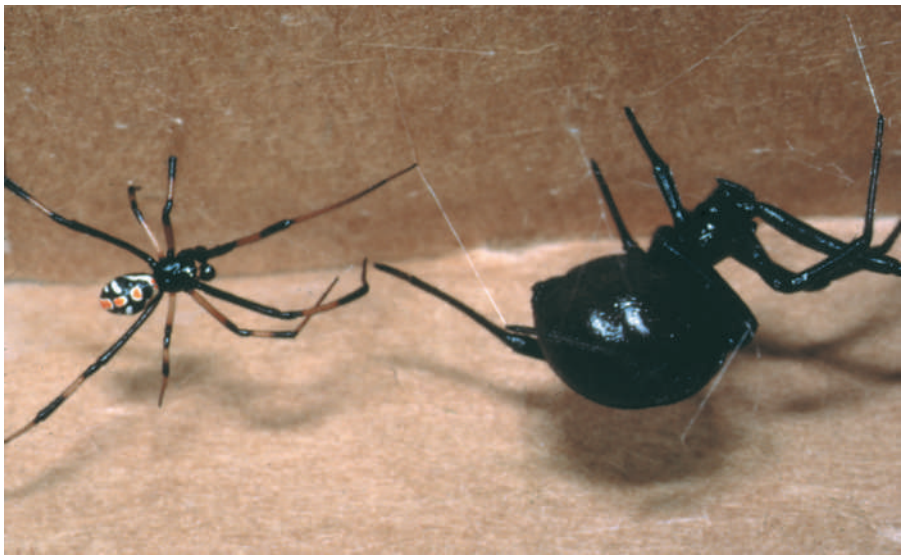
While both sexual selection and natural selection are evolutionary processes that increase an organism's fitness, they differ in several important ways. Environmental, physical, or biological factors often drive natural selection, whereas sexual rivals and mates are the exclusive agents of sexual selection. Furthermore, the evolutionary effects of sexual selection differ markedly from those of natural selection. Sexual selection frequently produces sexual dimorphism and exaggerated male traits, often in opposition to the forces of natural selection.

For example, male widowbirds have extraordinarily long tails (more than twice their body length) that make flight more difficult. When researchers manipulated the tail length of several males, they found that female widowbirds preferred males with longer tails to males with short or normal length tails. Thus, while the long tails of widowbirds may be selected against by natural selection, they are favored by sexual selection.

There are two broad categories of sexual selection: intrasexual selection (members of one sex compete among themselves for reproductive opportunities with individuals of the other sex) and intersexual selection (members of one sex choose among members of the other sex).

Intrasexual Selection

Many examples of intrasexual selection are readily observable. Males of many species fight, display, vocalize, and otherwise compete for the opportunity to mate with available females. Male deer fight with their antlers and enormous male elephant seals fight with their bulk to establish dominance and



Male (left) and female black widow spiders. Mate choice is a widely popular topic of study.

consequently the right to mate with females. Male red-winged blackbirds display and sing to establish their territories, the quality of which determines the number of mates they will attract.

Post-mating competition also occurs. Male dragonflies often guard their mates after copulation to ensure that the female lays her clutch of eggs before remating. Male fruit flies sometimes transfer a substance to their mate that inhibits courtship by subsequent males. Male dunnocks (a small European bird) often peck the **cloaca** of their mate until she everts it, sometimes ejecting sperm.

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

Once the male has successfully rid the female of the sperm from a previous mate he will proceed to reinseminate her. Some male parasitic worms cement the **genitalia** of their mates after copulation to form a copulatory plug. These male worms take intraspecific competition one step further by occasionally "mating" with rival males and cementing the genitalia of their rivals to prevent subsequent sperm transfer.

genitalia reproductive organs

Intersexual Selection

For several decades after Darwin presented his theory of sexual selection, most naturalists discounted the importance of intersexual selection, or mate choice. However, in the 1950s a few scientists began to revisit this subject, and by the 1980s mate choice had gained wide popularity as a topic of study.

Many exaggerated male traits are now thought to have evolved as a result of female mate choice, although several competing hypotheses exist to explain the origin and maintenance of these female preferences. Ronald A. Fisher proposed an explanation called "runaway sexual selection" in *The Genetical Theory of Natural Selection* (1930). Fisher suggested that as females began to evolve a preference for a particular male trait, such as tail feather length, these females would be more likely to mate with males who displayed the preferred trait. The offspring of these matings would inherit the genes for both the male trait and the female preference, resulting in a genetic correlation between the preference and the trait. Consequently, as the male trait spreads because females prefer it, the female preference itself also

spreads because it is linked with the male trait. This is called a self-reinforcing choice, and is one way that exaggerated male traits can evolve without conferring any direct benefits on the females who prefer them.

Another explanation for the evolution of female choice is called the handicap hypothesis. In his study "Mate Selection—A Selection for a Handicap" (1975), Amotz Zahavi suggested that exaggerated male traits indicate to females that the male is healthy enough to survive despite his substantial handicap. The exaggerated trait is a signal through which females can assess a male's genetic quality, and therefore is often called a good genes hypothesis. This is another way that exaggerated male traits can evolve without directly benefiting the females who prefer them.

Other explanations of the evolution of female mate choice include sensory bias (for example, female frogs prefer males who call loudly or in a low pitch because they can hear them better) and direct benefits (for example, females might prefer males who provide superior resources, defense, or parental care).

Experimental Techniques

The refinement of several genetic analyses in the late 1980s and the 1990s have contributed greatly to the study of sexual selection. Using deoxyribonucleic acid (DNA) fingerprinting, microsatellite DNA typing, and related techniques, researchers can confidently assign paternity to offspring using genetic markers, whereas in the past they had to rely on behavioral cues. These techniques are particularly well used in **avian** studies, where scientists are learning that many birds thought to be monogamous actually have a high frequency (30 to 95 percent) of promiscuity. Using molecular techniques to definitively assign paternity has and will continue to further the study of sexual selection, particularly mate choice and sperm competition. SEE ALSO Behavior, Genetic Basis of; Darwin, Charles; Evolution; Mating Systems; Natural Selection; Sexual Reproduction

avian concerning birds

Michelle J. Solensky

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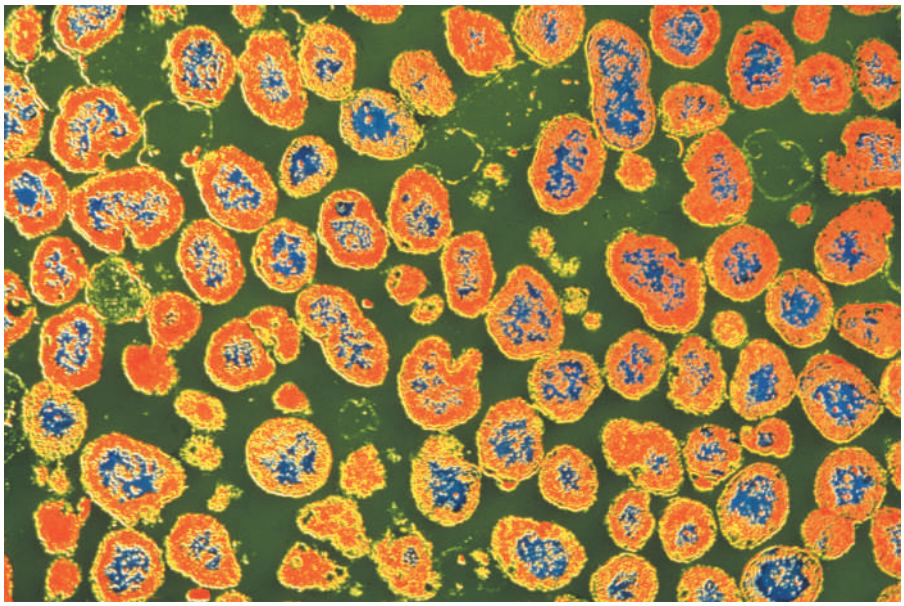
Sexually Transmitted Diseases

A sexually transmitted disease (STD) is any disease whose primary (though not necessarily only) mode of transmission is some form of sexual contact. STDs may be viral, bacterial, protistan (protozoan), or fungal. Certain



Colorized micrograph of gonorrhea cells. Because of the permanent reproductive tract damage gonorrhea can cause, it is often called the "great sterilizer."

STDs, such as gonorrhea and syphilis, are classified as "reportable" because when diagnosed they must be reported to a proper health or government agency to prevent their spread.

Bacteria

Gonorrhea. Gonorrhea, one of the most widespread of the STDs, is caused by the bacterium *Neisseria gonorrhoeae*, some strains of which are resistant to treatment by penicillin as well as the other drugs of choice. The organism itself is quite fragile and cannot survive long enough outside the body to be transmitted from one person to another via infected toilet seats, clothing, or household utensils. It is readily killed by sunlight, drying, or ultraviolet light.

Although any **mucous membrane** may be affected, the usual gonorrheal infection is found in the genitourinary tract. In the female, the symptoms of gonorrhea are usually mild and may resemble a simple vaginal infection, or they may go completely unnoticed. If left untreated in females, the infection can cause a blockage of the **fallopian tubes** as well as other pelvic inflammatory diseases. Because of the permanent reproductive tract damage gonorrhea can cause it is often called the "great sterilizer."

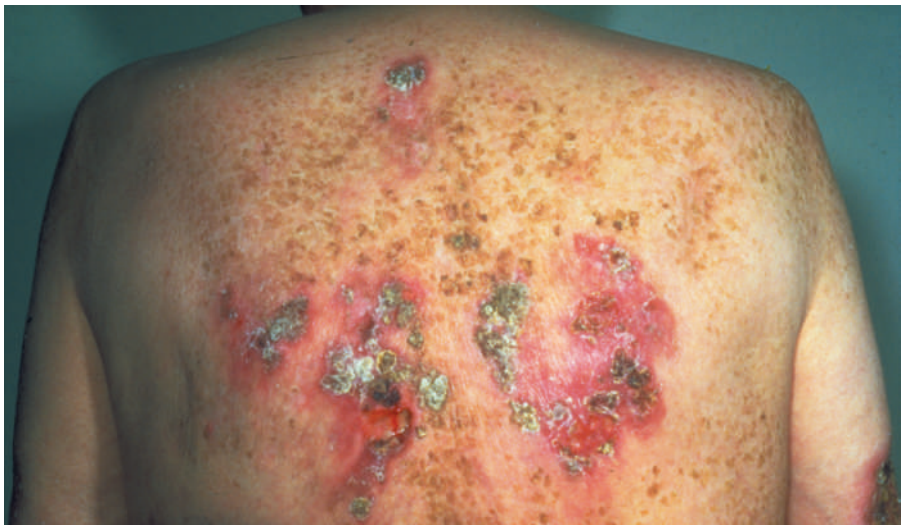
mucous membrane outer covering designed to secrete mucus, often found lining cavities and internal surfaces

fallopian tubes tubes through which eggs pass to the uterus

In males, the organism often causes a painful infection of the urethra and if left untreated, a complete blockage of the urethra can occur. Other complications of gonorrhea may include damage to the kidneys, heart valves, and joints. The rectal area, **conjunctiva**, and oral mucosa may also be affected. Because infants can acquire gonorrhea of the conjunctiva while passing through the birth canal of an infected mother, the eyes of newborns are routinely treated with silver nitrate or a penicillin ointment.

conjunctiva eye membrane that helps seal the eye socket

Syphilis. Syphilis begins when the spirochete bacterium *Treponema pallidum* enters the body through a tiny break in the skin. The primary lesion, forming at the site of entry between ten and ninety days after infection, is called a chancre and it is teeming with the spirochetes. This chancre is also normally painless and thus may go undetected, particularly in females if it



Syphilitic infection on a man's back. Syphilis is classified as a "reportable" disease: when a case of syphilis is diagnosed, it must be reported to a proper health or government agency to prevent its spread.

is high in the vagina. The chancre usually disappears, but the organisms disperse to various parts of the body. About six weeks later, secondary syphilis appears as a **hypersensitivity reaction** to the bacteria. Secondary syphilis is usually characterized by a generalized skin rash (including on the palms of the hands and the soles of the feet) and often by such flu-like symptoms as headache, fever, and general malaise.

In about half the cases, anywhere from several months to twenty or more years after the initial infection, syphilis progresses to the **tertiary** stage. (Of the remaining cases, about half appear to be cured, and the rest, while not cured, do not seem to progress to the tertiary stage.) Tertiary syphilis may be relatively mild, affecting only the bones or skin; or it may be serious or even fatal, affecting the cardiovascular system (causing such conditions as aortic **aneurysms**) or the **central nervous system** (causing paralysis or syphilitic insanity). In **congenital** syphilis, the fetus acquires the disease prenatally; the chancre of primary syphilis is bypassed.

Syphilis is usually treated with penicillin, which is especially effective in primary and secondary cases. Other drugs can be used. Treating a pregnant woman also treats her child. As with the gonorrhea organism, *Treponema pallidum* is quite fragile and cannot survive long enough outside the body to be transmitted from one person to another via infected toilet seats, clothing, or household utensils.

Nongonococcal Urethritis (NGU). Nongonococcal urethritis is a categorical term for any of a number of inflammatory diseases of the sexual organs. By far the most frequently observed of the STDs is chlamydial NGU. Other chlamydial infections include trachoma, an eye disease, and possibly certain arterial plaques and other **coronary artery** diseases.

Chlamydial NGU. Chlamydial NGU, caused by the **obligate intracellular** bacterium *Chlamydia trachomatis*, is also a reportable STD. Chlamydial NGU is often a secondary infection following a gonorrheal infection. Although asymtomatic infections are common in both sexes, in males chlamydial NGU causes urethritis, and in females it causes urethritis, cervicitis, and pelvic inflammatory disease (PID). In serious cases, acute complications such

hypersensitivity reaction immune reaction characterized by rapid and severe response, often with swelling of airways

tertiary third level

aneurysm bulging of the wall of a blood vessel

central nervous system brain and spinal cord

congenital present at birth; inherited

coronary artery artery supplying blood to the heart

EHRLICH, PAUL (1854–1915)

German physician who discovered an effective drug treatment for the sexually transmitted disease syphilis. Ehrlich's drug was the first example of a modern antibiotic, a substance that specifically kills disease-causing organisms without significantly hurting the patient. He won many awards and prizes, including the 1908 Nobel Prize in medicine.

as testicular or prostate swelling in males or the **lysing** of fallopian tube cells in females can occur.

Pelvic Inflammatory Disease. Pelvic inflammatory disease is a categorical term for any of several inflammations of the pelvic organs. The most common causative agents of PID are *Chlamydia trachomatis* and *Neisseria gonorrhoeae*. The specific drug of choice for treatment depends on the cause of the PID. PID is more commonly associated with females than with males. Untreated PIDs can be extremely serious. PID is a leading cause of sterility, particularly among females.

Lymphogranuloma Venereum (LGV). Lymphogranuloma venereumis caused by a specific strain of *Chlamydia trachomatis* and is one of the most serious of the chlamydial infections. This disease occurs more frequently in males and is characterized by swelling in the groin and in the lymph nodes. The bacteria may also cause proctitis (inflammation of the rectal tissues). Doxycyline is the drug of choice.

Viruses

Herpes. Herpes is a virus or family of viruses (the herpes viruses) causing cold sores, fever blisters, and genital infections. Herpes virus type I (HV1) was formerly thought of as causing problems "above the belt," while Herpes virus type 2 (HV2) has been credited with problems "below the belt." Today it is known that either HV1 or HV2 (including their many **serotypes**) can infect any area of the body.

Genital (or anogenital) herpes results in painful blisters of the anus, penis (in males), and cervix, **vulva**, or vagina (in females). The disease, which can recur at sporadic intervals, is most contagious during the blister stage. Although the disease is incurable, it can be treated. Acyclovir is the drug of choice. Because genital herpes can be passed on through the birth canal, babies of pregnant women with this infection are often delivered by caesarian section. A significant correlation exists in females between genital herpes and cervical cancer.

Genital Warts. Genital warts are caused by a group of papilloma viruses. The presence of these warts in women has been associated with an increased risk of cervical cancer. Warts can be removed surgically, chemically, or by cryotherapy (freezing).

The Hepatitis Viruses. The hepatitis viruses, often identified today as A, B, C, D, and E, are not strictly STDs. However, hepatitis B and hepatitis C can be spread by sexual contact and hepatitis B can be spread in utero.

Protozoans and Yeast

Trichomoniasis. Trichomoniasis is an NGU caused by the protozoan *Trichomonas vaginalis*. Although usually sexually transmitted, this disease is occasionally acquired from infected toilet or sauna seats, paper towels, or clothing. The organism infects the vagina and urethra of females and affected women experience vaginitis, vaginal discharge, and painful urination. In males the organism can infect the prostate, seminal **vesicles**, and urethra. The disease seems to be more prevalent among females than males, although males are more likely than females to be **asymptomatic**.

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

intracellular within a cell

lysing disintegration or dissolution of cells

serotype identity of an organism or virus based on reaction to an antibody

vulva external female genitalia

vesicle membrane-bound sac

asymptomatic without symptoms

HAZEN, ELIZABETH LEE (1885–1975)

U.S. biologist who, with Rachel Brown (1898–1980), developed the first fungicide. Nystatin is still used to treat dangerous oral and intestinal yeast infections. Hazen was orphaned at age two, attended the first state-supported college for women in the United States, and succeeded against great odds to become a biologist. Hazen and Brown donated all royalties from nystatin—worth more than $13 million—to academic science.

Candidiasis. Candidiasis, caused by the fungus (yeast) *Candida albicans*, is an **opportunistic** disease that often infects the vaginal tract, oral cavity, or respiratory system. The organism can also cause **systemic** tissue damage. SEE ALSO AIDS; Bacterial Cell; Bacterial Diseases; Birth Control; Female Reproductive System; Fungal Diseases; Male Reproductive System; Parasitic Diseases; Protozoan Diseases; Viral Diseases

Roberta M. Meehan

opportunistic infectious in an immunosuppressed person but not a healthy person

systemic throughout the body

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Shoots

The shoot is the production center for a plant. It is the organ system that gives rise to stems, leaves, and flowers. Therefore, the shoot system is functionally responsible for food production (photosynthesis) and reproduction. Shoots can be classified as vegetative or floral. Vegetative shoots are described in this article.

Anatomy

Vegetative shoots consist of stems and leaves. The stem is the major structural support for the plant, but also contains vascular tissues that transport water, **minerals**, and food throughout the plant. Examining the organization of plant tissues within a stem highlights these functional characteristics. The outer regions of the stem are covered with dermal tissue made up of epidermal cells. These cells protect the stem and help to prevent water loss. Internal to the epidermis lies the ground tissue and vascular bundles. The organization of these tissue types within a stem varies with the type of plant. For example, monocotyledons have vascular bundles of **xylem** and **phloem** scattered throughout the diameter of the stem with ground tissue surrounding them. In contrast, dicotyledons have vascular bundles that are arranged in a ring surrounded by ground tissue. The ground tissue that lies to the exterior of the vascular bundle ring is called cortex, and the ground tissue that lies interior to the vascular bundles is called pith.

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

xylem water-transporting system in plants

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

Vascular Functions

Regardless of the organization within the stem, the function of the vascular components is essentially the same in all higher plants. The xylem transports the water and minerals absorbed by the root up through the stems to the leaves and flowers. On the other hand, the phloem transports the sugars and other nutrients, made by the leaves throughout the plant, to the root for immediate use or for storage during periods of dormancy and to flow-

Young shoots of fiddlehead ferns.

ers for growth or fruit production. The ground tissue, which constitutes the bulk of the stem, is mainly composed of parenchyma cells that produce **carbohydrates** (via photosynthesis) and store nutrients. However, the ground tissue also contains collenchyma and sclerenchyma cells that provide support with their rigid cell walls.

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

Branching

On a larger anatomical scale, stems contain nodes, where leaves are attached, and internodes, the stem segments between nodes. There is usually a main shoot and side shoots, called branches. The side shoots grow from axillary buds that form at the nodes. In a young plant, most of the growth in the shoot system occurs in the main shoot and the developing leaves. During this stage, the growth is concentrated in the terminal bud at the shoot tip. The plant invests its energy into growing taller in order to maximize the plant's exposure to light. In fact, certain cells in the shoot tip produce a **hormone**, called auxin, that is transported down the shoot and functions to inhibit the growth of axillary buds. As the plant ages, the stimulatory effects of a group of hormones called cytokinins overcome the inhibitory control of auxin and the axillary buds begin to develop into **lateral** branches. This results in a bushier plant that allows for more leaf growth and greater exposure to the plant's environment. These hormonal effects are often taken advantage of in agriculture and gardening to manipulate the shape of a plant. Removing the shoot tip ("cutting back") will remove the source of auxin and will stimulate the growth of axillary buds, and make the plant thicker and bushier.

hormone molecule released by one cell to influence another

lateral side-to-side

Modified Shoots

Some plants have modified stems that serve a variety of different functions. Strawberries have modified stems called stolons that grow on the surface of the ground and allow the plant to spread and occupy a large section of

nutrient-rich soil. Tubers, such as the modified stems of white potatoes, are specialized for food storage. Bulbs are also modified stems that are specialized for storage, and rhizomes are stems that grow laterally underground and are often mistaken for roots.

Leaves

Leaves are the major sites of photosynthesis in most plants. They are joined to the stem via a petiole and extend from the stem at nodes. While leaves of different plants vary greatly in size and shape, they have several similar cellular features that optimize photosynthesis. Like stems, leaves are covered with epidermal cells that protect the leaf from excessive water loss. Leaves, however, have specialized epidermal cells called **guard cells**, which surround pores called **stomata**. Stomata facilitate the exchange of gases in the leaf. CO_2 diffuses into the leaf through the stomata for use in photosynthesis, and O_2, the waste product of photosynthesis, diffuses out of the leaf through stomata. The vascular tissue within a leaf is organized into veins. The remaining tissue in the leaf is ground tissue. This ground tissue is composed mostly of parenchyma cells that have numerous chloroplasts in which photosynthesis takes place. SEE ALSO DIFFERENTIATION IN PLANTS; FLOWERS; LEAVES; MERISTEMS; ROOTS

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

Susan T. Rouse

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Signaling and Signal Transduction

All cells are able to sense and respond to substances present in their external environments. For example, **motile** bacteria will move toward a source of sugar but away from a toxic chemical such as phenol. Cells are not only able to sense chemical substances in their environments, but also such things as heat and cold. Sudden exposure to elevated temperatures results in the synthesis of a set of **proteins** that protect the cell from heat damage.

motile able to move

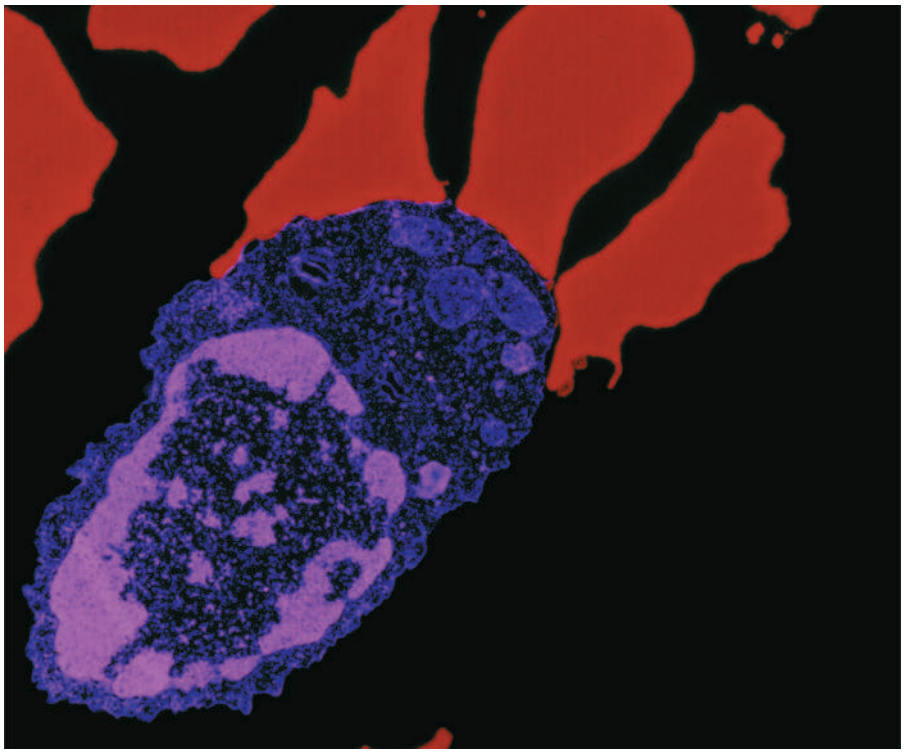
protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

The ability to respond to external stimuli enhances a cell's chance of survival, but in addition, especially in multicellular organisms, responding to external stimuli can be part of a cell's moment-to-moment function. For example, nerve impulses are transmitted through the body by the action of extracellular signaling molecules called **neurotransmitters**. Insulin, a **hormone** circulating in the bloodstream, promotes the absorption of sugar into a variety of cell types. Neurotransmitters and hormones are two important examples of extracellular signaling molecules released by one cell to influence another.

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

hormone molecule released by one cell to influence another

Extracellular signaling molecules exert their effects on a cell by binding to cellular receptors. In some cases these are inside the cell, and the signaling molecule must pass through the membrane to bind with the receptor. In most cases, however, the receptor spans the plasma membrane and the signal remains outside the cell. A membrane receptor is ideally positioned to sense signals on the outside and transmit them to the cell's interior. The



A scanning electron micrograph of lymphocytes (T cells) and three red blood cells. Responding to external stimuli (in the case of lymphocytes, to infectious agents) can be part of a cell's moment-to-moment function.

binding of a signaling molecule to its receptor activates the receptor, setting off a chain of events, much like a row of falling dominoes, called a signal transduction cascade. Activation of the receptor transmits the signal (but not the signaling molecule) to the first in a series of **enzymes** inside the cell, which in turn activates others, until the ultimate enzyme (or enzymes) is reached that causes the final response.

enzyme protein that controls a reaction in a cell

The different kinds of signal transduction pathways that exist are discussed below, followed by a more detailed description of a few of those that are the best understood, and that are **ubiquitous** throughout the animal kingdom.

ubiquitous found everywhere

Modes of Signaling

The different signaling pathways in multicellular organisms are often divided into three categories: **endocrine**, paracrine, and autocrine signaling. In endocrine signaling, a signaling molecule, called a hormone, acts on a cell located at a distance from where it was synthesized. An example of this is stimulation of **glucose** uptake by insulin. Insulin is a hormone produced by the **β** cells in the pancreas and is secreted into the bloodstream, from where it can act on many different cells, even those located far from the pancreas.

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

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

β the Greek letter beta

Paracrine signaling refers to signaling between neighboring cells. Paracrine signaling is common during development, where a cell's fate is determined by interactions with its neighbors. In addition, the passing of nerve impulses between nerve cells is an example of paracrine signaling: neurotransmitters secreted by a nerve cell into a synapse (the space between two nerve cells) bind receptors located on the neighboring nerve cell, thus transmitting an impulse.

T cell white blood cell that controls the immune response

In autocrine signaling, a cell responds to stimulants it produces. An example of this occurs during the immune response. The **T cells** of the immune system help destroy harmful invaders, and upon detecting their presence they produce and secrete growth factors to which they themselves respond. The result is an increase in their numbers, and an ensuing increase in the magnitude of the defensive response. Whether a cell responds to a signal, and how it responds, is determined by the set of receptors it has and the transduction pathways it has in place when it receives the signal. Much of the development is based on using these differences in receptors and pathways.

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

enzymatic related to function of an enzyme

The kinds of signaling molecules that exist are almost as varied as the types of proteins that exist in an organism. As would be expected, many are proteins, but many, such as neurotransmitters and **steroid hormones**, are nonprotein molecules, and still others, such as nitrous oxide and carbon monoxide, are gaseous. The types of receptors to which they bind are varied in structure and possess a variety of **enzymatic** activities, however, they are all protein in nature.

The Logic of Complex Pathways

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

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

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

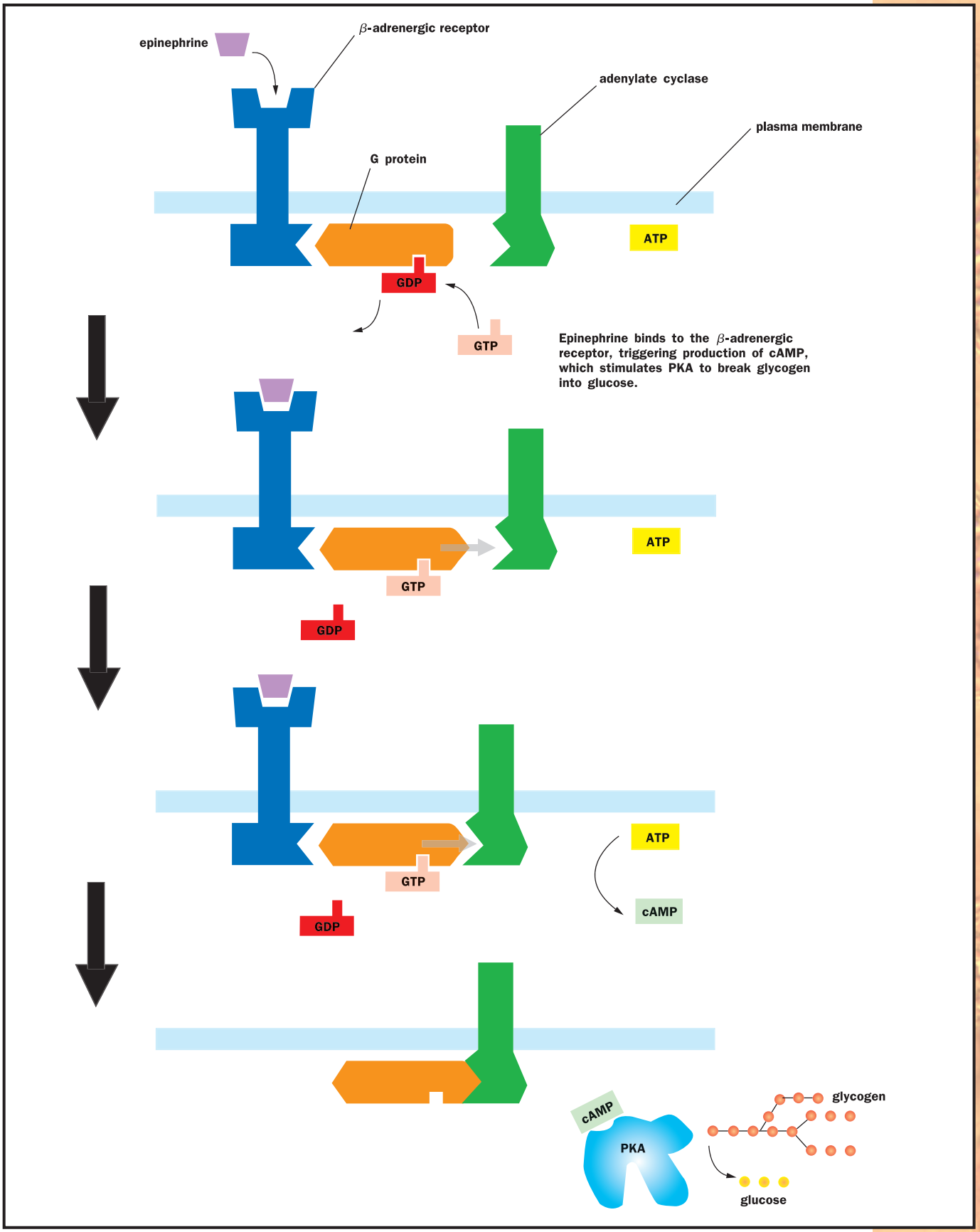
The three signaling pathways described below may seem overly complex. Why not have much simpler relay systems, say, involving just a cell surface receptor spanning the plasma membrane and a direct **effector**, such as a metabolic enzyme or a **transcription factor**? The answer may lie in the flexibility that such complex pathways afford. Having many different components in a pathway gives the cell many points at which to stimulate or inhibit the pathway, or the opportunity to use the components in different ways (see the mating pathway in yeast, for example). In addition, the relay system allows for amplification of the signal at each step. Thus, for example, the binding of a single molecule to a cell surface receptor may activate one hundred G-proteins, each of which may then activate one hundred **kinase** molecules and so on. Thanks to this type of amplification the cell can be made sensitive to even very low concentrations of extracellular stimulants.

Also, each of these pathways has been shaped over millions, or perhaps billions, of years of evolution. The features and functions of each pathway have been modified many times during evolution, with new levels of control added on top of older systems. The result is not necessarily the most efficient (although it may be in some cases), but it was what worked and was chosen by natural selection.

Stimulation of Glucose Production by Epinephrine: A Cyclic AMP-Dependent Pathway

Upon anticipation of muscular activity, such as when a fearsome predator appears in one's vicinity, the hormone epinephrine (also called adrenaline), is released into the bloodstream by the adrenal medulla. At the surface of its target cells (muscle cells, and to a lesser extent, liver cells) it binds to a receptor called the β-adrenergic receptor. The β-adrenergic receptor spans the plasma membrane. The **intracellular** portion of the receptor is bound to a member of the G-protein class of proteins. In the absence of epinephrine, the G-protein is bound by GDP and is inactive, but binding of the hormone to its receptor induces the exchange of GDP for GTP.

intracellular within a cell



Stimulation of glucose production by epinephrine.

Epinephrine release is part of the "fight or flight" response.

Through a series of steps, this activates an enzyme located in the plasma membrane called adenylate cyclase. Adenylate cyclase converts adenosine triphosphate (**ATP**), a ubiquitous molecule in the cell, into cyclic **AMP** (cAMP). cAMP is called a *second messenger* because it mediates the effects of the *first* messenger, the original inducer, which in this case is epinephrine. cAMP then activates an enzyme called protein kinase A (PKA), which activates another enzyme that stimulates the breakdown of **glycogen** into glucose, the cell's primary energy source.

Stimulated by a different enzyme, PKA acts to inhibit the incorporation of glucose into glycogen, which is the cell's energy storage molecule. Thus, by this two-pronged approach, PKA keeps the cell's usable pool of energy at a maximum during epinephrine stimulation.

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

AMP adenosine monophosphate, form of ATP after removal of two phosphate groups

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

α the Greek letter alpha

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

trimeric of a structure composed of three parts

phosphorylate add a phosphate group to

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

The Yeast Mating Pathway: A Map Kinase-Dependent Pathway

The yeast *S. cerevisiae* can be one of two mating types, called *a* and **α**, and when the two mating types encounter one another they can mate (or fuse), and subsequently give rise to offspring. Each mating type secretes its own mating factor (or mating **pheromone**), a small molecule that can be detected by receptors on the surface of cells of the opposite mating type. When an *a* cell detects α-factor in its vicinity, a variety of physiological changes occur (such as growth toward the α cell) that prepare it to undergo mating.

The α-factor receptor, like the β-adrenergic receptor described previously, is coupled to a **trimeric** G-protein. In this case, however, the next member of the pathway is a kinase called Ste20 (for *ste*rile *20*). Ste20 then stimulates a Map kinase (*m*itogen *a*ctivated *p*rotein kinase) cascade, which is a group of three kinases that are activated sequentially.

Each of the three kinases in the cascade of the mating pathway **phosphorylates** the next. Finally, the last one phosphorylates and thereby activates a transcription factor called Ste12, which activates a set of **genes** whose products prepare the cell for mating.

A fourth protein, called Ste5, plays a critical role in the activation of the Map kinase pathway, yet it possesses no known enzymatic activity. It is thought to serve as a scaffold, binding all three kinases and keeping them in close proximity, thus maximizing the efficiency of the chain reaction. This kind of scaffolding molecule has been found in other pathways as well, and may turn out to be a common mechanism for keeping signaling pathways rapid and specific.

Map kinase cascades are extremely common in animal cells and are involved in many different processes, including cell proliferation in mammalian cells (hence their name), development in fruit flies and nematodes, and programmed cell death in fruit flies and mammalian cells.

An interesting aside to the mating pathway is that a second pathway, called the filamentous growth pathway, uses some of the same components as the mating pathway. The filamentous growth pathway is stimulated by nitrogen starvation and is characterized by morphologic changes very different from those observed during mating. Two of the same three kinases (plus Ste5) are required for filamentous growth; however, a different Map kinase called Kss1 substitutes for the last member of the pathway. Both pathways converge on Ste12, which is the ultimate recipient of the signal in both cases.

If the last domino is the same in both cases, how do the different responses come about? The answer is complex and is still being deciphered;

however, part of the solution appears to lie in the ability of Ste12 to associate with different partners. Ste12 functions as a **dimer** and, depending on the identity of its partner, will activate a different set of genes. Thus, low nitrogen levels promote the association of Ste12 with one partner (and activation of a specific set of genes), while mating factor promotes association with another partner (and activation of another set of genes). Further experimentation is needed for a more complete understanding of this enigma.

dimer a polymer formed from two molecules of a simpler compound.

The Phosphoinositide Pathway

A third ubiquitous eukaryotic pathway is the phosphoinositide pathway. Its activation signals many different processes including cell proliferation, hormone **secretion**, smooth muscle contraction, and transduction of visual information. A key enzyme in the pathway is called phospholipase C (PLC), which cleaves PIP_2 (phosphatidyl inositol 4,5 bisphosphate), a minor phospholipid component of the plasma membrane, into IP_3 (inositol 1,4,5 trisphosphate) and DAG (diacylglycerol), as represented by PIP_2 PLC→ IP_3 + DAG. Receptor stimulation results in the release of both IP_3 and DAG, each of which then goes on to elicit a separate cellular response.

secretion material released from the cell

IP_3 is a small **hydrophilic** molecule that diffuses into the **cytoplasm** and binds its receptor, located in the membrane of the **endoplasmic reticulum** (ER). This stimulates the release of calcium from the ER into the cytoplasm, increasing the cytoplasmic concentration approximately tenfold. Calcium binds a small molecule called calmodulin, through which it exerts most of its effects. One of these is stimulation of a kinase called calcium/calmodulin kinase II (CaM kinase II), which phosphorylates many different target proteins, such as **ion** channels, metabolic enzymes, and transcription factors.

hydrophilic "water-loving"

cytoplasm material in a cell, excluding the nucleus

endoplasmic reticulum network of membranes within the cell

ion an electrically charged particle

Meanwhile, DAG, which remains bound to the cytoplasmic side of the plasma membrane, binds and activates a kinase called protein kinase C (PKC), which exists in many different forms in the cell. Interestingly, calcium also stimulates the activity of some forms of PKC, and thus these forms of the enzyme integrate signals from both arms of the phosphoinositide pathway. PKC activates many different pathways in the cell including a Map kinase pathway (see above) that leads to cell proliferation. In addition, it activates the transcription factor NF-κB by phosphorylating its inhibitor, IκB, thus targeting it for degradation. SEE ALSO Blood Sugar Regulation; Control Mechanisms; Endoplasmic Reticulum; Enzymes; Hormones; Membrane Proteins

Kirstie Saltsman

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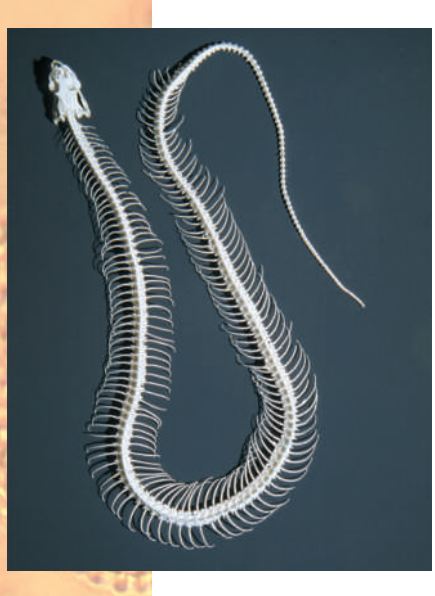


A snake skeleton.

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

Skeletons

Everyone is familiar with the human skeleton and its role in supporting the body. Less familiar is the variety of skeletons in other animals and the additional functions they provide. Zoologists generally recognize three types of skeletons: a hydroskeleton, an exoskeleton, and an endoskeleton.

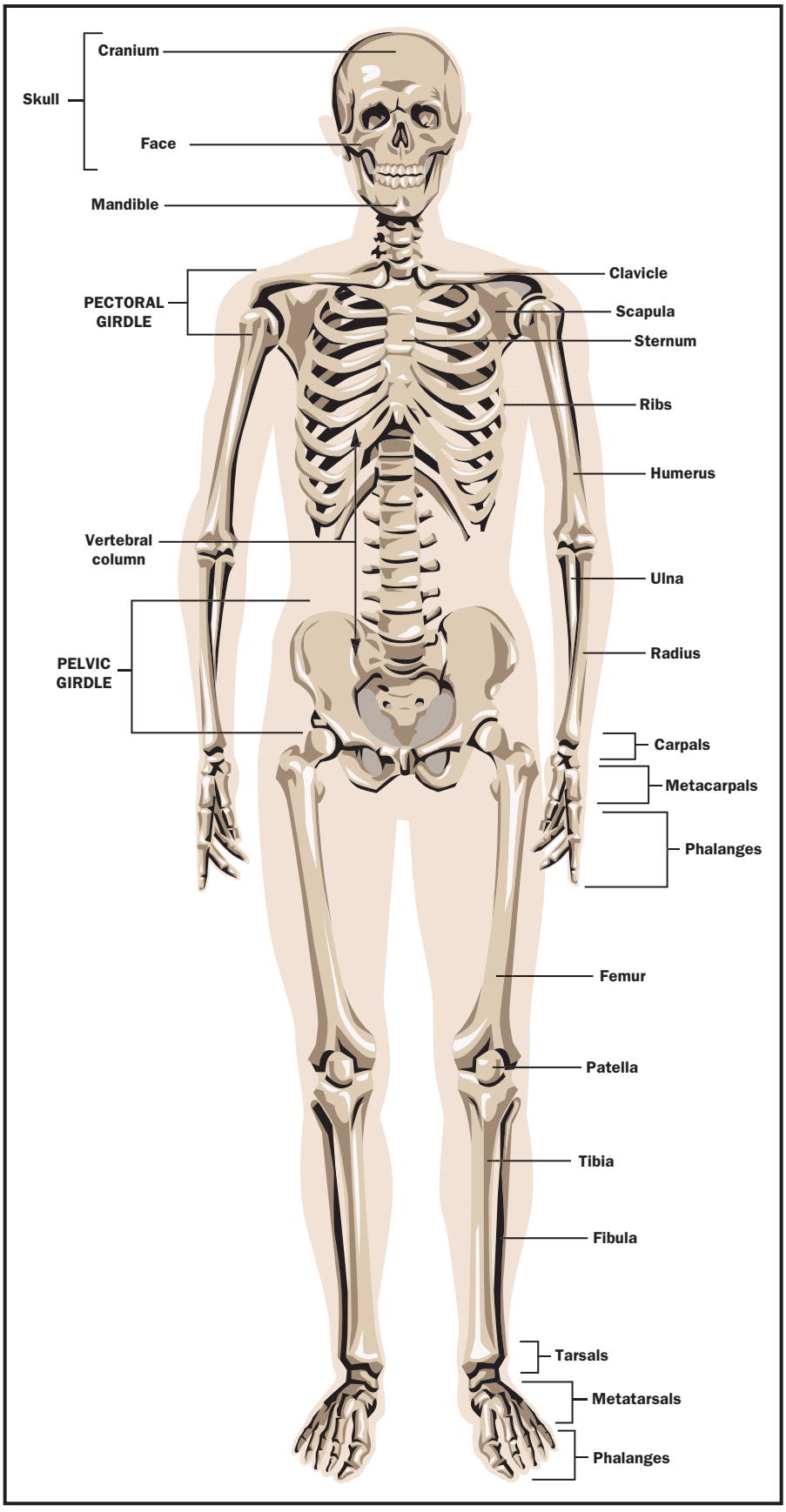
A hydroskeleton, also called hydrostatic skeleton, occurs in many soft-bodied animals, such as earthworms. A hydroskeleton is not bony, but rather is a cavity filled by pressurized fluid. Like air in a truck's tires, the pressurized fluid keeps the body from collapsing from the forces of gravity or movement. By manipulating the pressure in different parts of the cavity, many soft-bodied animals can change shape and produce considerable force. Earthworms (annelids), for example, can burrow through soil using pressure in the hydroskeleton.

An exoskeleton is a hard, nonliving structure that encloses the rest of the body. The exoskeleton may consist of a single hard piece, like the shell of a snail, or it may have two or more hard pieces linked together by flexible tissue, as in a clam. In crustaceans, insects, spiders and other **arthropods** (Arthropoda), and also in some other groups of animals, the exoskeleton is called a cuticle. Animals with exoskeletons of two or more pieces can generally move the parts by means of muscles that attach to the inner surface. Exoskeletons have the advantage of providing protection from predators. (Consider the work it takes to eat a lobster.) One disadvantage, however, is that it restricts the growth of the animal inside it. Snails and many other mollusks solve that problem by continually enlarging their shells as they grow. An arthropod sheds (molts) the old cuticle as it grows, then it secretes a new and larger one.

Endoskeletons are enclosed in other tissues. The human endoskeleton does not offer much protection from predators, but it does a good job of keeping the body from collapsing into a helpless pile. It also provides sites for attachment of muscles. Most muscles connect two different bones, and almost all movements result when muscle contraction moves some bones relative to others.

The skeletons of humans and other vertebrates consist of differing proportions of cartilage and bone. Cartilage, being flexible yet resilient, is well suited to cushioning joints and changing size and shape easily. Cartilage serves as a temporary skeleton in the embryos of vertebrates. In sharks and a few other vertebrates, cartilage persists as the skeleton throughout life. In humans and most other vertebrates, most cartilage is gradually replaced by bone, but some remains as cushions for joints and flexible supports in the nose, ears, and trachea. Bone is, of course, harder and more rigid than cartilage, but it is still living tissue that can slowly adapt to strains imposed upon it.

The 206 bones of the adult human skeleton occur in several distinctive parts of the skeleton. The skull, vertebrae, and ribs belong to the axial skeleton. The bones of the arms and legs and the pectoral and pelvic girdles are parts of the appendicular skeleton, which attaches to the axial skeleton.



Some of the major bones of the human skeleton.

SEE ALSO ANNELID; ARTHROPOD; BONE; CONNECTIVE TISSUE; INSECT; MUSCULOSKELETAL SYSTEM

C. Leon Harris

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Skin

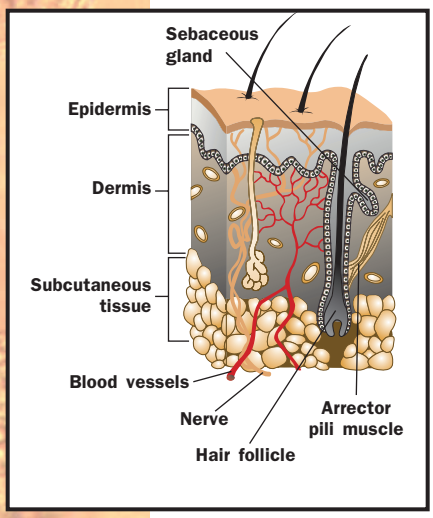
How is the skin, the largest organ in the body, constructed? The skin has two layers: the upper layer is the epidermis, and the lower layer is the dermis. Below the dermis is the hypodermis, or **subcutaneous** layer, composed of fat or other **connective tissue**.

subcutaneous below the skin

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

epithelium one of four tissue types found in the body, characterized by thin sheets and usually serving a protective or secretory function

The epidermis itself is an **epithelium** made up of sublayers. The outermost portion consists of many layers of flat, dead, dry epithelial cells called keratinocytes. Clearly this barrier of dead cells needs no blood supply. The waxy surface coating of these cells allows the skin to be waterproof and dry. In effect, the body surrounds itself with a hostile desert where few germs can live.



Living keratinocytes in the deepest layer of the epidermis undergo rapid cell division and push the overlying cells toward the surface. Melanocytes are also deep and produce the dark pigment in the skin, melanin. Upon exposure to ultraviolet light, melanin production is increased, a process called tanning. The melanin helps protect other cells from the damaging effects of ultraviolet light. Ultraviolet light from any source can harm the skin by causing skin cancer and wrinkling.

The dermis is composed of fibrous connective tissue. The upper part of the dermis exhibits many hills, called the dermal papillae, which prevent slippage between the dermis and the epidermis and increase surface area. There are blood capillaries and small organs of fine touch inside the papillae. In the fingertips, the papillae occur in ridges and help to form the fingerprints. The lower parts of the dermis are home to larger blood vessels, nerves, hair follicles, oil glands, sweat glands, and fibrous connective tissues.

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

Hair follicles contain the root of a hair and have a bulb at the deep end. A small muscle, the arrector pili, attaches to the hair and raises it when the body is cold or frightened. In hairier mammals, the raised hair creates an insulating layer of air to preserve the animal's warmth, but in humans this reaction merely causes goose bumps. There is a sebaceous (oil) gland associated with the follicle. **Parasites** called follicle mites are found in the hair follicles of many people, especially on the face.

matrix a network, usually of threadlike fibers

Other organs related to the skin are the finger- and toenails. These are made of plates of hardened keratin and are dead and dry, like the upper layer of the epidermis. The nails begin as new cells added in the nail **matrix**, under the skin.

Two types of glands also start out in the dermis: merocrine sweat glands and apocrine sweat glands. Merocrine sweat glands are those that increase

their watery **secretions** when the body starts to overheat. The evaporation of the secretions off the skin cools the body off. Sweat is only responsible for about one-fifth of the cooling in a resting person; most is due to radiation, in which heat is given off as infrared rays. Apocrine sweat glands are found around the breasts, armpits, and **genitalia** and produce sex-attracting chemicals called **pheromones**. Other glands include the ceruminous (earwax) glands, sebaceous glands, and mammary glands. SEE ALSO CONNECTIVE TISSUE; EPITHELIUM; ORGAN; TEMPERATURE REGULATION

David L. Evans

secretion material released from the cell

genitalia reproductive organs

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

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Sleep

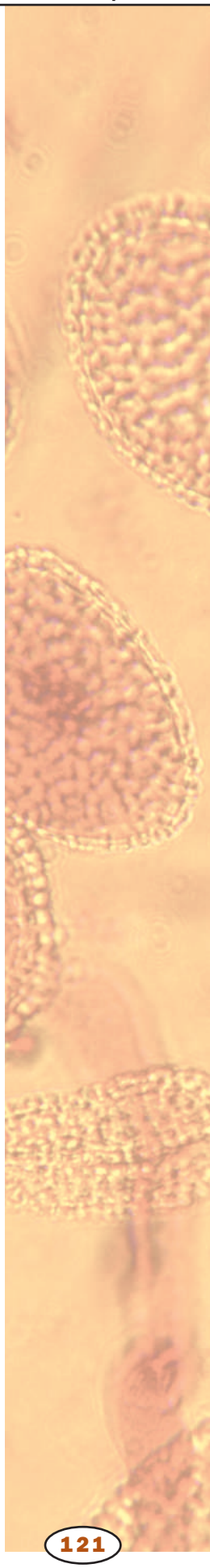
Sleep is a very important process and is characterized by a stereotypical posture, little movement, and a decrease in response to stimuli. These characteristics might also describe coma, but in sleep, unlike in coma, the characteristics are reversed each morning. Because creatures are not eating or mating and are also very vulnerable to attack by predators during sleep, sleep must have a very important function to make it worthwhile.

Sleep is also a very insistent drive. Whereas a person can voluntarily stop eating until he or she dies, the human body cannot force itself to stay awake indefinitely. In fact, there are situations when falling asleep might mean death (while driving a car, for example), yet the desire to sleep is so insistent that body will still succumb to it.

Stages of Sleep

Sleep is divided into two main stages: REM sleep (which stands for "rapid eye movement"), and non-REM (NREM) sleep. These stages are characterized by changes measured on instruments such as the electroencephalograph (EEG), which measures changes in electrical signals in the brain; electrooculogram (EOG), which measures eye movements; and the electromyogram (EMG), which measures muscle movements. In humans, REM and NREM sleep alternate in ninety-minute cycles approximately three to six times per night. During the first part of the sleep cycle, REM sleep takes approximately ten minutes of each cycle, but REM sleep periods become longer and closer together as the course of sleep progresses (see figure 1).

Non-REM sleep is divided into four stages. As one progresses from stage one to stage four, sleep gets deeper and EEG waves become taller and slower; stages three and four are often grouped together and called slow wave sleep (SWS). During SWS, muscle movements and eye movements are diminished in comparison to wakefulness, and the EEG is more synchronized, indicating that large portions of brain tissue are firing together.



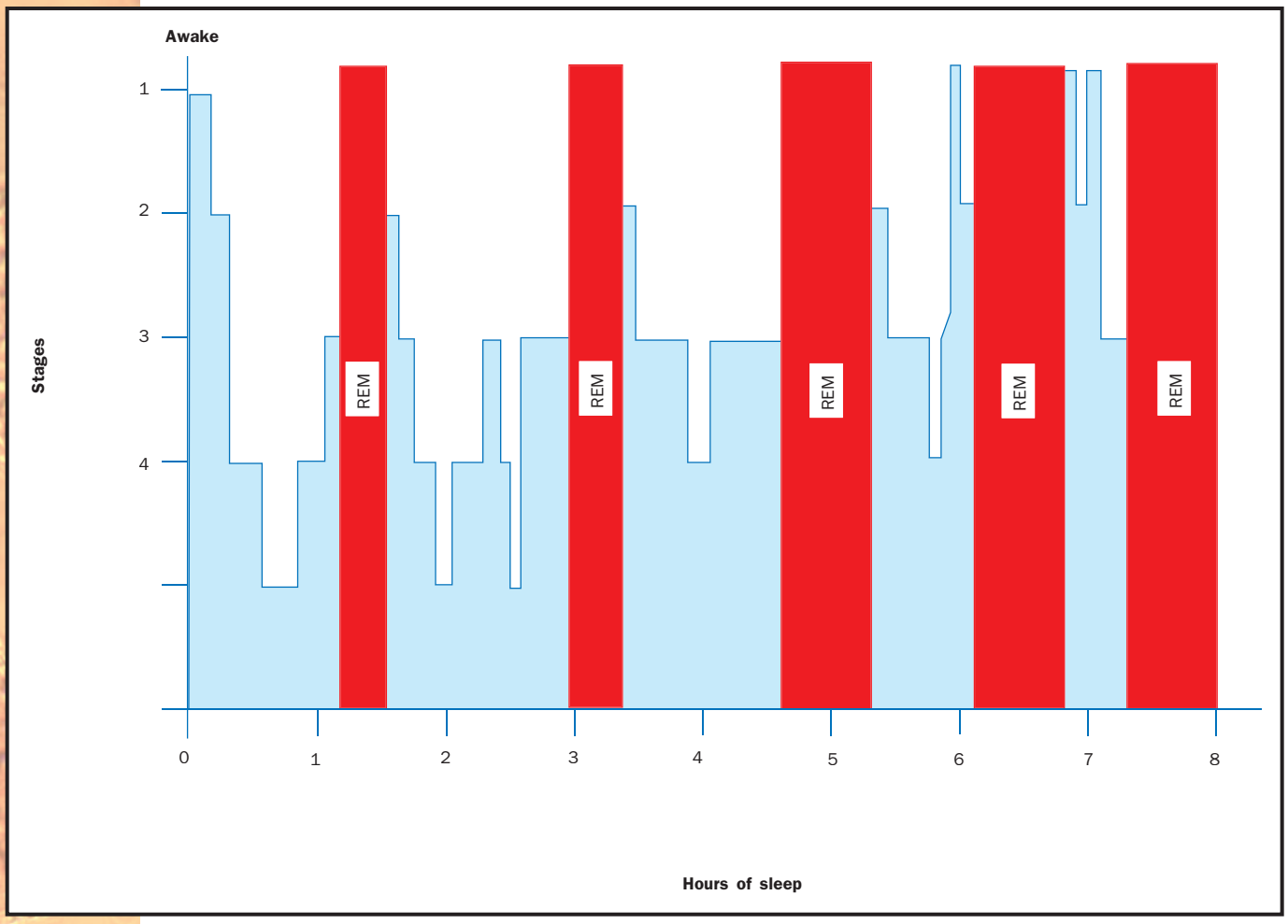


Figure 1. Stages of sleep.

desynchronized not happening at the same time

thermoregulation temperature regulation

muscle tone low level constant muscle contraction

REM sleep is characterized by a **desynchronized** EEG, a lack of **thermoregulation**, loss of tone in the skeletal muscle, erections of the penis or clitoris, rapid eye movements, and dreams. As seen by the desynchronized EEG, which is similar to the brain patterns seen during wakefulness, the brain is very active during REM sleep. However, one part of the brain that does shut off during REM sleep is the part of the hypothalamus that is responsible for temperature regulation. During REM sleep, the body does not thermoregulate and therefore does not shiver or sweat.

Skeletal muscles are also less active during REM sleep and thus lose **muscle tone**. This loss enables the muscles to relax during REM sleep. It also prevents people from acting out their dreams (sleep walking occurs during NREM sleep, when muscle tone is maintained but diminished). Not all muscles lose their tone during REM sleep. The diaphragm, necessary for breathing, continues to contract. Muscles are also active in the eyes: although the lids are closed, the eyes dart back and forth during REM sleep, which gives REM its name.

During REM sleep the penis and clitoris often become erect, but this is not necessarily related to dream content. Although REM sleep is associated with dreams, dreams actually occur during all stages of sleep. The dreams that occur during REM sleep have characteristics different from those dreams in NREM sleep. REM dreams are longer, more emotional,

and more visual than NREM dreams, and they usually do not follow the events of the day as closely as NREM dreams.

Neurological Control

A common misconception is that the brain shuts down during sleep. In truth, parts of the brain may be even more active during NREM or REM sleep than during wakefulness. The level of consciousness depends upon the activity of the **reticular** activating system, a network of **neurons** in the brainstem that send projections throughout the thalamus, hypothalamus, and **cerebral cortex**. Certain areas of the brain have been found to be responsible for causing different sleep stages. Whereas NREM sleep is controlled by the **basal** forebrain (the **anterior** hypothalamus and adjacent forebrain areas), REM sleep is mostly controlled by an area in the brainstem called the pons.

reticular netlike

neuron nerve cell

cerebral cortex outermost wrinkled portion of the brain

basal lowest level

anterior toward the front

Functions of Sleep

Although humans spend approximately one-third of their lives asleep, no one knows for sure what the function of sleep is. It is known that sleep is necessary for life. Constant sleep deprivation in rats leads to death. Studies suggest that constant deprivation of REM sleep alone causes metabolic changes in rats that can also lead to death.

There are a number of theories on the function of sleep. Sleep may help the body recover from an active day and give it the chance to restore substances that are lost during the day. However, since simply resting the body without sleep does not fulfill the same function as sleep, it is thought that there is more to sleep than resting.

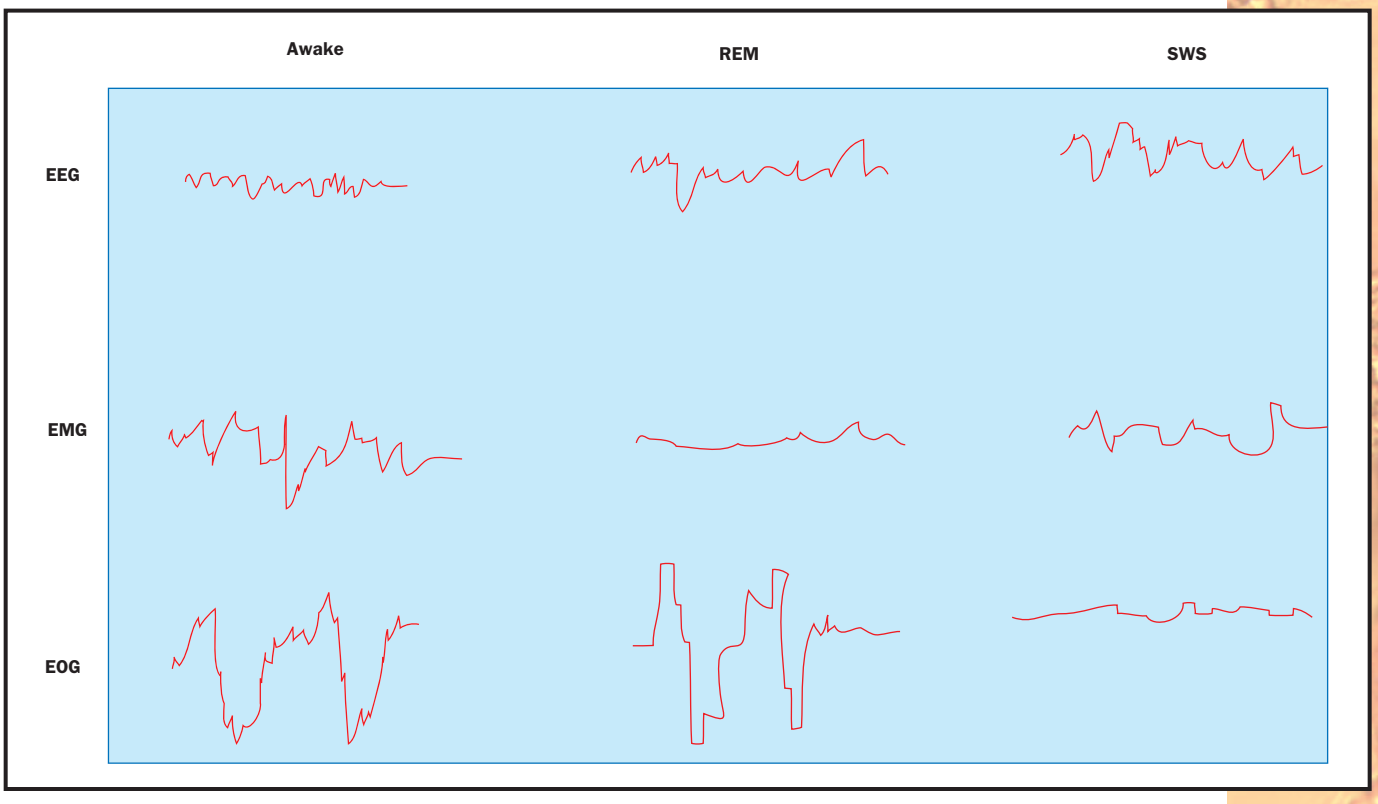


Figure 2. Electroencephalogram (EEG), electromyogram (EMG), and electrooculogram (EOG) show activity of the brain, muscles, and eyes during three different states: wakefulness, REM sleep, and slow-wave sleep (SWS).

Sleep may have developed evolutionarily as an adaptive mechanism to keep animals out of harm's way, preventing them from wandering around in the dark, vulnerable to accidents and attack by predators, during a time when food foraging may be less efficient. It is interesting to note that small animals with safe hiding places and large predators sleep a lot, whereas large prey sleep less often, suggesting sleep may be related to an animal's relative safety, although the evidence for this is far from clear. The question remains, however, why the complex process of sleep would have evolved to merely keep animals out of danger.

It is known that REM sleep is a necessary stage of sleep; however, the function of REM sleep is also unclear. Temporary REM sleep deprivation can lead people to become bad-tempered and uneasy. If REM deprivation continues, and the subject is then allowed to sleep undisturbed, he or she experiences "REM rebound," which means that REM sleep occurs more frequently and lasts longer than normal. There is evidence that REM sleep is necessary for learning and memory. Furthermore, theorists are proposing that REM sleep may be important in the development of the brain. SEE ALSO BRAIN; HYPOTHALAMUS; TEMPERATURE REGULATION

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Slime Molds

multinucleate having many nuclei within a single cell membrane

protoplasm fluid portion of a plant cell within the cell wall

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

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

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

There are two major unrelated phyla of slime molds. The Myxomycota are the true (plasmoidal) slime molds, and the Dictyosteliomycota are the cellular slime molds. Both were formerly classified as fungi but are now considered protists. Slime molds are often found on old, well-rotted logs because there they can find the moisture and bacteria required for survival. Their small, delicate fruiting bodies tend to be fungal in appearance. Most of the fruiting bodies are only a millimeter or two in height, and therefore often difficult to notice.

Myxomycota

A myxomycete exists in nature as a plasmodium, a **multinucleate** blob of **protoplasm** up to several centimeters in diameter, without cell walls and only a cell membrane to keep everything in. It resembles a large **amoeba** and feeds much the same way, by engulfing its food (mostly bacteria) with **pseudopodia** ("false feet"), in a process called **phagocytosis**. Thus the slime mold ingests its food and then digests it. (In contrast, true fungi have cell walls and digest their food externally before ingesting it.) When the plasmodium runs out of food, or environmental conditions become harsh, fruit-

Pillows of the coral-colored slime mold *Myxomycetes* grow on damp wood.

ing bodies form. These fruiting bodies produce dormant, resistive spores. These later germinate to form **uninucleate** myxamoebae or flagellated swarm cells. These later fuse and then divide mitotically to form a plasmodium, completing the life cycle. Myxomycetes are important scavengers in dark, damp parts of the **ecosystem**. Occasionally, during rainy periods, large plasmodia (up to a few meters in diameter) crawl out of the woods and into people's lawns and gardens. These plasmodia were the inspiration for the science fiction movie *The Blob* and are eaten in parts of Mexico.

uninucleate possessing one nucleus

ecosystem an ecological community and its environment

Dictyosteliomycota

The Dictyosteliomycota are also known as the social amoebae. Their life cycle is considered among the most bizarre among microorganisms. It begins with free-living **amoeboid** cells (not to be confused with the Amoebae); there is no true plasmodium. As long as there is enough food (usually bacteria) the amoebae thrive. However, when food runs out, the amoebae send out chemical signals to surrounding amoebae. Next, they stream toward a central point and form a sluglike multicellular pseudoplasmodium, which can then migrate like a single organism. When conditions are right, the pseudoplasmodium stops migrating and forms a multicellular fruiting body. Some of the cells become spores that disseminate, while the rest form stalk cells whose only function is to raise the spores up into the air to be more easily caught in air currents.

amoeboid like an amoeba, especially in movement via extension of portions of the membrane

The Dictyosteliomycota pose an interesting challenge for evolutionary theory, since some of the cells (in the stalk) actually seem to sacrifice their own reproductive potential so that others (the spores) can be transported to a new location where there is more food and they can grow again. This altruistic sacrifice would seem to be counter to the reproductive interests of the cells that became the stalk (because they never reproduce) and **genes** for stalk-forming behavior would therefore be selected against. It may be

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

maintained if the spore cells are closely related to the stalk cells (and thus both have the stalk-forming genes) or if the allocation of cells to spore versus stalk is random, so that genes for stalk formation are preserved over time. However, evidence suggests that the position of the cells in the slug and thus in the fruiting body is determined by the timing of their coming into the aggregation stream, rather than by genetics. SEE ALSO ENDOCYTOSIS; FUNGI; PROTISTA; SOCIOBIOLOGY

Tom Volk

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Smell *See Chemoreception*

Smoking and Health

Smoking cigarettes sets into motion a chain reaction of changes that set the stage for infection, degenerative diseases, cardiovascular disease, and cancer. Smoke contains thousands of chemicals, but it is nicotine that causes the powerful addiction that compels a person to continually deliver the other harmful chemicals to the respiratory system. Nicotine binds to receptors on certain nerve cells in the brain, causing the cells to release dopamine, which produces the associated pleasurable sensations. Addiction happens when a person seeks the good feelings and wants to avoid withdrawal symptoms.

Many of the health problems associated with cigarette smoking stem from impairment of the ability of the respiratory tract to cleanse itself. Each inhalation slows the beating of the **cilia** that line the tract, so that they cannot move mucus and particles out of the respiratory system. Eventually, the cilia are lost. Accumulating mucus causes smoker's cough, which can develop into chronic bronchitis. In addition, the mucus entraps **pathogens**, increasing the likelihood of respiratory infections. Meanwhile, the bronchiole linings thicken, and breathing becomes strained. As the bronchioles lose elasticity, the respiratory tract cannot resist the pressure changes that coughing produces, and the microscopic alveoli (air sacs) may burst. This leads to emphysema. Symptoms include difficulty taking a deep breath, worsening cough, wheezing, and fatigue that results from impaired oxygen delivery to tissues. Smokers face a fifteen times greater likelihood of developing emphysema than nonsmokers. Chronic bronchitis and emphysema are the two most common forms of chronic obstructive pulmonary disease (COPD), which is a general term for conditions that block the airways.

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

pathogen disease-causing organism

The Centers for Disease Control and Prevention report that there were approximately 47 million smokers in the United States in the late 1990s.

Smoking cigarettes accounts for 85 percent of lung cancer cases. The process begins years before a person notices symptoms. First, cells of the bronchial linings begin to divide more often than normal, which displaces

the ciliated cells. If smoking continues, these errant cells break through to lung tissue, where they grow into a tumor. Lung cancer can also begin within a single alveolus. Smoking also increases the risk of cancers of the mouth and throat. In one case, a man who repeatedly placed chewing tobacco on his ear developed a skin cancer in that location. Smoking raises serum cholesterol, and can contribute to diseases of the blood vessels. About 21 percent of cases of coronary heart disease and 18 percent of strokes are directly related to smoking.

If a pregnant woman smokes cigarettes, the fetus is at greater risk of premature delivery or low birth weight. Spontaneous abortions and stillbirth are also more likely. Fetal growth becomes stunted because carbon monoxide in cigarette smoke crosses the placenta and binds to fetal **hemoglobin** molecules, blocking oxygen delivery. Other chemicals in cigarette smoke prevent nutrients from reaching a fetus.

hemoglobin oxygen-carrying protein complex in red blood cells

A person can regain health if smoking ceases before too much damage has occurred. Although emphysema cannot be reversed and cancer or cardiovascular disease must be treated, the ciliated cells that are the guideposts of the respiratory system can regrow, and the cough and susceptibility to infection abate. SEE ALSO CANCER; CARDIOVASCULAR DISEASES; HEART AND CIRCULATION; ONCOGENES AND CANCER CELLS; PSYCHOACTIVE DRUGS; RESPIRATION

Ricki Lewis

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Social Behavior

Social behavior is defined as interactions among individuals, normally within the same species, that are usually beneficial to one or more of the individuals. It is believed that social behavior evolved because it was beneficial to those who engaged in it, which means that these individuals were more likely to survive and reproduce. Social behavior serves many purposes and is exhibited by an extraordinary wide variety of animals, including invertebrates, fish, birds, and mammals. Thus, social behavior is not only displayed by animals possessing well-developed brains and nervous systems.

Benefits of Social Behavior

Social behavior seems to provide many benefits to those who practice it. Studies have shown that many animals are more successful in finding food if they search as a group. This is especially true if food resources are clumped together only in certain places. If more individuals are cooperating in the search, there is a greater chance one of them will find the clump of food. In some cases, foraging in a group makes it easier to capture a prey. Dolphins are known to surround a school of fish and to take turns darting into the center to eat the fish that are trapped in the middle. Many carnivores will band together when they try to capture large prey. For examples, wolves

Two gannets greeting each other on Bonaventure Island, Quebec.

will hunt together when hunting moose, and lions will hunt together when hunting large prey such as wildebeests. When these animals are hunting much smaller prey, they will often hunt singly.

Many animals live in social groups partly for protection. Although one baboon might not be able to fight off a leopard, a troop of baboons often is able to do so. In addition, with more individuals cooperating together, some can serve as sentries looking for danger while the other group members are eating or sleeping. Prairie dogs and large flocks of crows normally have some individuals acting as sentries, which makes it nearly impossible to sneak up on a prairie dog town or a flock of crows.

Many prey species, such as schools of fish and flocks of shorebirds, travel in groups in which their movements are highly coordinated. The entire group moves quickly, darting one way and then another as an entire group, as if they were all somehow physically connected with one another. It is believed this behavior creates confusion for the predator. Predators generally need to pick out a single individual in a group that they will focus on and try to capture. A rapidly moving and turning school of fish, flock of birds,

or herd of antelope is believed to make it very difficult for the predator to remain focused on a single individual. However, if one individual is unable to keep up with the group, the predator will then be able to focus on it and usually will succeed in catching it.

Some animals form social groups to make travel easier. Canada geese and other bird species typically fly in a V formation. Just like bicyclists who ride behind one another in order to reduce wind resistance, the geese fly in formation to reduce the wind they must encounter. In this situation, the lead bird has the most tiring job, which is why several birds usually take turns leading the V. Some animals congregate in close proximity to one another in cold weather in an effort to stay warm. Small birds are sometimes known to huddle so closely they form a single large ball of birds.

Breeding Behavior

Sometimes social behavior is exhibited by groups of males or females during the breeding season. In some cases, males may band together and try to chase the dominant male away so they have a better chance of mating success. In other instances, males are known to cooperate in making their courtship displays. Turkeys often perform their courtship display in pairs, even though only one of the turkeys ends up doing most of the mating. Why would the unsuccessful male agree to help? The two male turkeys are usually brothers. Since brothers share about 50 percent of the same genes, even if only one brother mates, many of the genes of the unsuccessful brother are passed on too.

In some species, the females form social groups during the breeding season. In certain circumstances, females will look after one another's offspring while the other mother goes out to find food. In other species, such as lemurs, females may form social groups as a kind of defense. Males of some lemur species will try to kill the offspring of females that mated with another male. By banding together, the females are sometimes able to ward off the attacking male.

Many animals form social groups only during certain times of the year. Many bird species flock together in foraging groups in the winter. However, these same birds that sought one another out in the winter set up breeding territories in the spring and will go to great lengths to keep the same birds out of their territory. Thus, for many species, social behavior is a flexible form of animal behavior, one that can be adopted or abandoned depending on the conditions of the environment and the time of year.

The male bower bird, of the Australian rainforest, has long interested scientists with its unusual courting behavior. The bower constructs a sort of bachelor pad on the forest floor, a complex structure of twigs, leaves, and moss. Further decorating it with berries and shells and feathers, scientists believe that it is specifically designed to attract mates.

Insect Societies

Some of the most well-developed social behavior is exhibited by insects such as ants, termites, bees, and wasps. Many of these species live in colonies with thousands or even millions of individuals. One benefit of social behavior for these insects is that different individuals specialize in certain activities. For example, some are the workers who build the colony and go out looking for food that they bring back. Other individuals are the soldiers of the colony. Their job is to continually patrol the colony perimeter and to protect the colony from possible attacks from other colonies. In many ant and bee colonies, all worker and soldier ants are females. Males are usually present in the colony, but do not contribute much. Finally, there is the queen ant

An olive baboon grooming another in Nairobi National Park, Kenya. Individuals who engage in social behavior are more likely to survive and reproduce.

or bee. The queen's only job for her entire life is to lay eggs that the workers will care for.

There are substantial benefits to forming social groups and there are also some definite costs to living closely with others of the same species. First, one competes most with others that are most like oneself, and thus a member of a social group always has to share or compete with others for resources. Second, because of the numbers and close proximity of individuals in many social groups, disease may spread through social groups relatively rapidly. SEE ALSO Behavior, Genetic Basis of; Behavior Patterns; Field Studies in Animal Behavior; Mating Systems; Natural Selection; Sociobiology; Symbiosis; Wildlife Biologist

Mark A. Davis

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Sociobiology

Sociobiology is the study of the biological basis of social behavior using evolutionary principles. The term was coined by a prominent entomologist E. O. Wilson in his book *Sociobiology: The New Synthesis* (1975). Wilson pointed out that just as physical characteristics such as beak length and fur color could be subject to natural selection, so too could aspects of social behavior.

The field of sociobiology was part of a broad conceptual shift during the late 1960s and throughout the 1970s. Sociobiology looked closely at the nature of interactions between individuals, replacing a cooperative view of social behavior with the idea that more often, from an evolutionary perspective, individuals should behave in their own self-interest. It was one of several fields that emphasized the genetic basis of behavior in all animals, including humans. In doing so, sociobiology shed light on a number of important aspects of animal behavior, including the evolution of altruism, the occurrence of infanticide and sibling rivalry, parental care, and social and mating systems. The extension of some aspects of sociobiology to humans initiated a controversy, which continues today.

E. O. Wilson, founder of sociobiology.

Altruism

Wilson's original focus was on the insects, such as ants, bees, and wasps, a group that commonly contains species that are eusocial. Eusocial species typically live in large highly cooperative groups or colonies, with reproduction limited to a very few members. Why would individual worker bees defend a colony from intruders, feed offspring that belonged to others, and forgo their own reproduction?

Such altruistic or helping behavior puzzled biologists. If natural selection works on behavior just as it works on other traits, why should individuals expend energy or time helping others survive or reproduce when that effort may reduce their own chances of reproduction? In 1964, William Hamilton developed the idea that individuals help their relatives because relatives share genes. Just as genes may be passed on by direct reproduction (producing offspring yourself), "your" genes can be passed on by increasing the reproduction of close relatives. In the social insects, cooperative behaviors associated with eusociality make evolutionary sense because these species have an unusual system of genetic relatedness, making colony members very closely related.

Competition and Cooperation

An evolutionary approach has shed light on other puzzling aspects of behavior. Infanticide or infant killing by males in social monkeys is now believed to be a strategy used by males to speed up female receptivity and prevent females from spending energy on offspring fathered by competing males. Using an evolutionary approach, even close relatives can have conflicts of interest. Natural selection is expected to favor offspring that compete with each other for food (sibling rivalry). Parents should care for offspring, but offspring may demand more attention and energy than parents are willing to give. Parents, after all, must balance the amount of time and energy they devote to any single offspring with demands of other offspring and potential future offspring.

Sociobiology has addressed broad questions concerning the social systems or kinds of groups in which species are found. For example, if groups of certain sizes have a greater likelihood of detecting predators, then they should be favored by natural selection. This may explain herding and flocking. An evolutionary approach to the study of mating systems has highlighted potential conflict of interest between males and females. Females produce few eggs, while males make many sperm. Because of this, females may be more selective in their choice of mates. In each of these cases, the field of sociobiology and an evolutionary approach to behavior led to insights that otherwise would have been missed.

Human Applications

The last chapters of Wilson's book extended the study of sociobiology to humans. Although not the core of his text, this final chapter generated heated controversy over the nature of human social behavior and, in particular, the role of genes versus environment in determining human behavior. Some scientists considered Wilson's ideas dangerous. Genetically determined behavior seems to leave little room for free will, and downplayed the importance of the social and physical environment within which individuals grow and develop.

Since the publication of Wilson's book, more evidence has emerged that aspects of behavior have a genetic basis. With the increasing evidence from genetic and inheritance studies, however, comes an appreciation of the critically important role of the environment. Biologists now appreciate that the environment works together with genes in complex ways to affect behavior.

SEE ALSO BEHAVIOR, GENETIC BASIS OF; EVOLUTION; FIELD STUDIES IN ANIMAL BEHAVIOR; MATING SYSTEMS; SEXUAL SELECTION; SOCIAL BEHAVIOR

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Soil

inorganic not bonded to carbon

organic composed of carbon, or derived from living organisms

ecosystem an ecological community and its environment

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

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

One of the first distinctions made by a soil scientist is that "soil" and "dirt" are not the same. Dirt is what collects on the car or in the corner of the bedroom when it has been months since the last time it was vacuumed. Soil, on the other hand, is a highly structured matrix of **inorganic** and **organic** particles that form the substrate for terrestrial **ecosystems**. The substrate is the foundation where plants, ranging in size from minute ferns to tall trees, are rooted. The inorganic particles are formed from **minerals** in rock through weathering; a process that produces them by physical means (for example, erosion, freezing and thawing, and wind abrasion) or chemical means (for example, **oxidation**, dissolving crystals, or the action of acids). The organic particles originate from plant and animal tissues through fragmentation, decomposition, and chemical transformation.

The climate, rainfall, and temperature determine the pattern of soil weathering in a particular area. The weathering process often produces hor-

izontal layers of soil of varying thickness called soil horizons because each layer is roughly parallel to Earth's horizon. The uppermost horizon often contains the most organic matter and others have differing nutrient contents and physical properties.

Soil provides physical support for plants, and the pores between particles provide spaces that contain water used by the plants and animals living within the soil. Oxygen from air diffuses into the pores when the water drains through the soil. This allows plant roots, **aerobic** microorganisms, and invertebrates to survive. Root systems may be located just below the surface, or may penetrate many meters deep. Too much water prevents air from reaching roots. Because of this, too much continuous water can kill many species of plants just as effectively as the absence of water during an extended drought. Only certain specially adapted plants are successful in water-saturated soils.

aerobic with oxygen, or requiring it

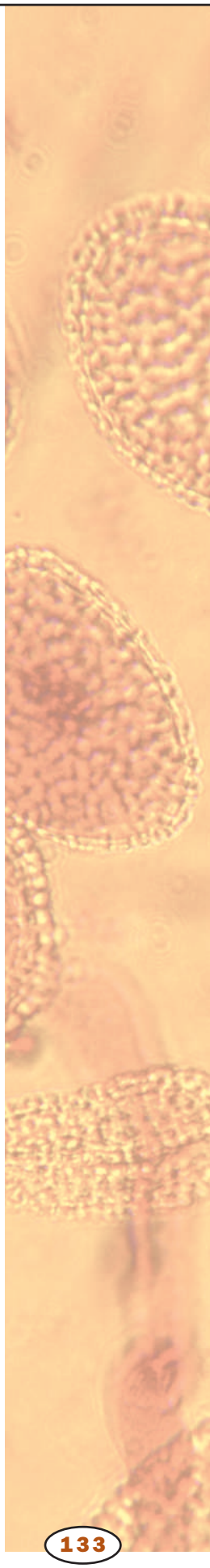
The particles that make up the soil may occasionally be all of the same size, as in the case of river sand deposits, or a silt layer that settled out on the bottom of ancient lakes. Sand particles are fairly large, only slightly smaller than gravel used in a fish tank, while silt particles are smaller than sand grains and clay particles are even smaller, approaching the fineness of talcum powder or baker's flour. Soils that are composed predominately of one of these particle sizes are known respectively as sands, silts, and clays. However, very often there is a mixture of particle sizes and the soil is referred to as a loam (a sandy loam has a mixture of particle sizes, but is mostly composed of sand). Loams are generally the best soils for plants to grow in. The larger sand particles facilitate drainage and oxygen penetration, while the small clay or organic humus particles provide a large amount of surface area where nutrient **ions** can become attached. Examples of these nutrients include nitrate, potassium, calcium, phosphate, and iron. They can be provided by commercial fertilizers, but are present naturally in nutrient-rich soils. The ions are attracted to electrically charged sites on clay or fine humus particles and gradually released into the water as they are exchanged with other ions. This nutrient-rich soil solution provides nutrition to plants through the roots.

ion an electrically charged particle

Finally, the soil is a habitat for millions of small organisms per cubic meter such as bacteria, algae, **nematodes**, insects, and mites. These organisms make nutrients available through metabolic activity or the production of feces. They also die and add to organic matter and in general contribute to good soil quality. Larger organisms also inhabit the soil. Earthworms are particularly important because they mix the soil and process organic matter, which passes through their intestinal tracts and is released as feces. This helps produce loose textured soils with a high organic content and nutrient-holding capacity. In addition, their burrowing increases oxygen penetration. Larger animals such as moles, rabbits, foxes, and groundhogs create burrows that provide them with amenities such as shelter and food storage areas. This allows them to survive and thrive within the subterranean part of the ecosystem. SEE ALSO Biogeochemical Cycles; Mycorrhizae; Nematode; Nitrogen Fixation; Plant Nutrition; Roots

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

Dean Cocking



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Speciation

Speciation refers to the genesis of a new species from an ancestral species. There are two basic ways this can happen. Anagenesis involves one species evolving into a different species. Cladogenesis occurs when one species splits into two or more species. Cladogenesis is of greater interest in terms of biodiversity and is the type of speciation discussed here. Speciation has two primary components: diversification and genetic isolation. The two principal types of cladogenesis are allopatric speciation and sympatric speciation.

Allopatric Speciation

Allopatric speciation is the better understood of the two types of cladogenesis. It occurs when one species is separated into two groups by some physical barrier, resulting from, for example, climate change, a geological event, or a human-induced change in the environment. For example, the uplift of a new mountain range might divide an ancestral species into two isolated groups. Once the species is separated into these groups, each group may accumulate genetic changes that serve to differentiate it from the other. This accumulation of changes may result from natural selection or from random events.

If the environment on either side of the barrier is different, natural selection may favor genes that produce different traits on either side of the barrier. Even if the environment on either side of the barrier is similar, it may be that when the two groups were separated, by chance one of the groups had a different subset of the total genetic diversity present in the species, and so that group has different "raw materials" for selection to act upon. It may also happen that a neutral mutation occurs in one of the groups, meaning it is neither favorable to the organism nor unfavorable to it. Selection will not act upon such a mutation, and it may persist in the population purely by chance. Also by chance, some versions of genes may become common in a small population while others disappear. This is called genetic drift.

So by a variety of processes, involving either selection or chance, two physically separated groups may accumulate differences between them. This is the first part of the process of speciation. The second part involves the lack of gene flow between the two groups. That is, individuals from one group do not cross the barrier to mate with individuals in the other group, resulting in the genetic isolation of each group from the other. This genetic isolation permits the development of differences in the two groups.

If these differences are to persist, there must be a persistent impediment to gene flow between them. If the two groups never come into contact again, they will almost certainly accumulate enough differences over time to become separate species. If they expand their ranges and come back into contact, some other mechanism must act to "preserve" the differences they

evolved in isolation (allopatry). Traditionally, this mechanism is known as **reproductive isolation**, and it is a byproduct of the diversification that has already taken place.

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

Reproductive Isolation

Reproductive isolation can operate prezygotically (premating) or postzygotically (postmating). Prezygotic reproductive isolation prevents **fertilization** from taking place. It may be that members of the two groups breed at different times of the day or different times of the year or in different habitats. They may have developed mechanical differences that prevent copulation, or perhaps copulation takes place, but the two groups have become chemically incompatible so that fertilization does not occur. Postzygotic reproductive isolation acts after fertilization. The embryo may not develop normally, or the offspring may be unhealthy or infertile as adults. In all these ways, reproductive isolation may prevent the gene pools of the two groups from mixing, allowing them to continue on independent evolutionary trajectories.

fertilization union of sperm and egg

There is some disagreement among scientists regarding the importance of reproductive isolation in the speciation process. If, as noted above, the two groups that have accumulated differences between them remain separated by a physical barrier preventing their members from ever meeting, it may not matter whether they develop reproductive isolating mechanisms. Proponents of the **phylogenetic** species concept, for instance, would say that the fact that the groups have accumulated diagnostic differences and are evolving independently is sufficient evidence to say that speciation has taken place.

phylogenetic related to phylogeny, the evolutionary development of a species

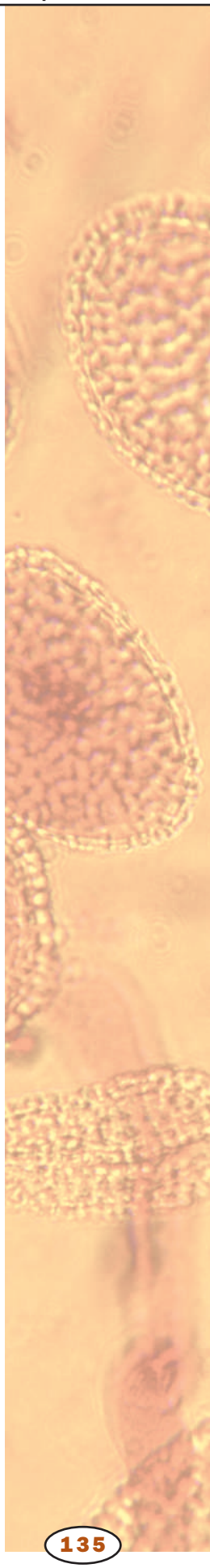
Sympatric Speciation

The other principal type of cladogenesis is sympatric speciation. In this type of speciation, a species splits into two groups that diversify and become genetically isolated while remaining in the same place. "Same place" typically means that individuals from both groups meet in the same habitat during the breeding season. Most of the mechanisms by which sympatric speciation may occur are poorly understood. There must be some impediment to gene flow if differentiation into two groups is going to take place.

Sympatric speciation can happen if a mutation results in an immediate reproductive barrier in a segment of the species. The most common example of this is polyploidy in plants. In this case, errors in cell division may cause a doubling of the normal number of chromosomes, which instantaneously produces a reproductive barrier.

Another possible mechanism for sympatric speciation is disruptive selection, which takes place when a species has a trait that is manifested in two very different ways, such as two different coat colors. In this case, natural selection operating in a highly partitioned environment (dark versus light background, for instance) may favor one expression of the trait in one particular portion of the habitat and the other expression of the trait in a different portion of the habitat. Selection may thus compound the differences in the trait's expression and in this way result in differentiation.

Polyploidy in plants is also an example of how quickly speciation can take place, even in a single generation. Usually, however, speciation takes



longer. Just how long is dependent on many variables, such as the generation time of the organisms involved, as well as factors of chance. There are two predominant schools of thought regarding the speed of speciation. "Gradualists," on the one hand, believe groups accumulate differences slowly over hundreds of thousands or millions of years. "Punctuationalists," on the other hand, believe that speciation takes place comparatively rapidly, over thousands of years, and little change occurs between these rapid bursts of differentiation. SEE ALSO BIODIVERSITY; EVOLUTION; EVOLUTION, EVIDENCE FOR; NATURAL SELECTION; POPULATION GENETICS; SPECIES

Ann E. Kessen and Robert M. Zink

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Species

There is little agreement among scientists about the definition of the word "species." However, most biologists would agree that a species is a detectable, naturally occurring group of individuals or populations that is on an evolutionary path independent from other such groups. Several more detailed definitions have been articulated over the years; two that have gained prominence are the biological species concept (BSC) and the **phylogenetic** species concept (PSC).

phylogenetic related to phylogeny, the evolutionary development of a species

In 1942 biologist Ernst Mayr defined the biological species concept as follows: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." This definition places emphasis on restriction of **gene** flow among groups. **Reproductive isolation** means that individuals from two groups are unable to interbreed successfully, that is, produce healthy, fertile offspring. So according to this definition, an individual is a member of a particular species if it can breed successfully with members of that species but not with members of other species.

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

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

Interbreeding between two different groups is called hybridization and is viewed differently by different scientists. In animals, hybrid offspring of two different species are thought to be unhealthy or infertile as adults, but in plants hybrid offspring are often thought to be more vigorous than their parents. As a result, plant biologists and animal biologists differ regarding the significance of interbreeding in answering species questions, and most plant biologists are not proponents of the BSC.

Objections to the BSC include the fact that the extent of hybridization can range from very little to extensive, making its interpretation subjective. Also, it requires guesswork regarding the species status of groups that do not occur in the same place and thus have no opportunity to interbreed, and

it cannot easily be applied to organisms in the fossil record or to those that lack sexual reproduction. Furthermore, it is now known that hybridization can occur between two independent groups that are not each other's nearest relatives. Thus, putting two hybridizing groups into one species could misrepresent evolutionary history by excluding other more closely related (and often reproductively isolated) groups.

A phylogenetic species concept was articulated by Joel Cracraft in 1987 as follows: "a species can be defined as an irreducible cluster of organisms, within which there is a parental pattern of ancestry and descent, and which is diagnosably distinct from other such clusters." This definition views a species as being the smallest possible grouping of organisms in time and space that can be differentiated from other groupings, with the basis for the differentiation being inherited. So an individual is a member of a species if it shares the inherited characteristics of the species, irrespective of whether it can hybridize with a member of another species. The primary objection to this definition is that it is too vague.

These are but two examples of the numerous definitions from a century of ongoing debate about the definition and meaning of species. Scientists often approach the species question differently depending on what organisms they are studying and the way in which they are studying them. Traditionally, organisms have been grouped into species based on aspects of their appearance or particular behaviors. More recently, analysis of deoxyribonucleic acid (DNA) has joined the list of techniques for differentiating or grouping organisms. Additionally, there are specific criteria used for different groups. In plants, for instance, plant chemistry, insect associations, and number of **chromosomes** may be important indicators of species status. As another example, scientists studying bacteria may use such characteristics as shape, biochemistry, and conditions favoring growth to help them answer species questions. Thus, there is no simple, universally agreed-upon definition of species. SEE ALSO BIODIVERSITY; BUFFON, COUNT; EVOLUTION; SPECIATION; TAXONOMY, HISTORY OF

Ann E. Kessen and Robert M. Zink

MAYR, ERNST (1904–)

German-born U.S. evolutionary biologist who helped found the "modern synthesis," the melding of evolutionary theory with genetics. Mayr's greatest contribution was to explain how new species can arise. When a population is isolated, on an island, for example, it can evolve separately from the rest of the species. Mayr's views have defined evolutionary biology for nearly three-quarters of a century, and he has won two prestigious prizes, the Balzan Prize and the Japan Prize.

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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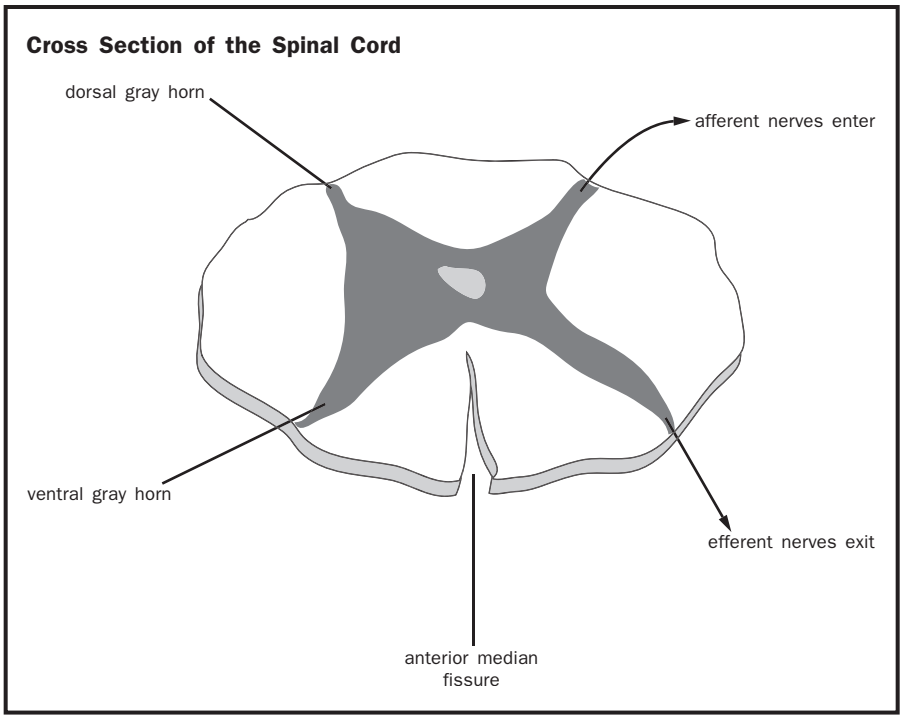
Spinal Cord

The spinal cord is a bundle of nerve fibers, no thicker than the human thumb, that links the brain with the rest of the body. The spinal cord is protected by the vertebral column, and together with the brain it comprises the central nervous system. The nerves that enter and exit the spinal cord form the peripheral nervous system.

Some nerves enter the spinal cord on its dorsal surface (which is closest to the back). These nerves carry sensory information to the spinal cord and are called afferent nerves. For example, they allow a person to determine if the pan on the stove is hot or cold, or if one's hand is touching



rough sandpaper or smooth silk. In contrast, the nerves that exit the ventral surface (closest to the stomach) of the spinal cord carry information from the spinal cord to the rest of the body. These nerves enable a person to jerk his or her hand away from a hot pan or throw a dog a ball. The term for nerves that conduct commands from the spinal cord to muscles and organs is efferent.

The afferent and efferent nerves are associated with an H-shaped area of gray matter in the center of the spinal cord. The gray matter is separated into dorsal and ventral horns. The ventral horn contains the cell bodies of efferent **neurons** that control muscles and organs. The sensory nerves enter the dorsal horn where they make connections with nerve cells that travel to the brain.

neuron nerve cell

The gray matter is surrounded by white matter, which contains the long projections of nerve cells (called **axons**) that carry information to other parts of the nervous system. Axons that carry similar information are grouped into bundles or tracts. Many tracts start in the dorsal horn and carry sensory information from the cord to the brain (for example, the message that the hand is touching silk instead of sandpaper). Since these neurons are traveling "up" the cord, they are often referred to as ascending tracts. In addition to ascending tracts, the white matter also contains descending tracts. As the name implies, these tracts begin in the brain and travel down the spinal cord to make connections with neurons in the ventral horn. They provide a person with voluntary control of his or her muscles, as well as the involuntary control over internal organs.

axon long extension of a nerve cell down which information flows

In short, the spinal cord carries all of the information that enters and exits the brain. Therefore, it is not surprising that when this flow of information is blocked by injury, the consequences are devastating. Patients suffer paralysis and loss of sensation in their legs (paraplegia) if the lower part

of the cord is damaged, or in their arms and legs (quadriplegia) if the injury is in the upper regions of the cord. In addition, control over urination, defecation, and sometimes respiration is lost depending on the level and extent of the damage. Once the spinal cord has been injured, the damage is usually permanent. Physical therapy can enable a patient to regain a small amount of movement over time, but the medical field has yet to discover a way to reconnect the severed nerve cells to produce normal function. SEE ALSO BRAIN; CENTRAL NERVOUS SYSTEM; NEURON; PERIPHERAL NERVOUS SYSTEM

Sheri L. Boyce

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Stress Response

The stress response is the human body's reaction to anything that throws off the balance inside it—injury, infection, fear, exercise, or pain. The body reacts with an alarm phase, then a resistance phase, during which it tries to fix the imbalance, and then, if that fails, an exhaustion phase.

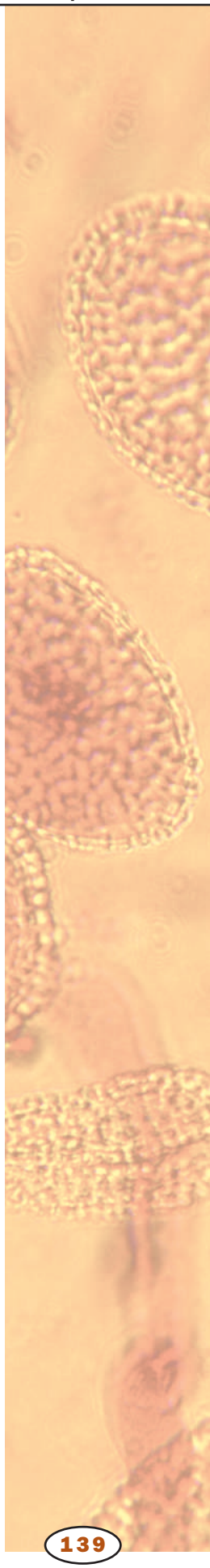
The response starts when a part of the brain called the hypothalamus detects stress. The hypothalamus starts the alarm phase by turning on the sympathetic division of the nervous system. The sympathetic nerves release adrenaline. The "adrenaline rush" makes the heart beat harder and faster, raising blood pressure. A person's skin turns pale as blood vessels to the skin constrict and direct the blood to the muscles. Blood vessels to the intestines and kidneys also constrict. The liver releases stored sugar into the blood, hair stands up, and the body begins to sweat. The body's natural response is to run away or fight back; that's why the sympathetic system is called the "fight or flight" system.

Next, the body must enter the resistance phase and fix whatever is causing this stress. If the body has lost blood from an injury, the kidneys can help minimize the loss. The hypothalamus makes the kidneys take water from the urine and put it back into the blood by releasing a **protein** called antidiuretic (which means "against urination") **hormone** (ADH).

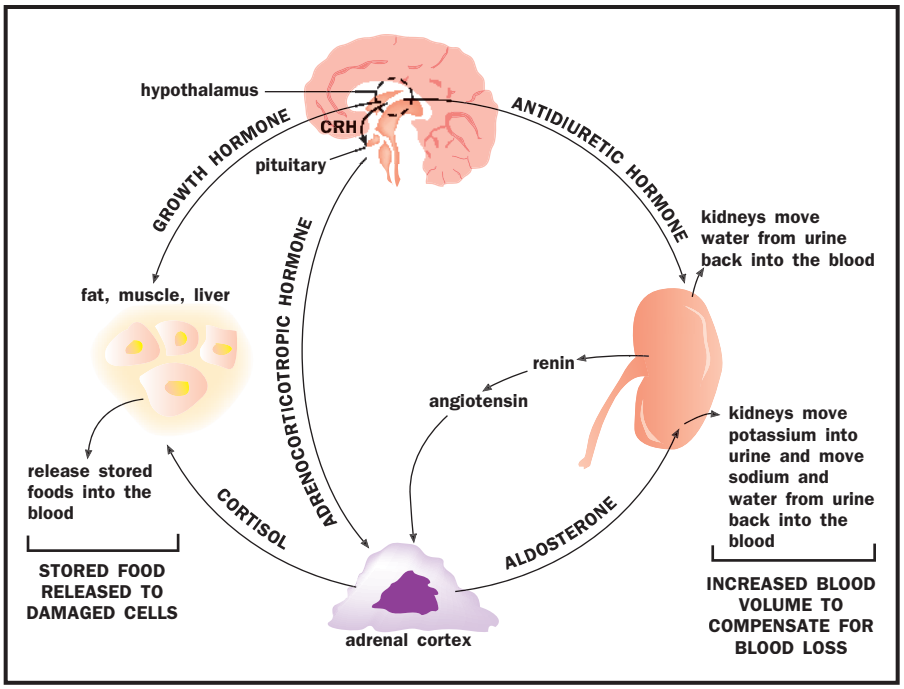
protein complex molecule made from amino acids; used in cells for structure, signaling, and controlling reactions

hormone molecule released by one cell to influence another

The adrenal glands (sitting right on top of the kidneys) can also make the kidneys move fluid from the urine back into the blood. But what makes them do it? It's the kidneys, located just below them. When the kidneys' blood supply is reduced during the alarm phase, they release a protein called renin (which means " kidney substance") into the blood. Renin reacts with other proteins in the blood to form angiotensin (which means "blood vessel constricting"). When angiotensin reaches the adrenal glands, their outer layer, the adrenal cortex, releases the hormone aldosterone. Aldosterone makes the kidneys secrete potassium into the urine and reabsorb sodium and water into the blood. This helps maintain blood volume.



The hypothalamus and adrenal cortex work together in the resistance phase to replace lost blood volume and send food to damaged cells.



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

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

As the stress continues, the body uses up its stored **glucose**. It will need to use its stored **carbohydrates**, fat, and proteins for energy and to heal damaged cells. Once again, the hypothalamus and adrenal glands tell the body what to do. The hypothalamus releases growth hormone and the adrenal cortex releases cortisol. Both of these hormones tell the body to release stored compounds from body fat, muscles, and the liver. In this case, the adrenals get their orders to release cortisol from the hypothalamus when it releases a protein called corticotropin (meaning "cortex stimulating") releasing hormone (CRH).

The hypothalamus does not affect the adrenals directly. Instead, the CRH goes to the pituitary gland, just below the brain. The pituitary sends the message on to the adrenals by releasing adrenocorticotropic (meaning "adrenal cortex stimulating") hormone (ACTH). This chain of command, in which the hypothalamus tells the pituitary what to do, and then the pituitary tells the adrenals, is called the hypothalamic-pituitary-adrenal axis. When ACTH reaches the adrenals, the adrenal cortex releases cortisol into the blood. Cortisol makes the body release stored chemicals into the blood.

With ADH and aldosterone helping the body preserve blood volume, and cortisol and growth hormone providing food for the cells, the body should recover. But if this isn't enough help, the body could become exhausted and suffer organ damage.

Long-term or chronic stress can keep the body's stress response too active. That can cause high blood pressure by increasing blood volume. It can make the body lose too much potassium in the urine or develop high blood sugar levels. Also, cortisol suppresses the immune and inflammatory systems (that is why the similar compound cortisone is used to treat rashes). With high cortisol levels, the body has trouble fighting off infections. Stress even makes some animals more prone to cancer. The stress response helps saves the body from life-threatening injury, but it may need to be controlled with

medications, biofeedback, or meditation to keep it from causing new illnesses or complications. SEE ALSO ADRENAL GLAND; BLOOD SUGAR REGULATION; HORMONES; HYPOTHALAMUS; IMMUNE RESPONSE; LIVER; NERVOUS SYSTEMS; PITUITARY GLAND

Patricia S. Bowne

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Structure Determination

Determining the structure of a molecule, especially a protein, is an important step in determining its function. In many diseases, changes in molecular structure are involved in the **pathologic** process, and understanding these changes can help in the design of therapy. The three-dimensional arrangement of atoms in a molecule can be determined using a variety of physical techniques. For large biological **macromolecules** the most common experimental techniques for structure determination include X-ray crystallography, electron microscopy, and nuclear magnetic resonance (NMR). Finally, approximate models depicting the three-dimensional arrangement of atoms can be built using computer modeling.

pathologic related to disease

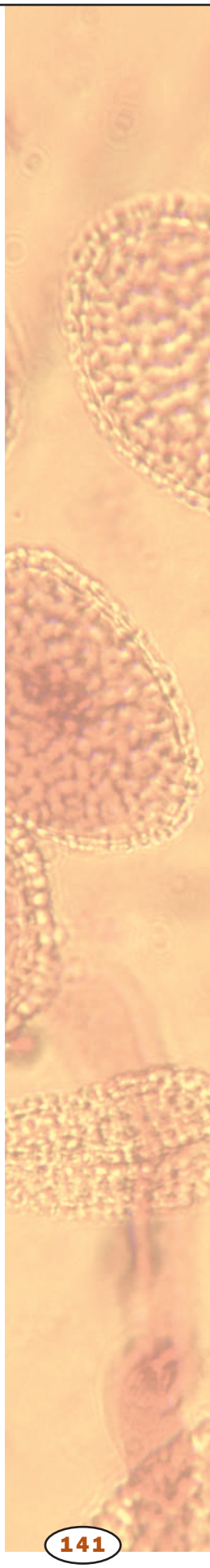
macromolecules large molecules such as proteins, carbohydrates, and nucleic acids

The principles behind the use of X rays for the determination of the structures of biological macromolecules are quite different from the use of "X rays" in the practice of medicine. A medical X-ray film shows a shadow revealing internal body parts depending on how easily the X rays penetrated them. In contrast, **X-ray crystallography** looks at how X rays are diffracted, or scattered, by the atoms in a sample and determines what the three-dimensional arrangement of the atoms must be to give rise to the observed pattern of scattering. (This is somewhat akin to determining the structure of a jungle gym by bouncing a tennis ball off it and recording the pattern of bounces.)

X-ray crystallography use of X rays to determine the structure of a molecule

The distances between atoms in a molecule are very small, on the order of 10^{-10} meters, and the wavelength of the radiation used to determine their relative positions must be correspondingly small. X rays have the necessary small wavelength. The amount of radiation scattered by one molecule is too small to measure; therefore, it is necessary to combine the diffraction from a large number of molecules. Crystals are used because they contain an ordered arrangement of many molecules. Computers are used to reconstruct an image of the molecules in the crystal. The technique of X-ray crystallography provides the most detailed and accurate information on the structure of biological macromolecules.

Electron microscopy uses an electron beam to study the structure of biological materials. By using a magnet to focus electrons scattered from a sample, an electron microscope can form an image in a manner similar to a conventional microscope. One problem is that the electron beam used in such a microscope has a very high energy and can destroy sensitive biological samples. To aid in its preservation, the sample is often maintained at a



very low temperature (this is called cryo-electron microscopy). As in the case of X-ray diffraction, it is an advantage to combine the electrons scattered from many molecules to get an average image. This can be done using ordered samples such as two-dimensional crystals or by orienting and averaging many images. Electron microscopy is especially useful for large complexes of macromolecules.

Nuclear magnetic resonance is not a scattering technique, but a spectroscopic technique that depends on the interaction of atomic nuclei with radio-frequency radiation and a magnetic field. This interaction is very sensitive to the environment surrounding an atom, and therefore can be used to determine what other atoms are nearby a given atom. Once the features in an NMR spectrum have been associated with specific atoms it is possible to combine this experimental information of the local arrangement of atoms with knowledge of the chemical structure of a molecule to derive a three-dimensional structure. An advantage of NMR is that it examines molecules in solution and can also provide information about their dynamic properties, or motion.

In addition to the experimental techniques for determining the three-dimensional structures of molecules, it is possible to use computational techniques to predict structures. The most successful approach to structure prediction utilizes the observation that proteins with similar **amino acid** sequences have similar three-dimensional structures. This allows one to predict an approximate structure if a structure of a related protein is already known. This starting point can then be combined with knowledge of the chemical structure and physical principles to improve the model. SEE ALSO ELECTRON MICROSCOPY; PROTEIN STRUCTURE

amino acid a building block of protein

Wayne F. Anderson

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Symbiosis

A wide array of interactions among plants, animals, and microorganisms occurs in nature. Some of these relationships are characterized by a close physical association among species that persists for a significant period of the life cycle. In 1879 German botanist Heinrich Anton de Bary coined the term "symbiosis" to describe these relationships, meaning the living together of different species of organisms.

An interaction is considered a symbiosis based on the closeness of the physical association among the organisms rather than on the effect or outcome of the interaction. Symbiotic relationships span a spectrum from beneficial to detrimental effects. Many people associate symbiosis with **mutualism**, interactions that are beneficial to the growth, survival, and/or reproduction of *both* interacting species. But symbiotic interactions also include commensalism (one species receives benefit from the association and

mutualism symbiosis between two organisms in which both benefit

Cleaner shrimp cleaning a zebra moray eel. Mutualistic relationships such as these promote the well-being of the host fishes and provide food for those that do the cleaning.

the other is unaffected), amensalism (one species is harmed, with no effect on the other), and parasitism. An example of commensalism is found in the anemone fish, which gains protection from living among the poisonous tentacles of the sea anemone, but offers no known benefit to its host.

In parasitic interactions, one species lives on or within a host organism and receives nourishment from the host, whereas the host is harmed by the interaction. In **obligate** interactions, the relationship is essential to at least one of the interacting species. Facultative interactions are those that are beneficial to at least one of the interacting species, but not essential.

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

Mutualisms in Plants

A common and widespread symbiosis occurs between terrestrial plants and fungi that colonize their roots. These associations are called "mycorrhizae," a word meaning "fungus-root." Unlike **pathogenic** fungi that cause disease, mycorrhizal fungi benefit the plant in several ways. These fungi germinate from spores in the soil to form thin threadlike structures called hyphae, which grow into the roots of plants. Once the roots are colonized,

pathogen disease-causing organism

the fungal hyphae grow out from the root in an extensive network to explore the soil beyond the reach of the roots, gathering essential mineral nutrients and transporting them into the plant, increasing its growth. In return, the plant provides **carbohydrates** as a food source for the fungus.

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

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

Mycorrhizal symbiosis occurs in about 80 percent of all plant species. It is essential to many plants in low-nutrient environments because their roots alone are incapable of absorbing adequate amounts of some essential **minerals** such as phosphorus. The symbiosis is essential to the fungus because, unlike plants, fungi cannot make their own food via photosynthesis.

ecosystem an ecological community and its environment

Mycorrhizal fungi provide other benefits to plants including improved resistance to drought and disease. The additional mineral nutrients acquired by these fungi have been shown to aid plants in coping with competitors and herbivores. This symbiosis plays a large role in the growth and functioning of plants in both natural and agricultural **ecosystems**.

Legumes and certain other plants are colonized by *Rhizobium* bacteria that form small swellings or nodules on their roots. These symbiotic bacteria carry out the process of nitrogen fixation, the conversion of nitrogen gas into ammonia. Nitrogen is an essential element required by all organisms. Although nitrogen gas is abundant in the air, plants are unable to use nitrogen in this form, but they can readily use the ammonia formed by these bacteria and thus benefit from this symbiosis. As with mycorrhizal associations, the host plant benefits its symbiont by providing a carbohydrate energy source.

Mutualisms in Animals

ungulate hoofed mammals such as cattle

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

enzyme protein that controls a reaction in a cell

In animals, a common mutualistic symbiosis occurs between many herbivores and microorganisms of their digestive tracts. **Ungulates** (hoofed animals) and some other animals eat plant material that is high in **cellulose**, even though they lack **enzymes** capable of breaking down cellulose molecules. They obtain energy from cellulose with the help of symbiotic bacteria and protozoa living within their digestive tracts. These microbes produce enzymes called cellulase that break down cellulose into smaller molecules that the host animal can then utilize. Similarly, wood-consuming termites depend upon symbiotic protozoans living within their intestines to digest cellulose. These are obligate symbioses. The termites cannot survive without their intestinal inhabitants, and the microorganisms cannot live without the host. In each of these symbioses, the host animal benefits from the food provided by the microorganism and the microorganism benefits from the suitable environment and nourishment provided by the host.

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

A variety of animals engage in a mutualistic relationship referred to as cleaning symbioses. Birds such as oxpeckers benefit their large ungulate hosts by removing their external **parasites**, benefiting in return from the food source the host provides. In the marine environment, certain species of fish and shrimp similarly specialize in cleaning parasites from the outside of fishes. This mutualistic relationship promotes the well-being of the host fishes and provides food for those that do the cleaning. Unlike herbivores and their gut microorganisms, these interactions do not involve a close association of one organism living exclusively within another. These and other mutualistic but not clearly symbiotic relationships, such as those between plants and their pollinators, are sometimes referred to as proto-cooperation.

Parasitism

Perhaps the most common type of symbiotic interaction in nature is parasitism. Many kinds of worms, protozoa, bacteria, and viruses are important animal parasites. Some, such as fleas or ticks, are ectoparasites, living on the outside of their host. Others, such as tapeworms or hookworms, are endoparasites that live inside their host.

A variety of parasitic **symbionts** also occur in plants. In some plants, insects deposit their eggs within the growing shoot tips or other plant part, at the same time producing chemicals that cause the development of a large swelling or tumorlike growth called a gall. The insect larvae then develop within the gall, feeding on the plant tissue as they grow. When its development is completed, the adult insect emerges from the gall to mate and then initiate the gall-forming cycle again. This is an obligate symbiosis because the insect larvae lives inside the plant and cannot complete its life cycle without its host plant. It is also a parasitic association because the insect living within the plant consumes plant tissue and causes harm to its host plant, while benefiting from the food resources and shelter provided by the plant. In addition to insects, other gall-forming symbionts include viruses, bacteria, and fungi.

symbionts organisms living in close association with another organism

Symbioses are widespread and important in the life of many organisms and ecologically important in the functioning of natural ecosystems. The patterns of adaptations of mutualists, parasites, and hosts suggest that these interactions are the product of coevolution, leading to increasingly specialized, and often increasingly beneficial, associations. In many mutualistic symbioses such as lichens (symbioses of algae and fungi) and corals (cnidarians and endosymbiotic algae), the adaptive value of the association is that one organism acquires from its partner some new metabolic capability (for example, photosynthesis) that it does not itself possess. SEE ALSO CNIDARIAN; CORAL REEF; MYCORRHIZAE; POPULATION DYNAMICS

David C. Hartnett

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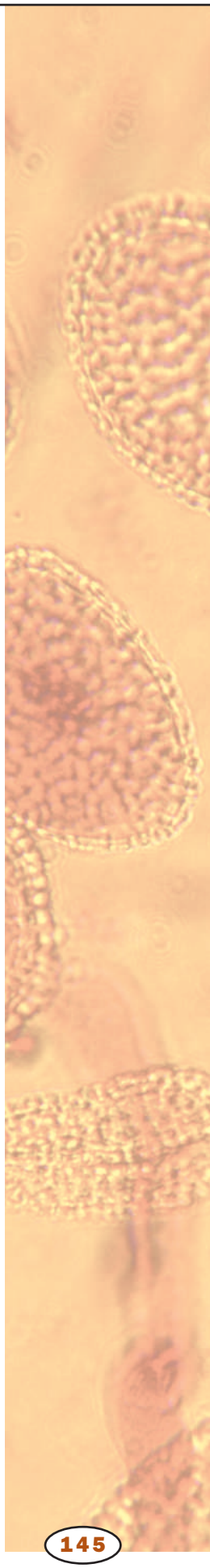
Synaptic Transmission

Synaptic transmission is the process whereby one neuron (nerve cell) communicates with other neurons or **effectors**, such as a muscle cell, at a synapse. A typical neuron has a cell body (soma), branching processes specialized to receive incoming signals (dendrites), and a single process (axon) that carries electrical signals away from the neuron toward other neurons or effectors. Electrical signals carried by **axons** are **action potentials**. Axons often have thousands of terminal branches, each ending as a bulbous enlargement, the synaptic knob or synaptic terminal. At the synaptic knob, the action potential is converted into a chemical message which, in turn, interacts with the recipient neuron or effector. This process is synaptic transmission.

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

axon long extension of a nerve cell down which information flows

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



Synapses

Synapses are junctional complexes between presynaptic membranes (synaptic knobs) and postsynaptic membranes (receptor surfaces of recipient neurons or effectors). The prefixes "pre-" and "post-" reflect the direction of synaptic transmission: presynaptic is the transmitting side (synaptic knob) and postsynaptic is the receiving side (dendrite, soma, or effector). Synaptic knobs contain many membrane-bounded synaptic **vesicles**, 40 to 100 **nanometers** in diameter. Synaptic vesicles contain the neurotransmitter. Synaptic knobs also contain **mitochondria**, microtubules, and other **organelles**.

vesicle membrane-bound sac

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

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

organelle membrane-bound cell compartment

Synapses are named according to their location on the postsynaptic neuron: Axospinous synapses are synapses on dendritic spines (tiny projections on the dendrites), axodendritic synapses are on shafts of dendrites, axosomatic synapses are on the soma of neurons, and axoaxonal synapses are synapses on other synaptic knobs. Synapses on skeletal muscle cells are neuromuscular junctions.

Neurotransmitter Release

Action potentials arriving at synaptic knobs trigger the release of neurotransmitter into the synaptic cleft. The molecular mechanism is not completely understood. A "synaptic delay" of one to two milliseconds occurs between the arrival of the action potential and the neurotransmitter release. Action potentials open calcium channels in the membrane of the synaptic knob, which causes an inward movement of calcium **ions**. Calcium ions trigger the release of neurotransmitter from synaptic vesicles into the synaptic cleft. The synaptic vesicles fuse with the presynaptic membrane during this process of exocytosis. The membranes of old vesicles become part of the presynaptic membrane and new vesicles pinch off from an adjacent area of membrane. These new vesicles are subsequently refilled with newly synthesized or "recycled" **neurotransmitters**.

ion an electrically charged particle

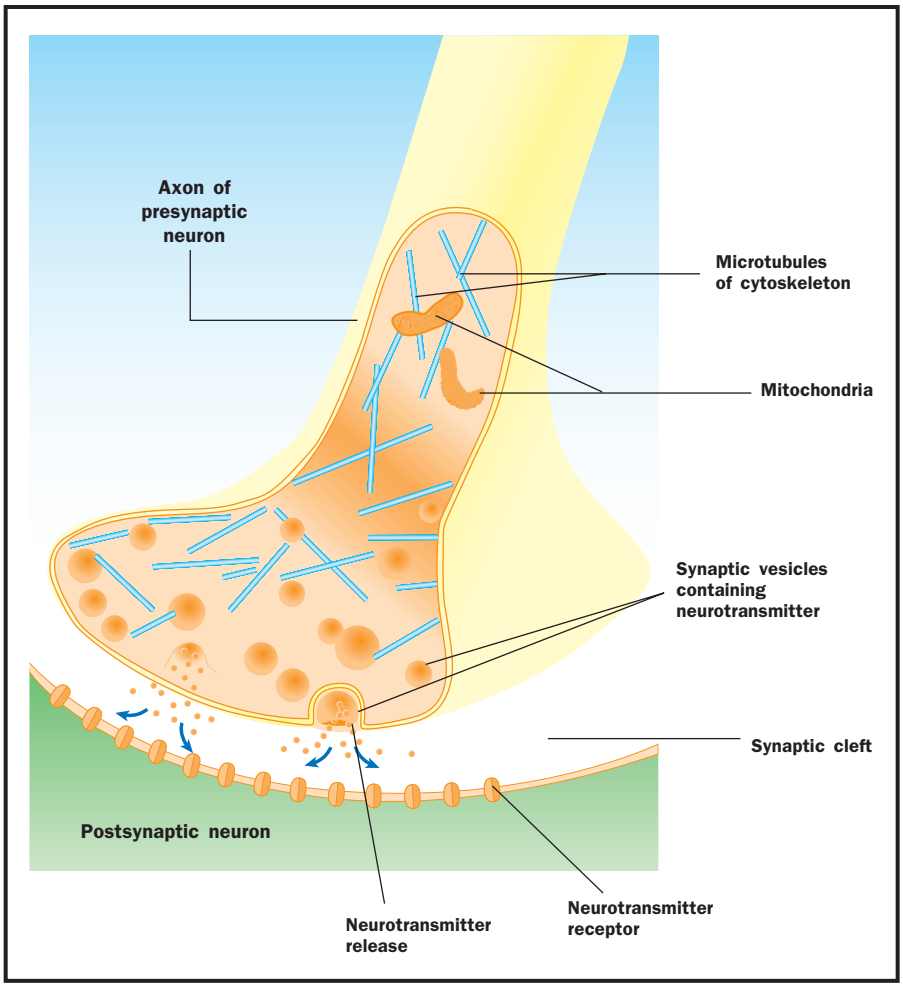
neurotransmitters molecules released by one neuron to stimulate or inhibit another neuron or cell

Released neurotransmitters diffuse across the narrow synaptic cleft. At the postsynaptic membrane, neurotransmitter molecules bind to membrane-bound receptor molecules with recognition sites specific for that neurotransmitter. Binding of the neurotransmitter to the receptor triggers a postsynaptic response specific for that receptor. These responses can be either excitatory or inhibitory, depending on the properties of the receptor. If receptor stimulation results in the postsynaptic membrane becoming more electrically positive (depolarized), it is an excitatory postsynaptic potential (EPSP). If more negative (hyperpolarized), it is an inhibitory postsynaptic potential (IPSP). Excitation and inhibition depend on the properties of the receptor and not the neurotransmitter. Receptors coupled to sodium or calcium channels are excitatory and produce a depolarization of the postsynaptic membrane, whereas receptors coupled to chloride or potassium channels are inhibitory and produce a hyperpolarization of the postsynaptic membrane. Such receptors coupled to ion channels are called ionotropic receptors.

Other receptors are coupled to "second-messenger" systems that initiate a series of biochemical reactions in the postsynaptic cell. These are metabotropic receptors. Metabotropic receptors can produce many different

LOEWI, OTTO (1873–1961)

German-born American physician who received, with Henry Dale, the 1936 Nobel Prize in physiology for the discovery of a substance that stimulates nerve cells. In the 1920s, Loewi provided the first evidence that chemicals transmit impulses between nerves and organs, such as the heart.



Synapses are junctional complexes between the presynaptic neuron and the postsynaptic neuron. Presynaptic is the transmitting side of the nerve impulse and postsynaptic is the receiving side.

postsynaptic events. These range from the direct activation of adjacent ion channels, to alteration of receptor sensitivity, to **transcription** of specific messenger ribonucleic acids (RNAs), or even the activation of specific **genes**. Chemical synapses are part of a very adaptable and flexible communications system. These are not static anatomical structures with fixed properties but are dynamic structures, able to change their molecular properties with changing circumstances.

transcription messenger RNA formation from a DNA sequence

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

There are literally hundreds of neurotransmitters. Some are fairly simple compounds such as acetylcholine, serotonin, the catecholamines (dopamine, norepinephrine, and epinephrine) and a number of the **amino acids**. Many are more complex and belong to the vast array of neuropeptide transmitters. Once released into the synaptic cleft, neurotransmitters remain active until they are either altered chemically or taken back into the synaptic knob by special carrier systems and recycled. At cholinergic synapses, acetylcholinesterase is present in the synaptic cleft. This **enzyme** cleaves the neurotransmitter into acetate and choline, neither of which is active. Serotonin and epinephrine, on the other hand, are taken up into the presynaptic terminal and recycled.

amino acid a building block of protein

enzyme protein that controls a reaction in a cell

Electrical Synapses

Electrical synapses, although rare in vertebrate nervous systems, do exist. In an electrical synapse, or gap junction, the presynaptic and postsynaptic membranes are partially fused. This allows the action potential to cross from the membrane of one neuron to the next without the intervention of a neurotransmitter. Electrical synapses often lack the directional specificity of chemical synapses and may transmit a signal in either direction. During biological activity, electrical synapses do not have the potential for as much variation as do chemical synapses. SEE ALSO Amino Acid; Exocytosis; Hormones; Ion Channels; Muscle

Alvin M. Burt

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T Cells

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

Vertebrate animals have two immune system mechanisms to specifically identify and remove infectious agents from the body. In humoral immunity, **proteins** called antibodies bind to the foreign invader, targeting it for destruction by nonspecific defenses. In cell-mediated immunity, immune cells directly attach to and destroy the invader. Both mechanisms require the actions of T cells.

T cells belong to a category of white blood cells called lymphocytes. Lymphocytes are slightly larger than red blood cells and are found in the blood, lymphatic organs, and many other structures in the body. The spleen, lymph nodes, and tonsils are examples of lymphatic organs. Lymphocytes have large, round nuclei that take up almost all of the space inside the cell. Other examples of lymphocytes include B cells and natural killer cells.

Like all blood cells, T cells are made in the bone marrow. The *T* is an abbreviation for the word "thymus," an organ found on the front of the trachea, near the lungs and heart. After T cells are made, they go to the thymus to become mature. Three important events occur in the thymus.

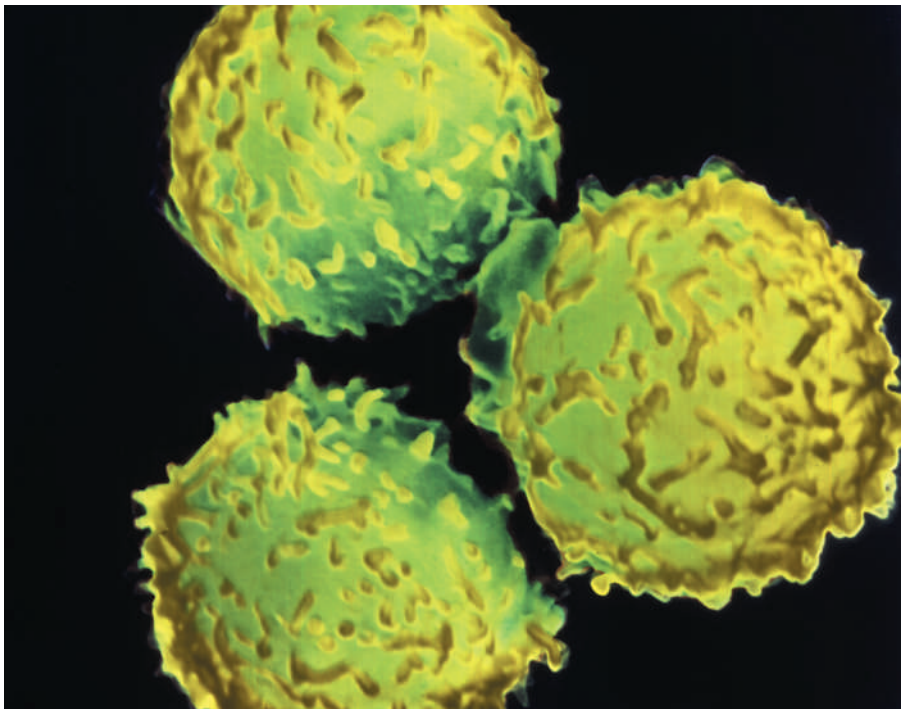
antigen foreign substance that provokes an immune response

First, each T cell begins to produce a protein called a receptor on its cell surface. T cell receptors recognize **antigens**, which are molecules that can start an immune response. Foreign invaders are made of many antigens. An antigen can fit inside the T cell receptor much like a key fitting into a lock. Each T cell receptor recognizes only one type of antigen. This explains how the immune system specifically identifies foreign invaders.

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

As a T cell matures, the **genes** that contain the information on how to build the T cell receptor are rearranged. Millions of possible T cell receptors can be produced by this rearrangement. However, once the genes are rearranged, a given T cell is committed to making only one type of receptor.

Unfortunately, some T cells express receptors that can recognize and damage the body's own antigens. Consequently, the second event that oc-



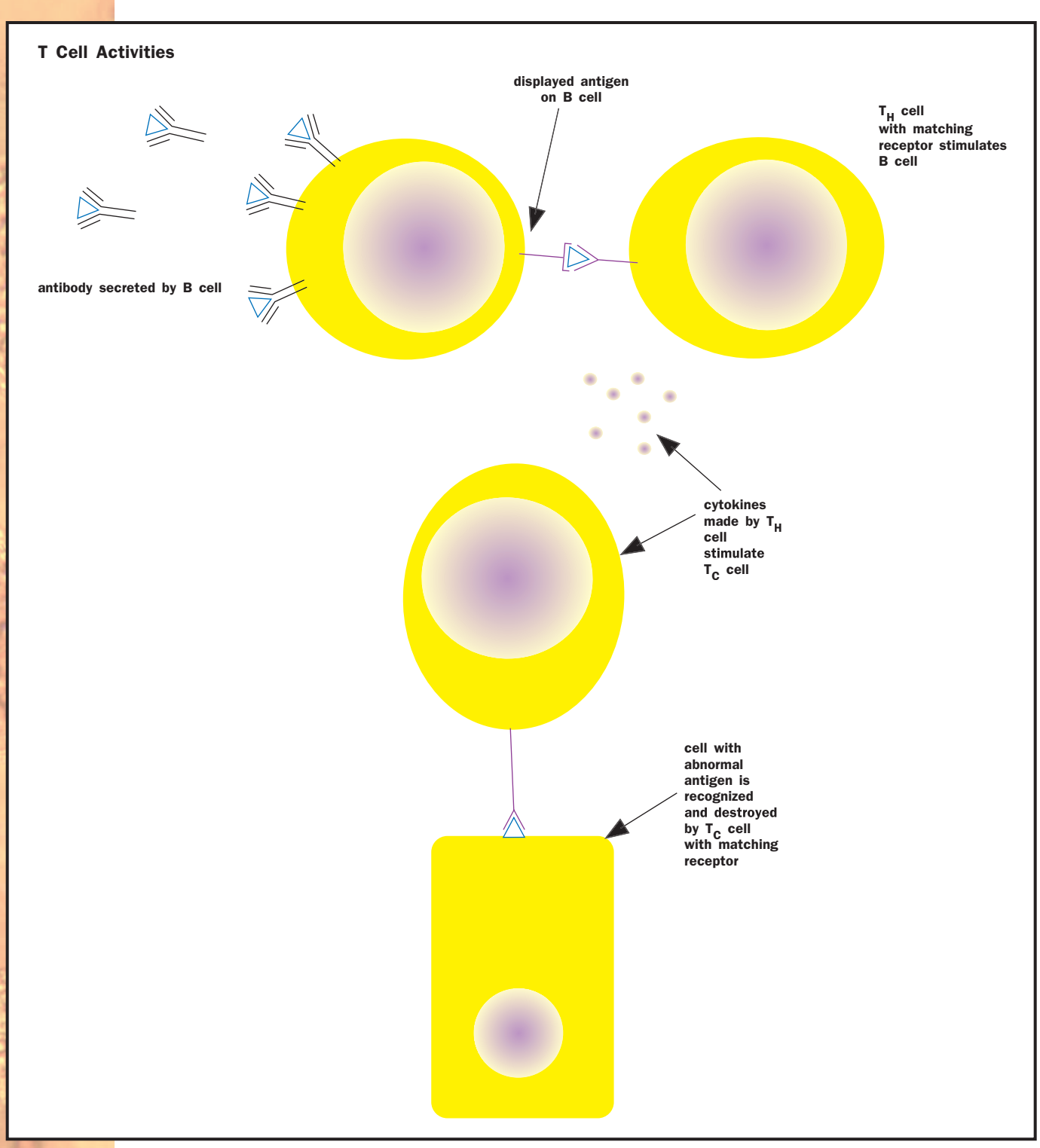
Scanning electron micrograph of three T cells.

curs in the thymus is the destruction of these T cells. This process is called clonal deletion. The surviving T cells can roam through the body's organs, searching only for invaders.

The third event that occurs before the T cells leave the thymus results in the production of T cells with different functions. Some of the T cells will produce a surface protein called CD4. These T cells are called helper T cells (T_H cells), T4 cells, or CD4 cells. As their name implies, T_H cells assist other immune cells. Other T cells in the thymus produce a surface protein called CD8. These T cells are called cytotoxic T cells (T_C cells), T8 cells, or CD8 cells. As their name implies, T_C cells destroy foreign invaders. Some CD8 cells seem to be able to control the immune system and are consequently called suppressor T cells.

T_H cells function in both humoral immunity and cell-mediated immunity. If foreign antigens enter the body, cells called antigen-presenting cells (APCs) engulf the antigen and attach it to a molecule called a class II major histocompatibility complex (MHC) protein. The antigen and class II MHC protein are then moved to the surface of the APC. The APC presents these molecules to a series of T_H cells with different receptors. If there is a match between a T_H cell receptor and the antigen, the T_H cell is stimulated to divide rapidly and produce chemicals called cytokines. The CD4 molecule on the T_H cell connects with the class II MHC protein on the APC to stabilize the cell-to-cell connection and provide additional signals. There are many other molecules on the surfaces of these cells that must interact, showing the complexity of the process.

In humoral immunity, stimulated T_H cells activate B cells. Like APCs, B cells bring foreign antigens inside and then display them with class II MHC proteins on the surface. The stimulated T_H cells then attach to the B cells just as they did with the APCs. This contact, along with the cytokines,



T_H cells interact with B cells and T_C cells to protect the body from infection.

stimulates the B cell to divide rapidly, and it produces antibodies. Antibodies can clear other copies of the foreign invader from the body.

In cell-mediated immunity, stimulated T_H cells activate T_C cells. All cells of the body produce surface proteins called class I MHC proteins. If the cell is abnormal (cancerous or infected with a virus), the abnormal antigen is displayed with the class I MHC protein. A T_C cell with the match-

ing receptor will recognize the abnormal cell. The T_C cell receptor binds to the abnormal antigen and the CD8 molecule binds to the class I MHC molecule. The T_C cell receives other signals from cytokines made by T_H cells. Now the T_C cell divides rapidly and searches for other abnormal cells. When the T_C cells find abnormal cells, they bind to them and release chemicals that destroy the target cell. Perforin, lymphotoxin, and tumor necrosis factor are examples of these chemicals. Both B cells and T_C cells can become memory cells. Memory cells eliminate an invader more quickly if it appears again.

T_H cells also aid nonspecific immunity by producing cytokines that cause inflammation and attract and activate white blood cells such as neutrophils, natural killer cells, and macrophages to the site of infection.

T cells may function abnormally, causing a variety of medical problems. For example, human immunodeficiency virus infects and destroys T_H cells. Consequently, many T_C cells and B cells are not activated. The invader gets the upper hand, and the body cannot easily rid itself of the infection or abnormal cell.

Sometimes T_C cells overreact to a harmless antigen and damage healthy tissue. This is what happens in individuals with allergies to poison ivy, latex, cosmetics, and metals. T_C cells are also responsible for the rejection of a transplanted organ. SEE ALSO AIDS; Antibody; Autoimmune Disease; Immune Response; Nonspecific Defense

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Taste *See Chemoreception*

Taxonomy, History of

Taxonomy, the field of biological classification, attempts to group types of organisms in meaningful ways. Modern taxonomy is based on similarities among organisms that reflect descent from recent shared ancestors, rather than similar solutions to environmental challenges. For example, a bird's wing and a human's arm reflect common descent from a vertebrate ancestor, whereas a bird's wing and an insect's wing are derived from different structures and therefore not characteristics on which modern classification might be based.

Taxonomic designations increasingly rely on deoxyribonucleic acid (DNA) sequence similarities. Because DNA mutates at a known rate, the

Carolus Linnaeus, the great eighteenth-century taxonomist, distinguished plants by their sexual parts.

more alike the DNA sequences are for two types of organisms, the more recently they diverged from a shared ancestor. By considering such data on pairs of species, biologists can construct evolutionary tree diagrams that depict how existing organisms are related to one another. In this way, taxonomy in the modern sense reflects evolution.

Early Classification Schemes

Humans have probably always classified life. Thousands of years ago, people designated plants, animals, and fungi by whether they were tasty and safe to eat, of medicinal value, or were foul-tasting or even poisonous. An early taxonomist was Greek philosopher Aristotle (384–322 B.C.), who organized five hundred types of animals according to habitat and body form. His designations were rather subjective: he considered animals that gave birth to live young and had lungs as the pinnacle of living perfection.

By the sixteenth century, explorers had discovered so many new species that Aristotle's plan could no longer suffice. Newer schemes continued to be based on what people could see, but the characteristics considered were often more mystical than scientific. For example, an early-sixteenth-century botanical classification assigns a high ranking to the plantain, because "more than any other plant, it bears witness to God's omnipotence." John Ray (1627–1705) was an English naturalist who classified more than twenty thousand types of plants and animals. His highly descriptive method distinguished animals by their hoofs, nails, claws, teeth, and toes. Yet the inability to see microscopic distinctions and reliance on **superficial** similarities led him to group together algae, lichens, fungi, and corals. A lichen is a compound organism that consists of an alga and a fungus, but a coral is an animal.

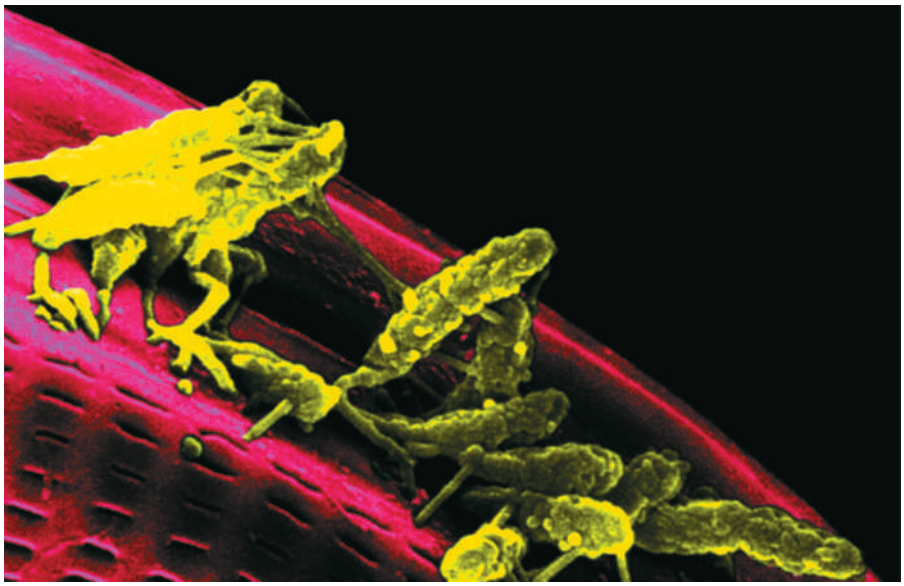
superficial on the surface; not deep

Carolus Linnaeus (1707–1778) is the best-known taxonomist. Heavily influenced by John Ray, Linnaeus compared, contrasted, and meticulously listed types of organisms from his earliest childhood. He started his first botanical listing at age eight, which evolved into a series of publications called *Systema Naturare*, reaching twenty-five hundred pages by its tenth edition. Linnaeus distinguished plants by their sexual parts. He is most noted for introducing the binomial name for a species, which includes an organism's genus and "specific epithet," an adjective that describes the species in some way. The human animal, according to Linnaeus's scheme, is *Homo sapiens*, *sapiens* meaning "wise." French anatomist Georges Cuvier (1769–1832) and others contributed broader levels of taxonomic classification: family, order, class, **phylum** or division, and kingdom. The full taxonomic classification of humans is: Animalia (kingdom), Chordata (phylum), Mammalia (class), Primates (order), Hominidae (family), *Homo* (genus), *sapiens* (specific epithet).

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

Beyond Plants and Animals

As biologists catalogued more of life's diversity, classification as plant or animal was no longer sufficient. For a while, biologists assigned to the plant kingdom anything that couldn't move, such as the fungi. These organisms are not plants because they do not photosynthesize, among other distinctions. Then the invention of the microscope revealed an entirely hidden, but vastly populated, world. In 1866, German naturalist Ernst Haeckel



The discovery of archaea in the 1970s led scientists to add a taxonomic level, called domain, above kingdom.

(1834–1919) proposed a third kingdom, Protista, to include one-celled organisms. But Protista according to this early definition lumped together some very different types of organisms. In 1937, French marine biologist Edouard Chatton made an enormous contribution to biology by introducing the terms prokaryote and eukaryote. The prokaryotes lack nuclei; eukaryotes have nuclei as well as other **organelles**, and include unicellular and multicellular life. The prokaryotes include bacteria, cyanobacteria, and the fairly recently recognized archaea.

organelle membrane-bound cell compartment

By 1959, it became clear that three kingdoms weren't enough. For a decade, several four-kingdom schemes reigned. One approach split single-celled life into prokaryotes and eukaryotes; another separated fungi from plants. Both changes were included in Cornell University ecologist Robert Whittaker's five-kingdom system. He introduced it in 1969 and it prevailed for many years. Whittaker's scheme recognized the Monera (prokaryotes), Protista (unicellular eukaryotes), Fungi, Plantae, and Animalia.

Enter the Archaea

Classification of life reflects the tools that scientists have to observe organisms and to compare their characteristics. With the ability to distinguish nucleic acid sequences in the 1970s came a new way to deduce evolutionary relationships and classify organisms on this basis. Carl Woese, a microbiologist at the University of Illinois, analyzed the ribosomal ribonucleic acid (rRNA) **genes** of various microbes, reasoning that these genes are so vital that they would be similar in sequence among different types of organisms. (That is, any major deviation would be lethal.) Comparing the differences in sequence, therefore, might be useful in establishing evolutionary relationships. He quickly learned that prokaryotes and eukaryotes have very distinctive rRNA gene sequences.

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

After examining the rRNA genes of all of the microbes in his colleagues' labs, Woese turned to an organism in a more natural habitat, *Methanobacter thermoautotrophica*, a methane-emitting microbe found in a nearby lake. Its rRNA genes were markedly different in sequence from the prokaryotic

lipid fat or waxlike molecule, insoluble in water

"signature." Woese found others like it. This new class of microbes also had different **lipid** molecules in their membranes than other bacteria. Eventually, when the list had grown, Woese published his work. In 1977 he introduced the archaebacteria and suggested that a new and broader taxonomic level, called the domain, embrace them.

Early use of the term "archaebacteria" led to much initial confusion, because these organisms are quite different from bacteria, although they are also small and lack nuclei. Because the first archaea that Woese worked with were found in what are termed extreme environments—high heat, salt, or pressure—the idea arose that this was one of their key characteristics. Since then, however, biologists have found archaea in many habitats, including rice paddies, swamps, and throughout the oceans. To identify them, biologists just had to know what to look for.

The three domains of life are the Archaea, the Prokarya, and the Eukarya. Both the Archaea and the Prokarya consist of unicellular organisms that are prokaryotic cells. The Eukarya includes the eukaryotes (protista, plants, fungi, and animals). This invention of domains to supercede kingdoms solved a problem that the identification of archaea brought to Whittaker's five-kingdom scheme. At first, the archaea were considered a sixth kingdom. The dilemma was that the differences between archaea and any of the other five kingdoms were greater than the differences among those other kingdoms. The three-domain organization has gained acceptance as distinctions among the groups have accumulated. Today scientists know that archaea lack nuclei and organelles like the bacteria, their cell walls are distinctive, and their mechanisms of DNA replication and **protein** synthesis are more like those of eukaryotes than other prokaryotes. The **genome** sequences of a few archaea have confirmed what Woese proposed a quarter century ago: that they share some characteristics with bacteria and eukaryotes, but are very much a distinct type of organism. On a more philosophical note, the addition of domains to biological classification indicates that taxonomy is very much a dynamic discipline. SEE ALSO ANIMALIA; ARCHAEA; EUBACTERIA; EXTREME COMMUNITIES; FUNGI; LINNAEUS, CAROLUS; PLANT

Ricki Lewis

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

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Temperature Regulation

Humans and other mammals are homeothermic, able to maintain a relatively constant body temperature despite widely ranging environmental temperatures. Although the average human body temperature is 36.7 degrees Celsius (98.2 degrees Fahrenheit), this temperature varies depending on individual differences, time of day, the stage of sleep, and the ovulatory cycle in women. Temperature regulation, or thermoregulation, is the balance be-

A pit bull panting. Thermoregulation is the balance between heat production mechanisms and heat loss mechanisms that occur to maintain a constant body temperature.

tween heat production mechanisms and heat loss mechanisms that occur to maintain a constant body temperature.

Heat flows from higher temperature to lower temperature. Conduction is the transfer of heat between objects that are in direct contact with each other. For instance, if a person sits on the cold ground, heat moves from the body to the cold ground. Convection is the transfer of heat by the movement of air or liquid moving past the body. This explains why a breeze across the skin may cool one down, whereas trapping air inside clothing keeps the body warm.

A lizard sunning itself on a rock on a warm summer day illustrates radiation: the transfer of heat energy via electromagnetic waves. Whereas conduction, convection, and radiation can cause both heat loss and heat gain to the body, evaporation is a mechanism of heat loss only, in which a liquid is converted to a gas. Perspiration evaporating off the skin is an example of this heat loss mechanism.

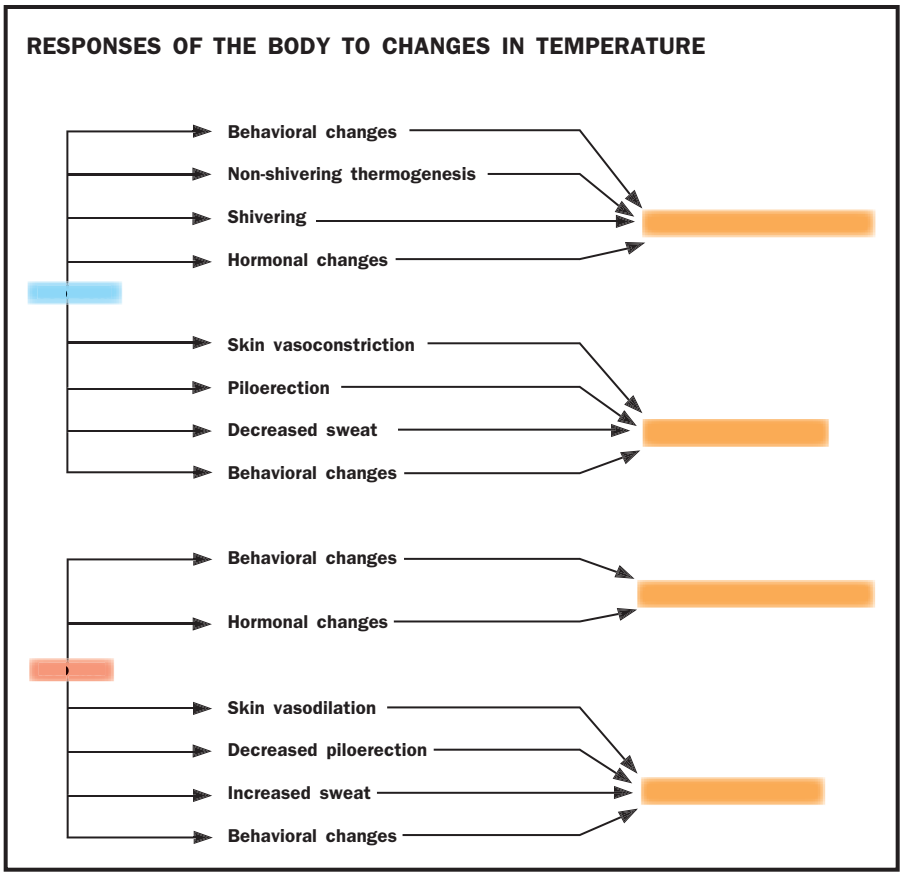
When the body is too hot, it decreases heat production and increases heat loss. One way of increasing heat loss is through peripheral vasodilation, the **dilation** of blood vessels in the skin. When these vessels dilate, large quantities of warmed blood from the core of the body are carried to the skin, where heat loss may occur via radiation, convection, and conduction. Evaporation of fluids from the body also causes heat loss. Humans constantly lose fluids from the skin and in exhaled air. The unconscious loss of fluid is called insensible perspiration.

dilation expansion or swelling

Although the body has no active control over insensible perspiration, the **sympathetic nervous system** controls the process of sweating and can stimulate secretion up to 4 liters (4.22 liquid quarts) of sweat per hour. In order for the sweat to evaporate and cool the body, the environmental air must have a relatively low humidity.

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

When the body is too cold, it increases heat production and decreases heat loss. Vasoconstriction, the constriction of the vessels of the skin, helps prevent heat loss. Shivering, which is a rhythmic contraction of skeletal



muscles, produces heat. Heat can also be produced by nonshivering thermogenesis, an increase in metabolic heat production.

hormone molecule released by one cell to influence another

Hormones such as epinephrine, norepinephrine, and thyroid hormone increase the metabolic rate by stimulating the breakdown of fat. Humans also change posture, activity, clothing, or shelter to adjust for fluctuations in temperature. The goose bumps that arise on the skin in the cold are another sign the body is trying to prevent heat loss. They are due to piloerection, the erection of the hair follicles on the skin. This is a vestige of the time when humans were covered in hair: piloerection would trap air and retain heat.

Body temperature is regulated by a system of sensors and controllers across the body. The brain receives signals regarding body temperature from the nerves in the skin and the blood. These signals go to the hypothalamus, which coordinates thermoregulation in the body. Signals from the hypothalamus control the sympathetic nervous system, which affects vasoconstriction, **metabolism**, shivering, sweating, and hormonal controls over temperature. In general, the posterior hypothalamus controls responses to cold, and the **anterior** hypothalamus controls responses to heat.

metabolism chemical reactions within a cell

anterior toward the front

Hypothermia, or low body temperature, is a result of prolonged exposure to cold. With a decrease in body temperature, all metabolic processes begin to slow. Hypothermia can be life-threatening.

Hyperthermia describes a body temperature that is higher than normal. One example of hyperthermia is fever. A fever is generally considered to be

a body temperature over 38 degrees Celsius (100.4 degrees Fahrenheit). A fever is the body's natural defense to an infection by a bacterium or virus. Fevers are one of the body's mechanisms for eliminating an invading organism. Fevers may even make the immune system work more effectively. Heat exhaustion and heatstroke are other examples of hyperthermia. These occur when heat production exceeds the evaporative capabilities of the environment. Heatstroke may be fatal if untreated. SEE ALSO HORMONES; HYPOTHALAMUS; METABOLISM, HUMAN; NERVOUS SYSTEMS; SKIN; THYROID GLAND

Martha S. Rosenthal

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Theoretical Ecology

The study of ecology involves investigations of specific organisms and environments and the development of general conclusions about how the natural world works. These generalizations are called theories. The goal of ecology, like all sciences, is to develop theories that aptly describe what human beings know about the natural world. For example, the statement "islands have fewer species than similar sized environments on the mainland because islands have higher extinction rates and lower immigration rates" is a theory. It does not describe the situation of a particular island but proposes a generalization regarding patterns and mechanisms for all islands.

Theoretical ecology is a branch of ecology that particularly focuses on the development of theory. To accomplish this, theoretical ecologists usually develop models of the patterns and processes about which they are interested in generalizing. These models usually consist of a series of mathematical equations intended to quantify the phenomenon under study. Ecologists do not pretend that their models include everything involved in the study system. In fact, the models are intentionally simplified representations of what they are studying. This simplification enables the ecologist to analyze in detail certain aspects of their system.

Virtually all aspects of ecology are of interest to theoretical ecologists. In the 1920s and 1930s ecologists Alfred Lotka and Vito Voltera developed some of the first theoretical models of ecology. These simple models consisted of equations intended to describe the growth of two interacting populations over time. The two populations could be competitors or predator and prey. These famous equations are referred to as the Lotka-Voltera model. These equations predicted the conditions in which one species would drive the other to extinction and also what conditions permitted coexistence of the two species. Although very simple models, the results prompted ecologists to think more deeply about species interactions and eventually to develop more complex, but realistic, models and theories.

A number of theoretical models have been developed to describe how animals make foraging choices. For example, optimal foraging theory predicts

that animals should forage in a way that maximizes the net intake of energy in the shortest period of time. Other theoretical models have been developed to explain how plants compete for resources, why animals sometimes behave altruistically toward kin but not unrelated individuals, why some species of plants reproduce many times in their lifetime while other species reproduce only once, how disease spreads through a population, and why sexual reproduction evolved.

One important value of developing models is that the formal process of modeling requires the ecologist to be very thorough and precise in defining the assumptions of the model. Thus, modeling helps ecologists think more clearly about the issues they are studying in the natural world. Another value of these theoretical models is that they often suggest field experiments that can be conducted to test certain predictions made by the model. Data collected from the field often then prompt the theoretical ecologists to revise their models or theories. Thus data collection and theory building work together to advance the ecological understanding of the world. SEE ALSO BIODIVERSITY; ECOLOGICAL RESEARCH, FIELD STUDIES IN PLANT ECOLOGY; ECOLOGY; ECOLOGY, HISTORY OF; ECOSYSTEM; POPULATION DYNAMICS

Mark A. Davis

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

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

amino acid a building block of protein

hormone molecule released by one cell to influence another

enzyme protein that controls a reaction in a cell

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

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

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

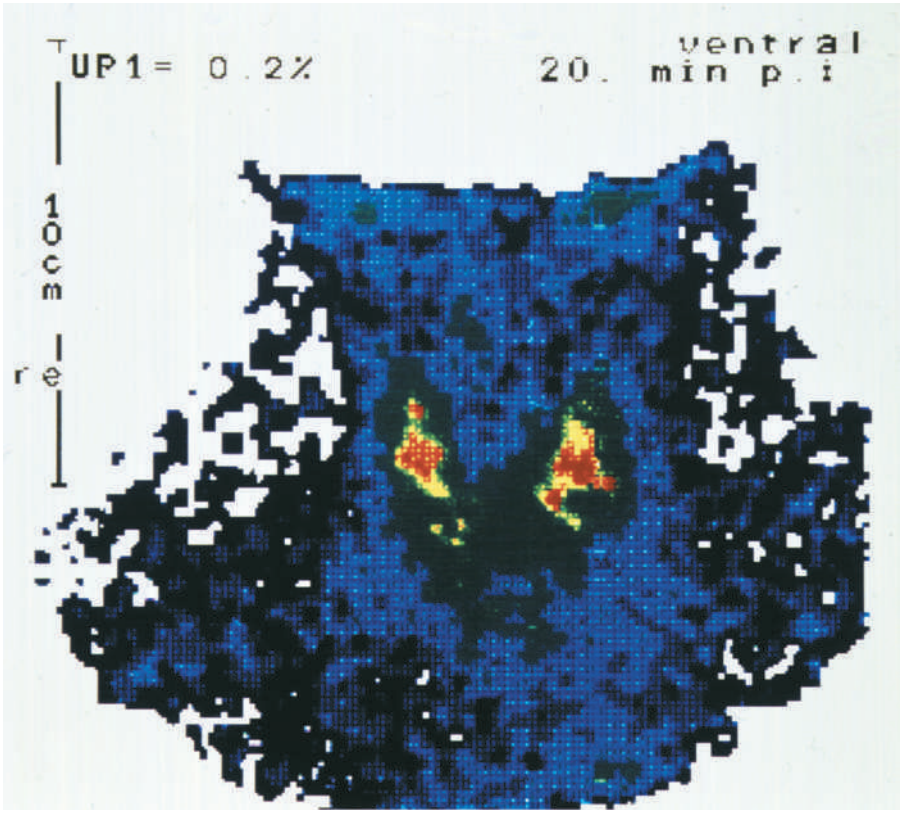
myxedema thyroid disorder characterized by dry skin, swelling in the face, and mental deterioration

Thyroid Gland

The thyroid gland, the largest of the **endocrine** glands, is located in the neck just below the thyroid cartilage of the **larynx**. It consists of two lobes, one on either side of the trachea, joined by a narrow band or isthmus. It is composed of numerous hollow ball-shaped follicles with small, interspersed clusters of parafollicular cells.

Follicle cells concentrate and attach iodine to the **amino acid** tyrosine, producing two forms of thyroid **hormone** (TH): thyroxine or tetraiodothyronine (T_4), and smaller amounts of triiodothyronine (T_3). Manufacture and release of these hormones into the blood is regulated by thyroid stimulating hormone, TSH, from the pituitary gland. The major effect of TH is to stimulate activity of **enzymes** involved in energy production through the **oxidation** (burning) of **glucose**, thus increasing basal metabolic rate. A side effect of this increased activity is the production of body heat.

Overactivity of the thyroid gland, called hyperthyroidism, causes elevated metabolic rate, nervousness, and weight loss. The most common form of hyperthyroidism, Graves' disease, is an **autoimmune disease**; it is accompanied by swelling of the thyroid (goiter) and bulging of the eyes (exophthalmos). Adult hypothyroidism, or underactive thyroid, causes **myxedema**, characterized by lowered metabolic rate, sluggishness, and weight gain. Additional consequences of low TH levels in infants are stunted growth and irreversible brain damage. Hypothyroidism resulting from low iodine intake, with consequent low TH manufacture, produces an enlarge-



A color-enchanced scintigram (gamma scan) of a human thyroid gland.

ment of the thyroid gland called endemic goiter. TSH is responsible for this enlargement.

Parafollicular cells produce the hormone calcitonin, which lowers blood calcium levels by suppressing the activity of bone-destroying cells called osteoclasts, and stimulating calcium uptake by bones. Calcitonin is important in children, where growing bones are being constantly remodeled. It has little effect on the normal adult skeleton, but may be prescribed in nasal spray form to help reduce bone destruction in osteoporosis. Parathormone, produced by the parathyroid gland, has opposing effects on blood calcium levels. SEE ALSO AUTOIMMUNE DISEASE; BONE; ENDOCRINE SYSTEM; HORMONES; METABOLISM, HUMAN

Patricia L. Dementi

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Tissue

A tissue is made up of a group of cells that usually look similar to one another and come from the same region in a developing embryo. The group of cells that make up a tissue have physiological functions that work together in a coordinated way to support special functions. The special function of

a tissue is also influenced by the kind of material that surrounds the tissue and by communication among the cells of the tissue. Different kinds of tissue have different physical properties. Tissues may be hard (bone), soft (muscle), or even liquid (blood).

In the structural organization of the body, tissues are located between the cell and organ levels of organization. Individual cells are a lower level of organization. Tissues are made up of many individual cells. Groups of different kinds of tissues are organized together to form organs, which have special functions with characteristic shapes and functional properties.

There are four kinds of tissues based on differences in their anatomy and function: epithelial tissue, connective tissue, muscle tissue, and nervous tissue. Epithelial tissue is made of layers of cells that are joined together and may cover the surface of the body (epidermis of the skin), line spaces in the body (lining of the abdominal cavity) and hollow structures (lining of blood vessels), or form glands (sweat glands). Connective tissue is usually made of cells and extracellular fibers that hold structures together (tendons), protect them (cartilage), store energy (fat), or produce blood.

Muscular tissue is made of cells that are organized to shorten and produce force when they contract (smooth skeletal and cordine muscle). Nervous tissue is made of **neurons** and accessory cells. Neurons are the cells that carry information in the form of electric **action potentials**. Accessory cells protect and support the function of neurons. SEE ALSO BLOOD; CONNECTIVE TISSUE; EPITHELIUM; MUSCLE; NERVOUS SYSTEMS; NEURON; ORGAN; SKIN

neuron nerve cell

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

Michael G. Scott

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Torrey, John

American botanist and chemist
1796–1873

John Torrey was the preeminent botanist in the United States during the nineteenth century. Born in New York City and trained as a physician, chemist, and mineralogist, he taught at West Point, the College of Physicians and Surgeons in New York City, and Princeton University. Torrey became the central figure in classifying the thousands of new plants discovered by explorers during the period of westward expansion, and he wrote numerous scientific monographs on the flora of the American West.

Torrey introduced to the United States the natural system of classification developed by his European contemporaries Antoine-Laurent de Jussieu and Augustin de Candolle, overthrowing the sexual system of classification of Swedish botanist Carolus Linnaeus. In 1833 Torrey began his work with American botanist Asa Gray, first as teacher and later as partner, and by 1843 Torrey and Gray had published two volumes of the *Flora of North America.*

Throughout his life, Torrey developed a large and significant herbarium, housing thousands of plant specimens. His collection is the heart of the herbarium of the New York Botanical Garden. Torrey's name is found in a genus of evergreen trees, *Torreya*, as well as numerous plant species names. The Torrey Botanical Society is a national scientific organization promoting interest in and understanding of botany. SEE ALSO GRAY, ASA; LINNAEUS, CAROLUS

Richard Robinson

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Touch

Touch is one of the five major sensory channels by which humans sample and experience their environment. The word "touch" describes the sensory experience resulting from gentle contact of the skin with the environment, including air moving over the skin and hairs. The sense of touch is so exquisitely sensitive that the brain can consciously experience the activity of a single **neuron** supplying the skin. Touch sensation not only informs one about the near environment but plays an essential role in guiding fine movements basic to such skills as playing musical instruments, reading Braille, typing on a computer keyboard, or performing surgery.

The fingertips are richly endowed with nerve endings and are very sensitive.

neuron nerve cell

Touch (mechanoreception) is distinguished from pain (nociception) and temperature perception (thermoreception). Pain is sensed by free nerve endings, mostly located in the skin, bones, and joint capsules, and around blood vessels. Two broad categories of painful sensations, fast pricking pain versus slow aching or burning pain, are carried to the spine by two different types of sensory neurons. Thermoreceptors are located immediately below the skin, with warmth receptors more numerous than cool receptors. They are most sensitive not to absolute level of temperature, but to rapid change in temperature, and quickly become quieter once the temperature has stabilized at a new level.

Detection of touch stimuli begins with mechanical deformation of several types of specialized touch receptors, distributed unevenly over the body surface. Nerve fiber endings in the skin may be free, "naked" endings (for light touch) or more commonly are associated with other, cooperating cells. Thus nerve endings that wrap around hair follicles are activated by hair movement; other nerve endings adhere closely to specialized accessory cells or have tiny cellular capsules. The latter include pacinian corpuscles for vibration, and Meissner corpuscles (abundant in sensitive, hairless skin of the fingertips) for light touch. Ruffini corpuscles and Merkel disks respond to pressure or to stretch of the skin with signals that continue as long as a stimulus is applied.

When any of these touch-sensitive nerve endings are mechanically deformed, electrical signals (action potentials) are transmitted along the **axons** of sensory nerve cells. These signals pass rapidly to the spinal cord and brainstem to activate a second set of neurons. As these secondary touch cells relay information up the brainstem, their axons cross the body's midline, so that the touch information they carry activates neurons in the thalamus on

axon long extension of a nerve cell down which information flows

the side opposite the stimulation. Thalamic neurons transmit the signal to the primary sensory cortex in the brain's postcentral gyrus, where touch is actually experienced.

cerebral cortex outermost wrinkled portion of the brain

All of the touch information transmitted from the various receptor types in a given body area is combined in the **cerebral cortex**. It provides sophisticated analysis of the total pattern of nerve signals so that one can instantly (and consciously) judge the texture, force, location, and movement of the skin stimulus with great precision.

Touch sensitivity varies in different body regions because of differential density of distribution of the specific nerve endings. Areas such as the fingertips and lips (glabrous skin) are richly endowed with nerve endings and are very sensitive. Hairy skin has fewer endings and different kinds, and so produces a different sensory experience; skin of the trunk and back, with a low density of touch receptors, is less sensitive to touch than skin elsewhere.

Touch receptors branch out at their ends, and a single neuron may receive input from a region of the skin several centimeters in diameter, called its receptor field. Receptor fields in the lips may be as small as 2 to 3 millimeters (.78 to .118 inches), while in much of the rest of the body they are 4 to 7 centimeters (1.5 to 2.7 inches). SEE ALSO CENTRAL NERVOUS SYSTEM; NEURON; PERIPHERAL NERVOUS SYSTEM; SKIN

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Transcription

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

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

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

ribosome protein-RNA complex in cells that synthesizes protein

template master copy

Each **gene** on a **chromosome** can be thought of as the instructions for making a particular **protein** in a cell. However, the genes themselves cannot direct the synthesis of the proteins they encode but must first be converted into a form that can be recognized by the cellular protein-making machine, the **ribosome**. This conversion process is called transcription. During transcription the instructions held in the genes (in the form of deoxyribonucleic acid [DNA]) are transcribed into a chemical form called ribonucleic acid (RNA). Because this RNA carries the message, or instructions, from the genes to the ribosomes, where it is ultimately converted into a protein molecule, it is called messenger RNA (mRNA).

Most genes in a cell code for protein and hence are transcribed into mRNA. However, a few genes code for different types of RNA that are not used as **templates** for protein synthesis but instead are ends in themselves and carry out a variety of functions in the cell. Examples of these other kinds of RNA are transfer RNA (tRNA) and ribosomal RNA (rRNA), which are both critical to the process of protein synthesis.

Transcription in Prokaryotes

prokaryote single-celled organism without a nucleus

Much of the pioneering work on transcription was carried out in **prokaryotes**, most notably in the bacterium *E. coli*. These studies laid the founda-

tion for work that was later carried out in the more complex eukaryotes. The **enzyme** that carries out transcription is called RNA polymerase, and it consists of four kinds of **polypeptides**, designated **α**, **β**, β′ and **σ**, which are bound together into a complex called a holoenzyme.

Transcription can be divided into three phases: initiation, elongation, and termination. Initiation occurs when the polymerase, sliding along the chromosome, encounters a **promoter**, a sequence of DNA that identifies the beginning of a gene. The promoter contains two sequence elements, six **base pairs** apiece, called the -10 and -35 elements, which are located ten and thirty-five base pairs respectively upstream of the transcription start site. DNA is double-stranded, but only one side serves as a template from which RNA is made. With the two strands bound to one another, the template strand must be made accessible if it is to serve as a template for RNA synthesis. To begin, the polymerase unwinds a region of approximately seventeen base pairs, setting the stage for the formation of the first **phosphodiester** bond. Unlike DNA, the synthesis of RNA can be initiated without the need for a **primer**.

RNA is made by linking together ribonucleotides in an order dictated by the DNA template strand. The essence of transcription is to use the sequence of **nucleotides** already on the DNA strand to dictate the sequence of RNA nucleotides that will be formed into the new RNA strand. The four DNA nucleotides are adenine, guanine, cytosine, and thymine (A, G, C, and T). RNA nucleotides are A, G, C, and uracil (U). RNA polymerase pairs up an RNA nucleotide with each DNA nucleotide. However, rather than matching the DNA sequence, the polymerase pairs up **complementary** base pairs. G is always paired with C, so that if the DNA sequence is GGCC, the resulting RNA sequence is CCGG. The A of DNA is paired with the U of RNA, and the T of DNA is paired with the A of RNA, so that if the DNA sequence is AATT, the RNA sequence is UUAA. Thus, like DNA replication, the rules of Watson-Crick base pairing apply during transcription.

The nucleotides used in RNA synthesis are triphosphates, meaning they have three phosphate groups attached. This energizes them, and **hydrolysis** of these phosphates powers the transcription process. Once the chain has reached a length of approximately ten ribonucleotides the σ subunit **dissociates**, leaving the core enzyme ($\alpha_2\beta\beta'$) to continue transcribing until the signal for termination is reached. Termination signals on DNA vary but the most common is a GC-rich region followed by an AT-rich region.

enzyme protein that controls a reaction in a cell

polypeptide chain of amino acids

α the Greek letter alpha

β the Greek letter beta

σ the Greek letter sigma

promoter DNA sequence to which RNA polymerase binds to begin transcription

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

phosphodiester the link between two nucleotides in DNA or RNA

primer short nucleotide sequence that helps begin DNA replication

nucleotide the building block of RNA or DNA

complementary matching opposite

hydrolysis splitting with water

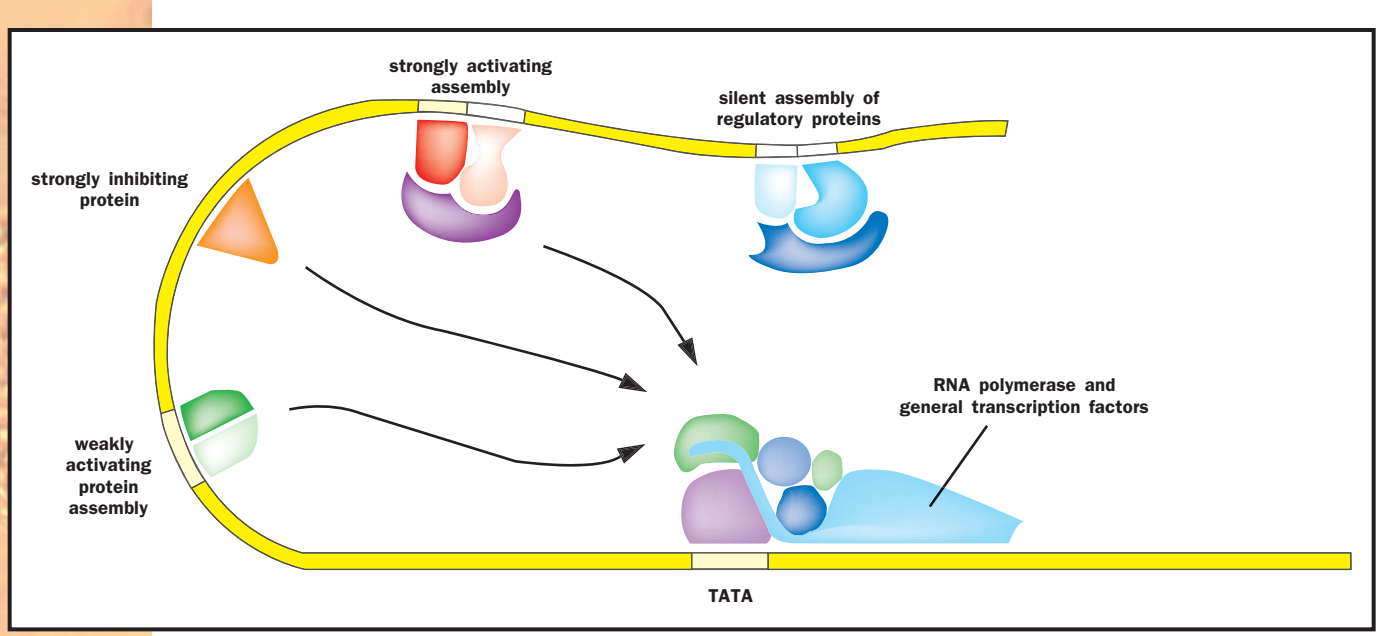
dissociate break apart

Transcription in Eukaryotes

The basic features of RNA synthesis are shared between prokaryotes and eukaryotes; however, transcription in eukaryotes differs in that it is significantly more complex. First, rather than having a single RNA polymerase, eukaryotes have three different RNA polymerases, each of which transcribes a different set of genes. RNA polymerase I transcribes three types of rRNA (the 18S, 5.8S, and 28S species), RNA polymerase II transcribes mRNA, and RNA polymerase III transcribes tRNA and the smallest rRNA (the 5S species). The eukaryotic RNA polymerases consist of between eight and fourteen subunits, with two of them corresponding to the β and β′ subunits of prokaryotic RNA polymerases.

OCHOA, SEVERO (1905–)

Spanish molecular biologist who received, with Arthur Kornberg, the 1959 Nobel Prize in physiology for discovering an enzyme that can be used to make ribonucleic acid (RNA). His work was fundamental to modern biotechnology.



Integration at a promoter.

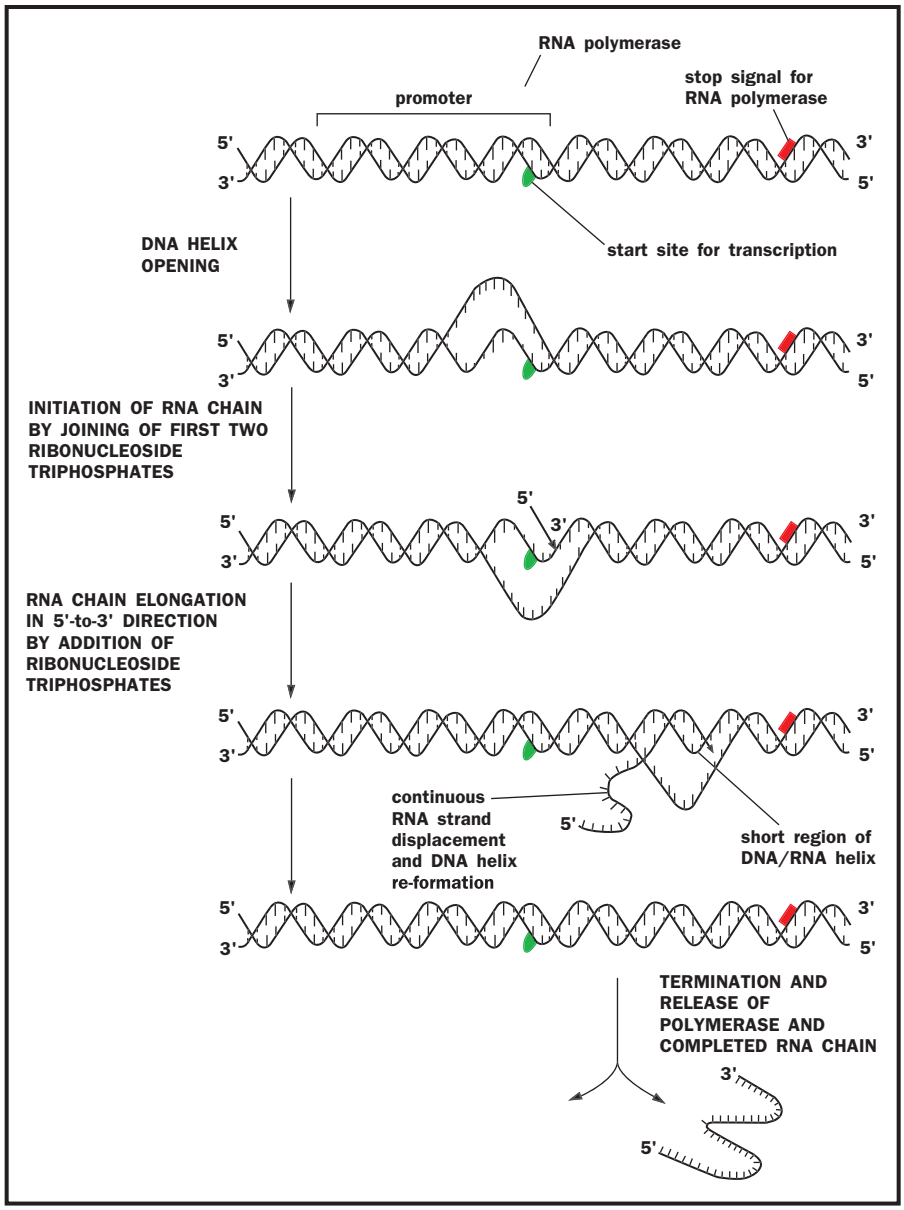
Unlike the bacterial RNA polymerase, eukaryotic RNA polymerases cannot initiate transcription by themselves but need the help of a set of proteins called the basic transcription factors. The basic transcription factors perform a number of functions, including binding to gene promoter regions and attracting the appropriate RNA polymerase to the initiation site, as well as unwinding the DNA double helix to allow access of the incoming ribonucleotides of the growing RNA chain.

RNA Polymerase II Transcription. The promoters of eukaryotic genes have been intensely studied, especially those transcribed by RNA polymerase II. Most genes transcribed by RNA polymerase II contain a sequence called a TATA-box located twenty-five to thirty-five nucleotides upstream of the transcription start site. The TATA-box contains the sequence TATAA, which is recognized by a multicomponent transcription factor called TFIID. One of the components of the transcription factor is the TATA-binding protein (TBP), which directly links to the TATAA sequence. RNA polymerase II genes contain additional binding sites in their promoters for transcriptional regulators and can even be affected by elements located at large distances called enhancers.

In contrast to prokaryotes, transcription termination by RNA polymerase II does not occur simply by release of the RNA molecule. Rather, transcription continues well beyond the termination point, and the transcript is later cleaved to the appropriate length. Following cleavage an enzyme called poly-A polymerase adds approximately 250 adenine residues to the tail end of the transcript.

Each polymerase has its own set of basic transcription factors, designated by a number and a letter. For example, TFIIA is transcription factor A, which functions with RNA polymerase II.

RNA Polymerase I and III Transcription. RNA polymerase I is exclusively devoted to transcribing the ribosomal RNA genes, which are present in many copies as tandem arrays (multiple copies, existing side by side). RNA polymerase I synthesizes one long RNA molecule containing the 28S, 18S, and 5.8S rRNAs, which is subsequently cleaved into separate parts. In contrast to the promoters for RNA polymerases I and II, the promoters of RNA polymerase III genes typically lie downstream of the



Synthesis of an RNA molecule by RNA polymerase.

transcription start site. Interestingly, although most of the basic transcription factors are not shared between the three polymerases, TBP, which was first discovered as a protein involved in RNA polymerase II transcription, has now been found to be required for transcription by all three polymerases. Thus, despite the differences between the polymerases, they have all incorporated TBP into their mechanism of transcription initiation. SEE ALSO CONTROL OF GENE EXPRESSION; GENETIC CODE; RNA; RNA PROCESSING; TRANSFER RNA

Kirstie Saltsman

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Transfer RNA

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

ribosome protein-RNA complex in cells that synthesizes protein

amino acid a building block of protein

polypeptide chain of amino acids

transcribe creation of an RNA copy of a DNA gene

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

genome total genetic material in a cell or organism

enzymatic related to function of an enzyme

nucleotide the building block of RNA or DNA

codon sequence of three mRNA nucleotides coding for one amino acid

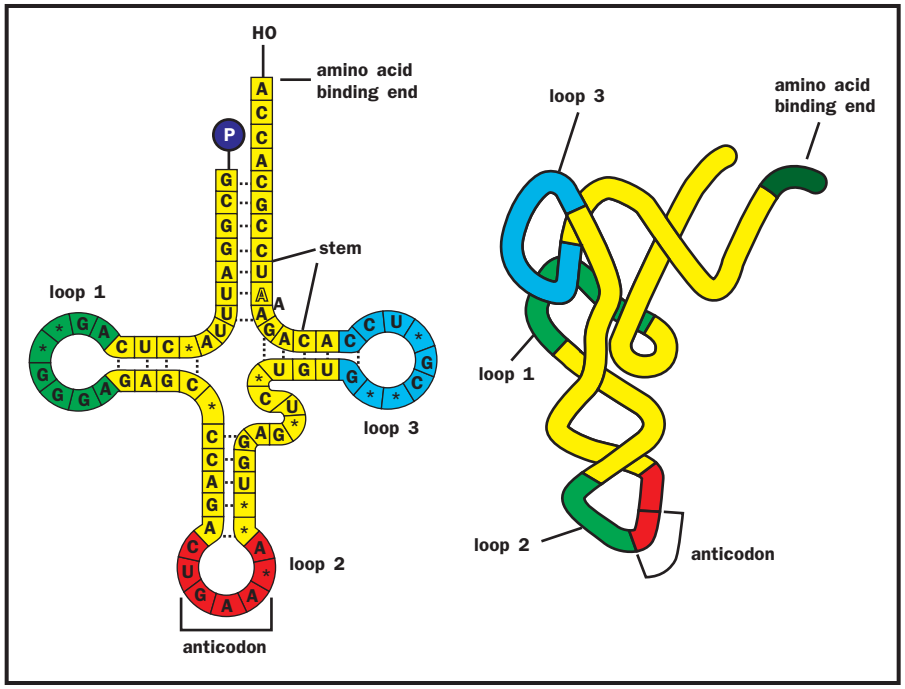
base pair two nucleotides (either DNA or RNA) linked by weak bonds

During **protein** synthesis at the **ribosome**, the nucleic acid sequence of deoxyribonucleic acid (DNA) and ribonucleic acid (RNA) is translated into the **amino acid** sequence of a protein. Transfer RNA (tRNA) is an important adapter that "reads" the nucleic acid code in the messenger RNA (mRNA) and "writes" an amino acid sequence. Transfer RNAs transfer individual amino acids onto the growing **polypeptide** chain.

There is at least one tRNA for each of the twenty naturally occurring amino acids. Each tRNA is **transcribed** from a different **gene** but the tRNA genes are clustered in the **genome** of some organisms. These clusters of genes are transcribed as a single unit, which results in the production of one large precursor RNA molecule. Individual tRNAs are then **enzymatically** separated from one another. Each tRNA is distinguished by a particular three-nucleotide sequence (the "anticodon") in one region, and by its ability to link up with a particular amino acid.

The **nucleotide** sequence of the first tRNA was determined in 1965. As of 2000, there are more than one hundred tRNA sequences known, and they are all quite similar. All tRNA molecules are relatively short, composed of less than one hundred nucleotides. Unlike those found in DNA and mRNA, many of the nucleotides found in tRNA are modified to enhance their interactions. Although the three-dimensional shape of tRNA molecules has traditionally been depicted as a cloverleaf, X-ray crystallographic methods have revealed that the actual shape of a tRNA is an upside down letter L.

During protein synthesis, the anticodon at one end of the L interacts with a triplet nucleotide in the mRNA called a **codon**. The correct tRNA will form "Watson-Crick"–type **base pairs** between the triplet anticodon



Unfolded transfer RNA (left) has a clover-leaf shape. In the cell, it folds into a more compact L shape (right). The sequence of each tRNA molecule differs, but includes an invariant amino acid binding end. The anticodon is unique for each type of amino acid. Asterisks indicate modified RNA nucleotides unique to tRNA.

on the tRNA and the triplet codon on the mRNA. The tRNAs must be exactly **complementary** at the first two codon positions (for example, A pairs with U, C pairs with G), but can vary in the third codon position. This flexibility in the third position is called "wobble," and it ultimately enables a single tRNA to bind to more than one triplet codon sequence. If the tRNA is not complementary as described above, it will be rejected from the ribosome, and its amino acid will not be incorporated into the polypeptide chain.

complementary matching opposite

At the other end of the L is the amino acid binding site. **Enzymes** (called aminoacyl tRNA synthetases) join the proper amino acid to its corresponding tRNA. This reaction requires **ATP** and the bond generated is a "high-energy" (that is, weak) bond. During the addition of the amino acid to the growing polypeptide, this bond is easily **hydrolyzed**, releasing the energy needed to power the process. SEE ALSO PROTEIN SYNTHESIS; RIBOSOME; RNA

enzyme protein that controls a reaction in a cell

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

hydrolyze to split apart using water

James E. Blankenship

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Transgenic Techniques

Transgenics describes the process of introducing foreign deoxyribonucleic acid (DNA) into a host organism's **genome**. The foreign DNA, or "transgene," that is transferred to the recipient can be from other individuals of the same species or even from unrelated species. In multicellular organisms, this is often done through experimental manipulation of **gametes** or early embryos. Usually the transgene is incorporated at a very early stage in embryonic development so that cells of the entire organism contain the transgene. A wide range of species can be made transgenic including plants, insects, worms, and vertebrates. The most commonly genetically manipulated vertebrate animal is the mouse because a variety of techniques exist to produce transgenic mice.

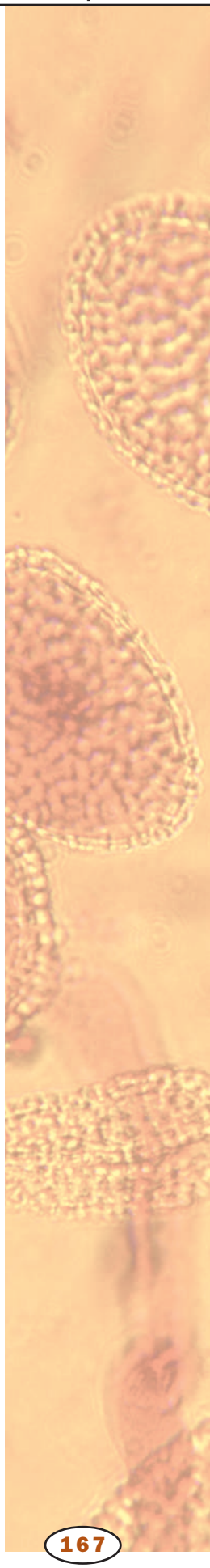
genome total genetic material in a cell or organism

gamete reproductive cell, such as sperm or egg

Transgenic techniques have been used for a number of goals: to determine an unknown gene's function; to analyze the malfunction of a mutated gene; to model human disease; and to provide better agricultural and pharmaceutical products by making transgenic plants and animals. For example, insect-resistant transgenic plants have been engineered. While the benefits of modified plants and animals are far-reaching, there is debate about the ethics of genetically altering plants and animals, and the impact these alterations may have on the environment.

There are several ways to introduce a transgene into the organism. Microinjection is one of these techniques. As its name suggests, microinjection is the process of injecting the transgene into the **nucleus** of a cell where it is randomly inserted into the host genome. This technique, initiated in 1981, is most commonly used to generate transgenic mice. DNA is injected into the nucleus of a fertilized egg, which is then transferred

nucleus membrane-bound portion of cell containing the chromosomes



to a foster mother. If the introduced DNA becomes integrated into the developing embryo's genome, the offspring will carry the transgene. Two other techniques for random insertion are retroviral and transposable element insertion.

An important application of transgenic technology, introduced in the 1990s, is gene targeting, or the production of "knock-out" organisms. The term "knock out" refers to the ability to disrupt a specific gene, so that it no longer encodes a complete **protein**. Genes are knocked out by being replaced by a transgene that has been disrupted *in vitro*, either by the addition of some sequence into the gene itself or by the deletion of part of the gene. Gene replacement occurs when the disrupted transgene is introduced into a cell. Here, it recombines with the recipient's copy of that gene, inserting itself into the **chromosome** by **homologous recombination**.

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

homologous recombination exchange of DNA segments between chromosomes

progeny offspring

homozygous containing two identical copies of a particular gene

In mice, transgenes can also be introduced with cultured embryonic stem (ES) cells, using selection techniques to recover the transformed cells. The altered ES cells are then injected into early mouse embryos, and result in a mosaic embryo with normal and transgenic cells. If the altered cells contribute to the germ cells of the mouse, **progeny** in a subsequent mating will inherit the knocked out gene. These mice can then be mated to produce mice that are **homozygous** for both copies of the altered gene (both copies of the gene are knocked out). These mice can then be carefully examined to determine what happens when the specific gene is absent. The knock-out technique is most commonly applied to mice, insects, and yeast.

Extensions of gene targeting are the "knock-in" approach and conditional mutation. The knock-in approach involves inserting a mutated gene or a similar gene in place of the gene of interest. The newly added gene is expressed at the same time and location as the replaced gene. This method allows scientists to study the effects of mutations in genes as well as discover if certain genes have redundant functions. Conditional mutation is a way of either turning on or turning off the gene of interest, and can be done either in specific tissues or at specific time points. SEE ALSO CLONE; RECOMBINANT DNA

Michelle Tallquist

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Translation

See Protein Synthesis

Translocation

Translocation is the movement of materials from leaves to other tissues throughout the plant. Plants produce carbohydrates (sugars) in their leaves by photosynthesis, but nonphotosynthetic parts of the plant also require

carbohydrates and other **organic** and nonorganic materials. For this reason, nutrients are translocated from sources (regions of excess carbohydrates, primarily mature leaves) to sinks (regions where the carbohydrate is needed). Some important sinks are roots, flowers, fruits, stems, and developing leaves. Leaves are particularly interesting in this regard because they are sinks when they are young and become sources later, when they are about half grown.

organic composed of carbon, or derived from living organisms

Phloem Structure and Function

The tissue in which nutrients move is the **phloem**. The phloem is arranged in long, continuous strands called vascular bundles that extend through the roots and stem and reach into the leaves as veins. Vascular bundles also contain the **xylem**, the tissue that carries water and dissolved minerals from the roots to the shoots. When plants increase in diameter (secondary growth) they do so by divisions of a layer of cells just under the bark; this cell layer makes new xylem to the inside (forming the wood of the tree trunk) and a thin, continuous cylinder of new phloem to the outside.

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

xylem water-transporting system in plants

The contents of the phloem can be analyzed by cutting off the stylets (mouth parts) of phloem-feeding insects such as aphids and collecting the drops of sap that exude. Phloem sap is composed largely of sugar dissolved in water. All plants translocate sucrose (table sugar) and some also transport other sugars such as stachyose, or sugar alcohols such as sorbitol. Many other organic compounds are found, including **amino acids**, **proteins**, and **hormones**. **Glucose**, the sugar found in the circulatory system of animals, is not translocated.

amino acid a building block of protein

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

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

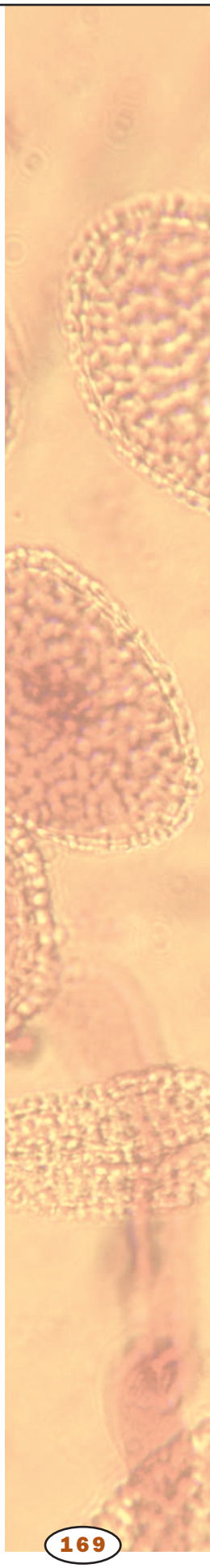
In order to accommodate the flow of sap, the internal structure of the conducting cells of the phloem, the sieve elements, is drastically altered. As the sieve elements mature, they lose many of the **organelles** commonly found in living cells and they modify others. The **nucleus** disappears, as do the vacuoles, microfilaments, microtubules, **ribosomes**, and Golgi bodies. Therefore, the inside (lumen) of the cell is left essentially open. The sieve elements are greatly elongated in the direction of transport and are connected to one another to form long sieve tubes. Large pores perforate the end walls of the sieve elements to facilitate flow through the tube. The connecting walls thus look like a sieve, giving the cell type its name.

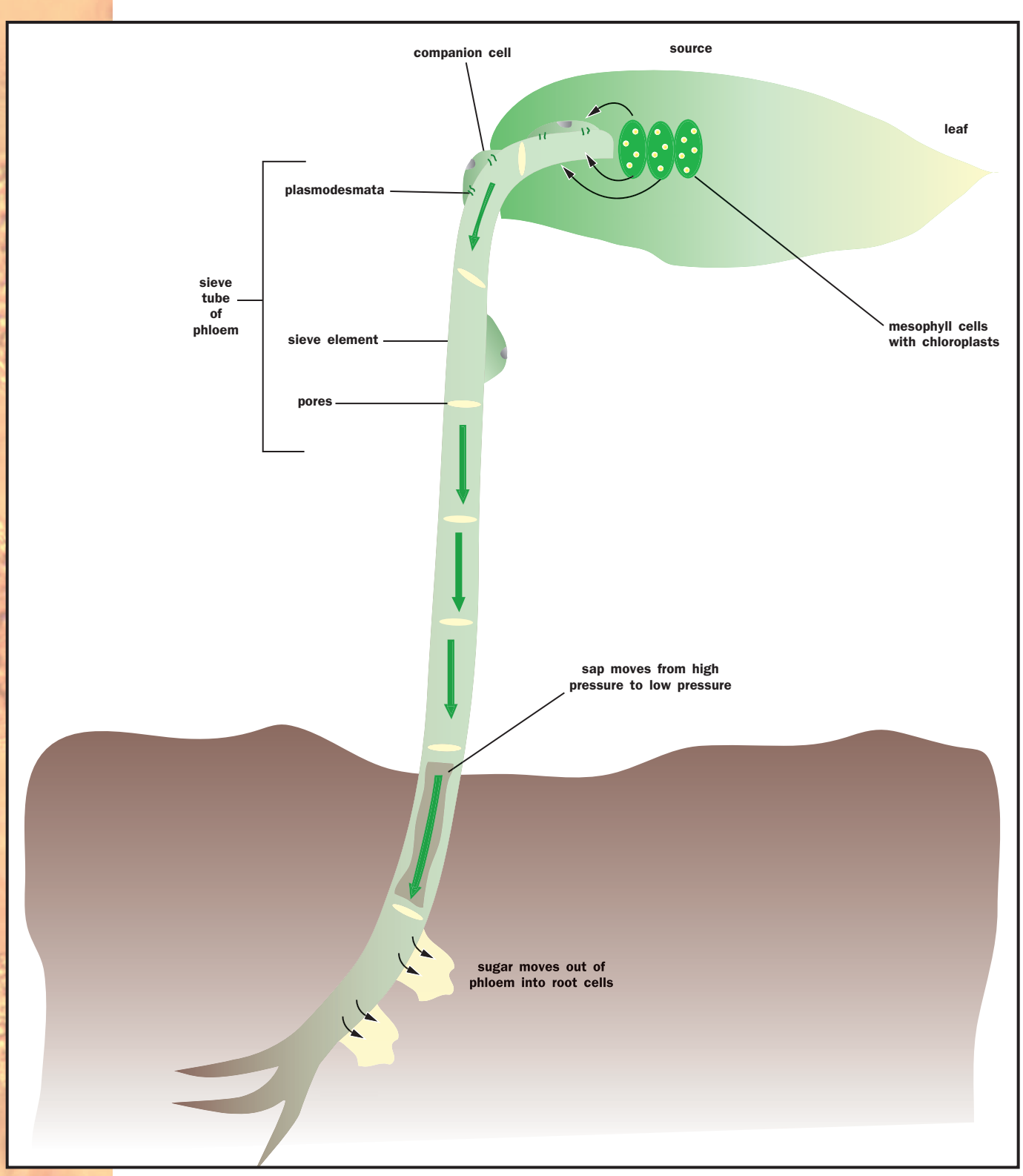
organelle membrane-bound cell compartment

nucleus membrane-bound portion of cell containing the chromosomes

ribosome protein-RNA complex in cells that synthesizes protein

Some sieve elements can live for a long time, as many as one hundred years in palm trees, even though they have no nucleus or any of the machinery needed for protein synthesis. Cells closely associated with them, called companion cells, apparently keep them alive. The association of sieve elements and companion cells is one of the most intimate and complex in nature, and one of the least understood. It now appears that both small and large molecules can move from companion cells to sieve elements through the plasmodesmata that connect them. Plasmodesmata are minute pores that traverse the common walls between plant cells. They have an intricate internal structure. Interest in plasmodesmata is high because viruses move through them to cause infections. If a virus enters the phloem this way it will travel with the sap, spread widely around the plant, and infect sink organs. Since viruses are much larger than plasmodesmata, they must be disassembled in one cell and reassembled when they get to their destination.





Sugars synthesized in the chloroplasts are actively pumped into the sieve tubes. Water follows by osmosis, creating high pressure. Sugar is then removed by active transport, and water again by osmosis, lowering the pressure in the sieve tube.

The Pressure-Flow Mechanism

The rate of translocation in angiosperms (flowering plants) is approximately 1 meter per hour. In conifers it is generally much slower, but even so this is far too fast to be accounted for by diffusion. Instead, the sap flows, like a

river of dilute syrup water. What is the force that drives the flow of material in the phloem? It is pressure, generated in the sieve elements and companion cells in source tissues. In leaves, sugar is synthesized in mesophyll cells (the middle layer of the leaf), and is then actively pumped into the phloem, using metabolic energy. By using energy, the sugar is not only transferred to the phloem but is also concentrated. When a **solute** such as sugar is concentrated inside cells, water enters the cells by **osmosis**. Since the plant cells have a rigid cell wall, this influx of water creates a great deal of internal pressure, over ten times the pressure in an automobile tire. The pressure causes sap to move out through the pores of the sieve element, down the tube.

solute dissolved substance

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

At the other end of the transport stream, in the sinks, sugar is constantly leaving the phloem and being used by surrounding cells. Some is consumed as an energy source, some is stored as sugar or starch, and some is used to make new cells if the sink tissue is growing. Since sugar leaves the phloem in the sink, water exits too (again by osmosis) and the pressure goes down. Therefore, there is a difference in pressure between source and sink phloem. This causes the solution to flow, just as water flows along a pressure **gradient** in a garden hose. This process is known as the pressure-flow mechanism.

gradient difference in concentration between two places

Sugar Loading and Unloading

How is sugar actively pumped (loaded) into the phloem? There are two known mechanisms, operating in different species. In one, sucrose enters the cell walls near the phloem in the smallest (minor) veins of the leaf. It then enters the phloem by attaching to sucrose transporter proteins embedded in the plasma membranes of the sieve elements and companions cells. In the second mechanism, sucrose enters the companion cells of the minor vein through small plasmodesmata, and is converted to larger sugars, raffinose, and stachyose. These larger sugars are unable to diffuse back through these plasmodesmata due to their size. Therefore they are trapped in the phloem of the leaf and build up to high concentration. They enter the sieve elements through larger plasmodesmata and are carried away toward the sinks.

When sugars and other nutrients arrive in sink tissues they unload from the phloem and enter surrounding cells, either through plasmodesmata or by crossing from one cell to another across the cell walls. The size and metabolic activity of the different sinks determines the amount of material that is delivered to them. Thus, the use of sugar in the sinks determines how much sugar flows to them. SEE ALSO ANATOMY OF PLANTS; CARBOHYDRATES; LEAVES; MEMBRANE TRANSPORT; PHOTOSYNTHESIS; ROOTS; WATER MOVEMENT IN PLANTS

Robert Turgeon

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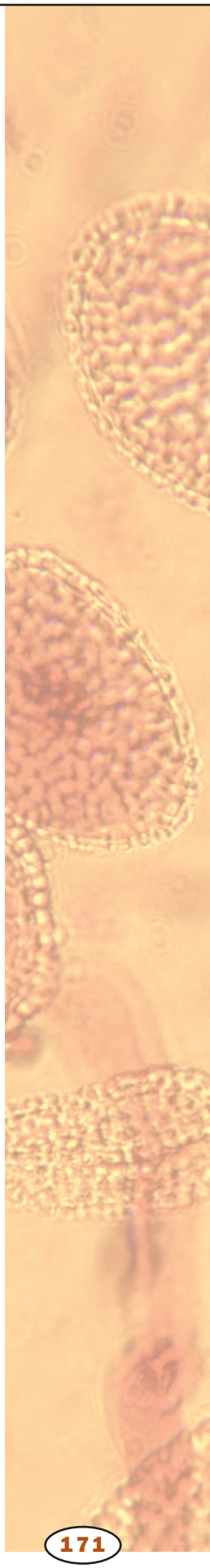

Transplant Medicine

When conventional medical and surgical procedures are insufficient to help a patient, organ and tissue transplants are sometimes the only solutions. From a blood transfusion to multiple organ transplants, the procedures and mechanisms associated with these diverse medical interventions all fall under the common area of medical practice known as transplant medicine.

TRANSPLANTS PERFORMED IN THE U.S. IN 1999

Type of Transplant	Number
kidney alone (4,153 were living donors)	12,518
liver	4,696
pancreas alone	383
kidney-pancreas	944
intestine	70
heart alone	2,184
heart-lung	49
lung alone	877

The beginnings of successful tissue and organ transplant can be attributed to Karl Landsteiner, an immunologist and pathologist who received the 1930 Nobel Prize in physiology and medicine. In 1901, Landsteiner discovered that there were four different blood types. He called these the A, B, AB, and O types and established that transfusion was possible between individuals having the same type, while mixing of incompatible blood could lead to death due to immune system actions. Because the goal of histocompatibility and immunosuppression transplantation is to insure that the recipient does not reject the transplant but lives with it for the rest of his or her life, histocompatibility and immunosuppression are critical aspects of transplant medicine.

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

antigen foreign substance that provokes an immune response

A tightly linked cluster of **genes** known as the major histocompatibility complex (MHC) governs tissue and organ compatibility between individuals. This complex is located on chromosome 6 in humans. These genes regulate the expression of the human leukocyte **antigens** (HLA) on the cell surface that, in turn, regulate the immunologic reactions associated with organ and tissue transplantation. Because the donor tissue is seen as foreign, it is necessary to suppress the body's natural defense systems to prevent rejection. The drugs cyclosporine, prednisone, and azathioprine are used to accomplish this goal.

Organ and tissue transplants are also called grafts. Homografts (allografts) are obtained from individuals of the same species. Homografts are usually rejected unless immunosuppressive methods are used to prevent the recipient from immunologically attacking the donor tissue. If a tissue is removed from one part of an individual's body and grafted onto another part of the body, it is termed an autograft. This is a common procedure in the treatment of burn victims. Isografts involve transplants between identical twins or between members of a very **inbred** species. In these situations there is no tissue rejection due to the similarity in the HLAs expressed on both the donor's and the recipient's cells. Heterografts (xenografts) involve tissue transfer between individuals of different species, such as transplanting a heart valve from a pig to a human.

inbred repeatedly bred with close relatives, creating organisms with very little genetic variation

While tissue compatibility is the principal determinant in the success of a transplant, some grafts, such as the skin allografts, are intended for short-term use, to prevent the loss of fluids and infection in severely burned individuals. Even though the graft will be rejected relatively soon, it allows the victim time to recover.

Organ Transplants

Transplantation procedures range in complexity from simple tissue replacement procedures, such as a cornea or tendon transplant, to single-organ

Surgeons at the University of Pittsburgh Medical Center prepare a human kidney for transplanting.

transplants such as the heart, liver, and kidney, to multiple-organ transplants involving the heart and lungs or the kidney and pancreas.

Corneal transplant is considered in cases of deformity in the shape of the cornea or corneal disease preventing the proper transmission of light to the retina. Corneal transplants were first performed in 1920. Due to a lack of extensive blood supply to this tissue, it was thought that histocompatibility issues would not be significant. While this was generally true, it has been shown that corneal graft rejection is an issue in approximately 10 percent of the surgeries.

If a person's kidneys fail to remove metabolic wastes from the blood, the only available options are usually hemodialysis or a kidney transplant. A kidney obtained from a living relative or an unrelated histocompatible donor, or from a cadaver, is used to replace the diseased organ.

The liver is responsible for filtering the blood and also for producing blood-clotting factors. Conditions such as cirrhosis and cancers involving the hepatocytes (liver cells) or the bile ducts (which convey the bile juice to the duodenum) are treatable by liver transplant. This is a complex procedure that needs to be done rapidly due to critical functions of the liver that cannot be duplicated artificially.

In 1967 in Cape Town, South Africa, a surgical team led by Dr. Christian Barnard performed the first heart transplant. His patient survived for a few weeks after the operation, but died of pneumonia soon after. His second patient, however, survived for a year and a half after the operation. Heart transplants were not a very successful procedure until the discovery of cyclosporine in 1980. Since then, heart transplant operations have become much more common with the average postoperative survival period being close to five years.

Heart transplants may be the only solution if a patient experiences **coronary artery** disease (blockage of the arteries supplying blood to the heart itself), **cardiomyopathy** (thickening of the heart walls), heart valve disease with congestive heart failure (weakening of the heart muscle and an

coronary artery artery supplying blood to the heart

cardiomyopathy heart muscle disease

associated failure of the heart valves to regulate the passage of blood), or severe **congenital** heart disease.

congenital present at birth; inherited

Individuals who have conditions such as emphysema, pulmonary fibrosis, or cystic fibrosis and accompanying heart failure, or who have pulmonary hypertension with associated heart failure, are potential heart-lung transplant candidates.

Strategies involving the development of artificial tissues and organs are also being developed. In May 1998, the U.S. Food and Drug Administration approved Apligraf, an artificial skin manufactured by Organogenesis, Inc., as a biomedical device. It is made up of the same two layers, the dermis and epidermis, that make up human skin. This was the first living, tissue-engineered product to become commercially available. It has demonstrated effectiveness in the repair of skin lesions, and its use in patients with burns and diabetic ulcers is being investigated. Additionally, cartilage obtained from damaged knees has been used to engineer tissues for knee repair. Complete structural recovery is possible in about a year. Research is occurring in the development of "neo-organs," which involves injecting cells into a three-dimensional matrix made of biodegradable **polymers**. These cells gradually replace the matrix, leaving behind a new organ. SEE ALSO ANTIBODY; BLOOD; IMMUNE RESPONSE; SKIN; T CELLS

polymer molecule composed of many similar parts

David A. Woodman

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Transposon

Transposons, also called transposable elements or jumping **genes**, are stretches of deoxyribonucleic acid (DNA) that can move around an organism's **chromosome**. These "transpositions" occur at a very low frequency. A transposon can contain one gene or a set of genes, and transposons are found in both **eukaryotes** and **prokaryotes**. The transposon encodes **enzymes** that cut the transposon from the DNA sequence and reinsert it elsewhere. This cutting and pasting requires short DNA segments at either end that are inverted repeats of each other called insertion sequences. These insertion sequences are duplicated by the transposon enzymes at the insertion site, also called the target site. No particular DNA sequence serves as the target site for transposons. However, during insertion each transposon duplicates a set number of **nucleotides** at the chromosomal target site.

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

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

eukaryote a single-celled or multicellular organism in which the cell or cells have a nucleus

prokaryote single-celled organism without a nucleus

enzyme protein that controls a reaction in a cell

nucleotide the building block of RNA or DNA

Prokaryote transposons may replicate DNA as well as cut and paste it. Transposons in eukaryotes do not replicate DNA. They move either by cutting and pasting, or by creating a ribonucleic acid (RNA) intermediate. These so-called retroposons are thought to be related to retroviruses whose genetic material is RNA. Retroposons are also thought to have created the repetitive *Alu* sequences that make up a very large fraction of human chromosomes.

Although transposition occurs at a low frequency, evolution has provided ample time in which to transpose elements. In addition to the *Alu* sequences in humans, about 3 percent of the fruit fly *Drosophila melanogaster* **genome** is made up of transposable element DNA.

genome total genetic material in a cell or organism

gene expression use of a gene to create the corresponding protein

In the 1940s, Barbara McClintock first discovered mobile genetic elements in corn that caused differences in **gene expression**, resulting in kernels containing dots of different colors against a background predominant color. Because transposons can be inserted anywhere in a chromosome, they can cause genetic mutations by disrupting whole genes, which they do in pigment genes in corn. They can also disrupt expression of genes downstream of the target site by inserting between the regulatory and the expressed parts of a gene. If two transposons end up flanking a gene, the ends can work together as one large transposon, duplicating that gene within the genome. Gene duplication is a mechanism of evolution. One copy of the gene can mutate further, perhaps resulting in a new function, while the other is retained. SEE ALSO CHROMOSOME, EUKARYOTIC; DNA; GENE; MCCLINTOCK, BARBARA; RETROVIRUS

Mary Beckman

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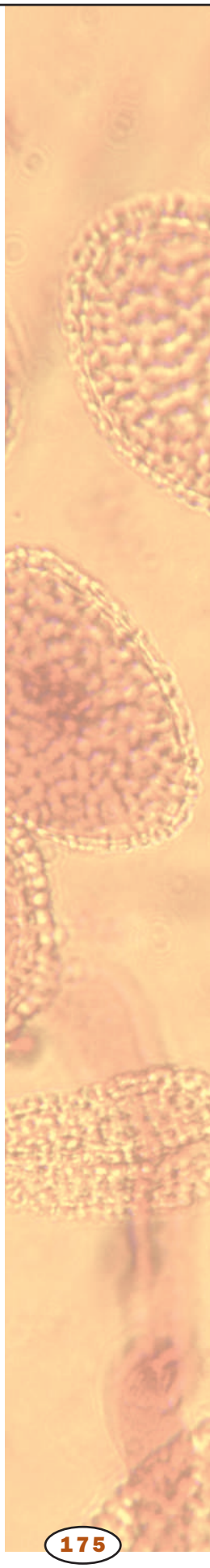
Tropisms and Nastic Movements

Tropisms are growth responses of plants that result in curvatures of plant organs toward or away from certain stimuli. Tropisms can be positive, in which case the plant will bend toward a stimulus, or negative, in which case the plant will bend away from a stimulus. Important tropisms in plants include phototropism, gravitropism, and thigmotropism.

Phototropism is the tendency for plant organs to bend in response to a directional light source. For example, light streaming in a window from one direction will often cause the stems of plants placed nearby to bend toward the window, a positive phototropism. Gravitropism is the tendency for plant organs to bend in response to gravity. In most plants, roots grow downward with gravity while shoots grow upward against gravity. Within hours, the shoot of a plant placed on its side will usually bend upward and the roots will bend downward as the plant reorients its direction of growth in response to gravity. Thigmotropism is the tendency for a plant organ to bend in response to touch. For example, the specialized touch-sensitive tendrils of many vining plants, such as pea, will bend toward the side receiving a touch stimulus. Continual stimulation can lead to the coiling of the tendril around an object, which enables vining plants to grasp objects on which they can climb.



For a plant organ to bend in response to a stimulus, differential growth of cells on either side of the organ is required. For example, for the stem of a plant to bend toward a light source, cells on the shaded side of the stem near the shoot tip must elongate faster than cells on the lighted side. Differential cell growth results from either the accumulation of growth-promoting substances on the shaded side, accumulation of growth inhibitors on the lighted side, or both. One substance that appears to mediate many tropisms is auxin, a plant **hormone** that promotes cell elongation. When the tip of a plant is lighted from one side only, auxin appears to accumulate on the shaded side of the tip, where it promotes more rapid cell elongation than occurs on the lighted side, resulting in the bending of the stem toward the light source.

hormone molecule released by one cell to influence another

Nastic movements are rapid movements of plant organs in response to a stimulus that results from alterations in cell volume in a specialized motor organ called a pulvinus. For example, handling of the touch-sensitive leaves of *Mimosa pudica* results in the folding of its leaflets within a few seconds and is an example of a thigmonastic movement. Leaf folding is due to the rapid uptake of water and increase in volume of some cells in the pulvinus located at the base of each leaflet, coupled with the rapid water loss and collapse of adjacent cells. Because nastic movements occur so rapidly, the movement of plant hormones (which can be slow) does not appear to be involved. Instead, rapidly propagated bioelectrical signals appear to mediate many nastic movements. SEE ALSO HORMONES, PLANT; RHYTHMS OF PLANT LIFE

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Tuatara

Tuataras (class Rhynchocephalia) **superficially** resemble lizards (class Reptilia), but the two known species are actually members of the smallest terrestrial vertebrate class on Earth, the Rhynchocephalia, a unique and ancient evolutionary **lineage** whose fossils (from Asia, Europe, North and South America, and Africa) first appeared in the early Triassic more than 220 million years ago. Today, Tuataras are found only on about thirty islands off the coast of New Zealand; their ancestors on other continents became extinct around 65 million years ago.

superficial on the surface; not deep

lineage ancestral line

Male Tuataras lack a penis or other copulatory organ (unlike mammals, turtles, reptiles, crocodilians, and birds), possess a skull with two pairs of arches (like crocodilians), exhibit teeth on the **palatine bones** of the jaw (unlike lizards), and have teeth that are set squarely on the jawbone (with limited ability for replacement when lost, unlike the class Reptilia); old individuals may have teeth worn entirely away. Tuataras lay shelled eggs on land (unlike the class Amphibia), and the eggs may take as long as fifteen months to hatch. Tuataras live in burrows, emerging mostly at night but sometimes during the day to bask in the sun.

palatine bone bone of the hard palate at the roof of the mouth

A Cook Strait Tuatara. *Tuatara* is a Maori word meaning "peaks or spines on the back."

Tuataras are long-lived, apparently reaching over one hundred years of age. Males are larger (up to 61 centimeters [2 feet] in length and 1 kilogram [2.2 pounds] in weight) than females (45 centimeters [1.4 feet], .15 kilograms [.33 pounds]). They are **insectivorous** (depending on insects for food), but will opportunistically prey on small vertebrates. *Tuatara* is a Maori word meaning "peaks or spines on the back," in reference to the conspicuous middorsal crest on the back and tail of males and, to a lesser extent, females. Access to much of the remote island habitat of this animal is difficult, providing it with protection from human disturbance; historically, on those islands where access was less daunting, humans arrived, and the tuataras became extinct. SEE ALSO AMPHIBIAN; CROCODILIANS; EXTINCTION; REPTILE

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insectivorous insect-eating

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Tundra

Tundra is the global biome that consists of the treeless regions in the north (Arctic tundra) and high mountains (alpine tundra). The vegetation of tundra is low growing, and consists mainly of sedges, grasses, dwarf shrubs, wildflowers, mosses, and lichens. The word "tundra" is derived from the Finnish word "tunturi," which refers to the upland treeless parts of hills and low mountains free of woodlands.

Tundra climates are extremely cold and snowy in winter. Summers are cool. The southern or lower limit of trees corresponds roughly to a mean July temperature between 10 and 12 degrees Celsius (50 and 53.6 degrees Fahrenheit), but in maritime areas the limiting summer temperature can be lower. Low shrubs, less than about 1 meter (3.2 feet) tall, and peaty

soils are common near treeline. In the northern extremes and at higher elevations, the landscapes are predominantly barren with scattered wildflowers, such as purple mountain saxifrage and Arctic poppies, mosses, and lichens. Most of the Arctic tundra regions are underlain by permafrost, ground that is permanently frozen beneath a shallow layer of soil that thaws annually.

ecosystem an ecological community and its environment

Tundra **ecosystems** have a variety of animal species that do not exist in other regions, including the Arctic hare, musk oxen, lemmings, Arctic ground squirrels, and ptarmigan. Other animals migrate annually to the Arctic including caribou and many species of birds.

The Arctic tundra is the least exploited of Earth's biomes. It is a unique biological laboratory for scientists to study unaltered ecosystems. The chief ecological concerns in the Arctic tundra are cumulative impacts of oil and mineral exploitation, roads, tourism, and long-range transport of air pollution from industrial centers to the south. Global warming is likely to have its greatest effect on tundra. Major concerns are the fate of permafrost and the carbon contained in Arctic peat. Decomposition of this carbon could increase the concentration of carbon dioxide in the atmosphere. SEE ALSO GRASSES; GRASSLAND

Skip Walker

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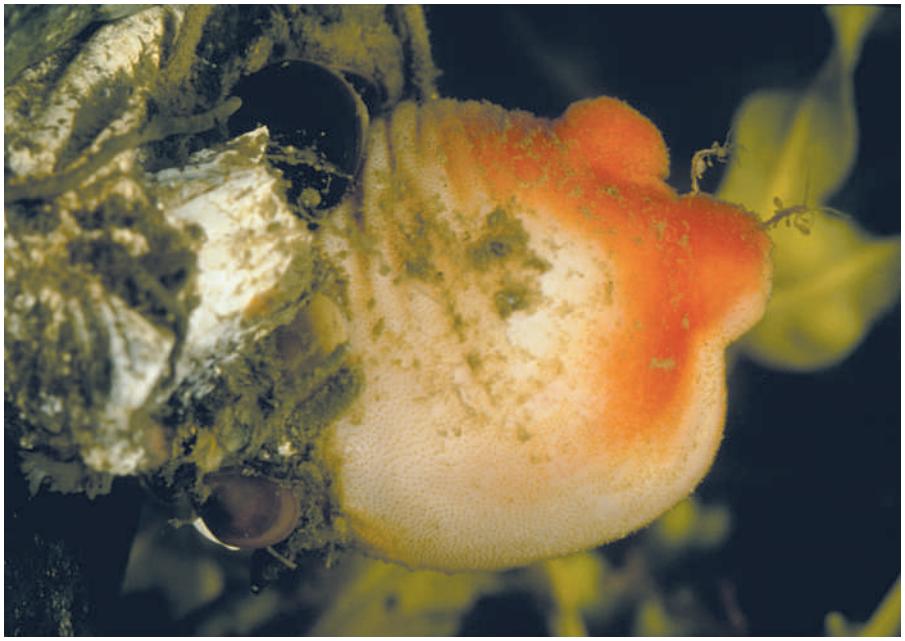
Tunicate

On such surfaces as marine dock pilings, rocks, ships, offshore oil rigs, and coral reefs, one can often find humble blobs of jelly among the sponges and hydroids. Some are as small as sesame seeds and some as big as potatoes. Some are solitary and others live in dense clusters. Some are transparent



A sea peach tunicate. Tunicates are named for the cloaklike tunics that support their saclike bodies.

and nearly invisible, while others are as brilliantly colored as a flower garden. These are tunicates, named for the cloaklike tunic that supports their saclike bodies. The tunic ranges from gelatinous to stiff. It often contains **cellulose**, a product normally associated with plants.

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

Tunicates, like humans, are in the animal **phylum** Chordata. Their swimming, tadpolelike larvae have a notochord and dorsal nerve cord as humans and other vertebrates do, but these are absent from the adults. Tunicates are classified in the subphylum Urochordata, signifying that the notochord is present only in the tail of the larva (*uro* means "tail").

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

Adult tunicates are filter-feeders, meaning they feed by pumping water through their bodies and straining **plankton** from it. Most of them are also **sessile**, or fixed in one place. Some, however, are swimming members of the marine plankton community. Adult tunicates have two body openings called siphons. They suck water into one opening, strain plankton from it with a filter called the branchial sac, and expel the water through the other siphon. When taken from the water, tunicates may expel a jet of water from this exit siphon, earning them the alternative name sea squirts. SEE ALSO ANIMALIA; CHORDATA; CORAL REEF; PLANKTON

plankton microscopic floating organisms

sessile attached and remaining in one place

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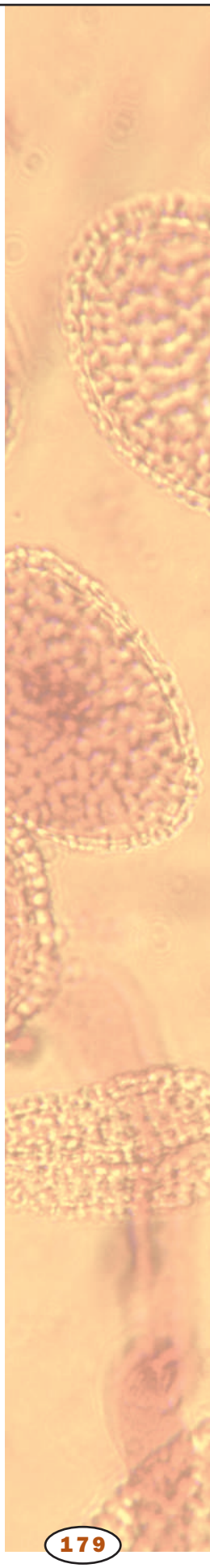
Turtle

There are about 260 species of turtles, tortoises, and terrapins. They range in size from the leatherback, a marine species reaching an upper shell length of about 190 centimeters (6.2 feet) and a weight of over 900 kilograms (1,984 pounds), to small freshwater species that average around 10 centimeters (3.9 inches) in length and weigh less than 100 grams (a few ounces). Turtles are no longer classified as reptiles but are considered a distinct and unique evolutionary **lineage** of terrestrial vertebrates, the class Chelonia. Possession of an upper (carapace) and lower (plastron) shell in combination with a skull that lacks temporal ("the temple") openings behind the eye socket sets turtles distinctly apart from amphibians, reptiles, tuataras, crocodilians, and birds. Over their 210-million-year history since the late Triassic, turtles have remained conservative in retaining a shell, their distinctive skeletal feature, but at the same time demonstrating an amazing diversity during their evolution, from sleek, flexible water-loving softshell turtles to high-domed, land-dwelling galapagos tortoises.

lineage ancestral line

All turtles are egg-layers; females dig nests in which to lay their eggs but like amphibians provide no maternal care after hatching (as in crocodilians and birds). Some turtles, such as softshells, snapping turtles, and diamondback terrapins, have commercial value and have been regularly consumed as food by people. Turtles are popular in the pet trade, and many species have been adversely impacted by overcollecting. In addition, the natural habitats of turtles are disappearing at an alarming rate, due to human



overpopulation worldwide. SEE ALSO AMPHIBIAN; CROCODILIANS; EXTINCTION; REPTILE

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Vaccines

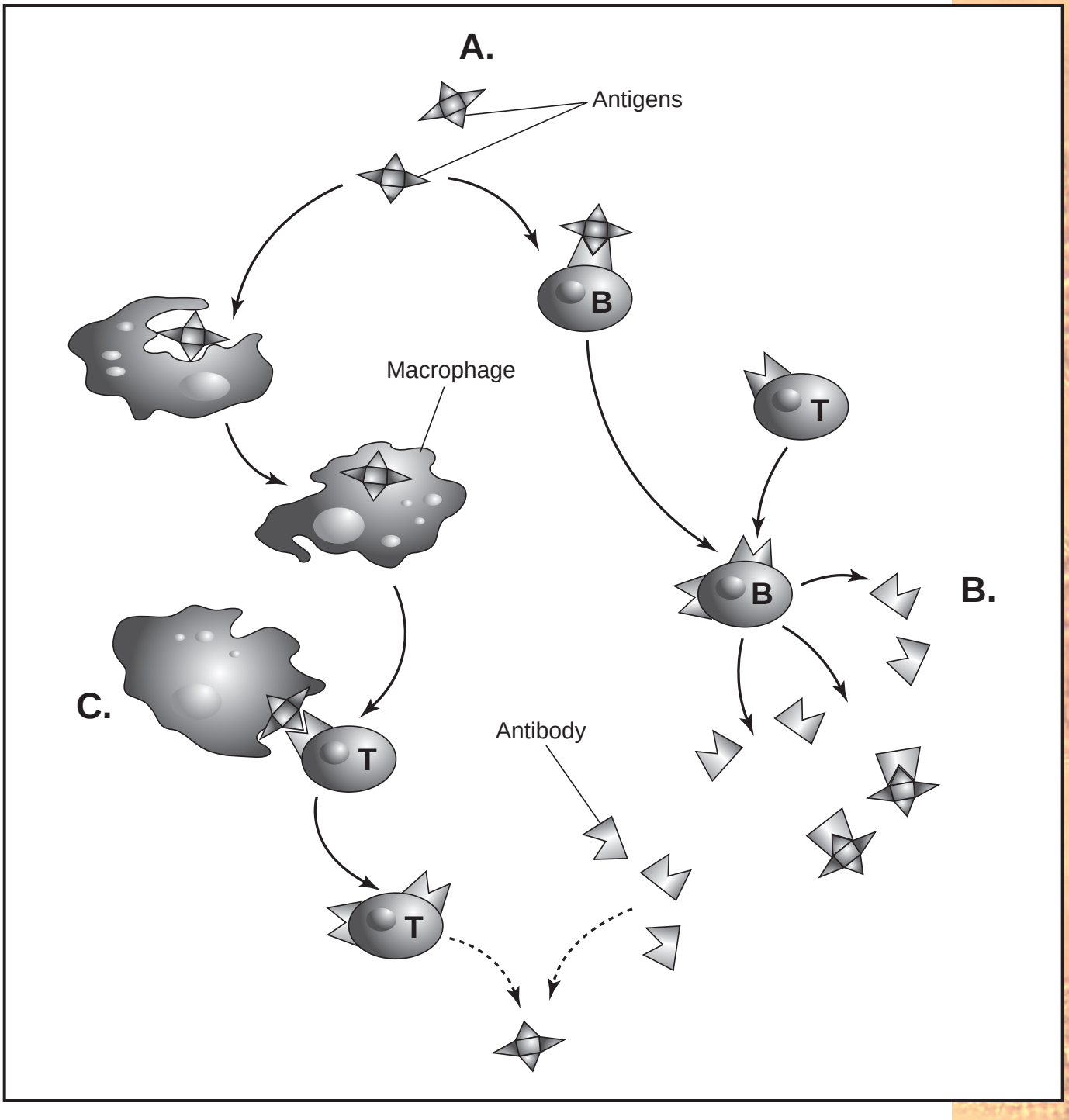
Vaccines are drugs used to increase the body's ability to combat disease organisms. Most vaccines are designed to help the body fight off a specific type of bacterium, protozoan, or virus. Some vaccines have been developed to stop the growth of cancer cells and to protect military troops from biological warfare. The administration of vaccines to animals and humans is called vaccination or immunization. Vaccination is one medical strategy for preventing the spread of infectious diseases. Vaccines encourage the body to build up immunity against disease organisms.

Vaccination

In 1796, an English physician named Edward Jenner developed the first vaccine to protect people from smallpox. Smallpox is caused by a potentially fatal virus that severely blemishes the skin and internal organs. Jenner noticed that cattle handlers infected with a related disease called cowpox did not contract smallpox. Jenner used this observation to test whether exposure to cowpox prevented people from getting smallpox. He introduced the fluids from a cowpox sore into the arm of a young boy. The boy developed cowpox, a mild disease in humans, but did not get smallpox after Jenner exposed the boy to the smallpox virus. (This highly unethical experiment could not be performed today!) The word "vaccine" comes from the Latin *vaccus*, meaning "cow." Today, smallpox has been effectively eliminated from the human population through vaccination.

Vaccines for vaccination are made from the disease organism. They are composed of either a weakened ("attenuated") form of the live disease organism, the killed disease organism, or chemical components of the disease organism. The cowpox fluids collected by Jenner contained live viruses that he scratched into the boy's body. Vaccination works by stimulating the immune system to produce antibodies against the disease organism. It takes a few days before the vaccine can protect the body, but the **antibody**-producing cells impart an immunity that can last several years to a lifetime. Booster shots are sometimes given years after immunization with an active vaccine to extend the body's immunity. Many vaccines must be given as several small doses over a six-month or one-year period. This prevents the person from being ill from a large dose given at once. Vaccination is used against a variety of common diseases including diphtheria, polio, rabies, and tetanus. Development of vaccines against HIV (human immunodeficiency virus) and malaria are two of the most active areas of research in twenty-first-century medicine.

antibody immune system protein that binds to foreign molecules



How vaccines work: A. Vaccines containing antigens are introduced into the body, stimulating the immune system response by instructing B cells, with assistance from T cells, to produce antibodies. B. Antibodies are produced to fight the weakened or dead viruses in the vaccine. The immune system prepares to destroy real and stronger viruses in the future. C. When new antigens enter the body, white blood cells called macrophages engulf them, process the information contained in the antigens, and send it to the T cells so that an immune system response can be mobilized.

French scientist Louis Pasteur was the first to develop a way to produce effective vaccines. Pasteur's first vaccine was derived from attenuated cultures of the disease organisms. Developed in 1879, it was for fowl cholera found in chickens. The first vaccine he used on humans was for the deadly viral disease rabies.

Adverse Effects of Vaccines

Many people are concerned that vaccines can have side effects in certain individuals. Several children have fallen ill from the DPT, or diphtheria-pertussis-tentanus, vaccination. Most illnesses from vaccinations are found in individuals who are allergic to the vaccine. Vaccines made from living organisms may cause the same illness physicians are trying to prevent. The oral polio vaccine, containing weakened virus, is designed to remain in the environment after defecation by the person ingesting it. This exposes other people to it, immunizing them. However, a few people exposed this way have contracted polio. The injected form of the vaccine does not carry this risk, but neither does it help immunize other people.

Passive Immunity

Another form of protection against disease, termed passive immunity, relies on injection of antibodies into the blood. These antibodies perform the same function as a person's own antibodies, attaching to the disease organism and acting as a label that tells immune cells to kill and remove the organism. These antibodies may be collected from laboratory animals immunized against the disease, or may be produced in cell cultures from special cells called monoclonal antibody cells. Passive immunization permits a person to have the protective antibodies already in the body before getting ill from the disease. Passive immunization works immediately after being administered, but gives only temporary immunity; the protective value may disappear after several weeks. Passive immunization is commonly given during influenza or "flu" outbreaks (but is not the same as a "flu shot," which is a true vaccine, given before exposure to the virus). Antivenoms used to treat the bites or stings of venomous insects and snakes are antibodies, and therefore are a form of passive immunization. SEE ALSO AIDS; Antibody; Bacterial Diseases; Disease; Immune Response; Immunization; Pasteur, Louis; T Cell; Viral Diseases

Brian R. Shmaefsky

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Vacuole

organelle membrane-bound cell compartment

ion an electrically charged particle

amino acid a building block of protein

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

A vacuole is a characteristic type of **organelle** found in plant and fungi cells and many single-cell organisms. The single large vacuole of the cell is surrounded by a membrane, called the tonoplast, and filled with a solution of water, dissolved **ions**, sugars, **amino acids**, and other materials.

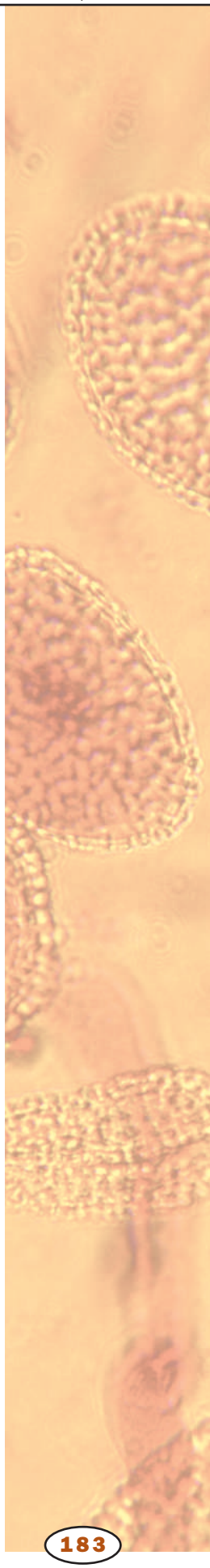
In plants, nicotine and other toxins are stored in vacuoles, since these are as toxic to the plant as they are to the herbivores they are meant to repel. The tart juice of the orange and other citrus fruits is stored in vacuoles, as are the bright pigments that give autumn leaves their color. The vacuole also serves as waste disposal and recycling center for worn-out organelles, such as **mitochondria** and chloroplasts, and in this function they are similar to lysosomes in animal cells. Expansion of the vacuole by water intake is the major driving force in plant cell growth, and is also the means for

maintaining cell rigidity, or **turgor**. To increase turgor, the tonoplast will pump ions or other material into the vacuole, causing water to infiltrate by **osmosis**. In a mature cell, the vacuole may occupy as much as 90 percent of the cell volume, such that the rest of the cell contents are flattened against the cell membrane. SEE ALSO ANATOMY OF PLANTS; CELL WALL; FUNGI; PROTISTA; SECONDARY METABOLITES IN PLANTS; WATER MOVEMENT IN PLANTS

Richard Robinson

turgor internal pressure

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



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van Helmont, Jan

Flemish physician and chemist
1579–1644

Jan van Helmont was an early pioneer in the study of gases, and performed numerous chemical experiments, including an analysis of smoke, distinguishing it from ordinary air by the particles it contained. However, van Helmont is best known for a single experiment demonstrating that the weight a plant gains during growth is not due to absorption of an equal amount of soil, but instead is due (at least in part) to water.

Van Helmont undertook his famous experiment in plant growth, in part, to learn more about water. In this experiment, he carefully weighed a young willow shoot, and then planted it in a large container whose soil he had also carefully dried and weighed. He watered the willow as needed for five years, and then reweighed both the willow and the soil. The willow had grown from 2.2 kilograms (5 pounds) to 77 kilograms (169 pounds), while the dry weight of the soil had lost only 57 grams (2 ounces). In this way, van Helmont demonstrated that plants do not simply take up soil as they grow, and concluded that water was the sole source of this increased weight. However, van Helmont did not suspect that gases in the air might contribute to plant growth, a fact demonstrated by Nicolas de Saussure more than one hundred years later. SEE ALSO SOIL; WATER

Richard Robinson

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Vavilov, Nikolay

Russian Plant Geneticist
1887–1943

Nikolay Vavilov is best known for attempting to apply the science of genetics to Russian agriculture, for his theories of the origin of crop plants, and for being persecuted during the Stalin Regime in the Soviet Union.

Vavilov studied genetics in Moscow and in England. Under Lenin, he became the head of the Bureau of Applied Botany in St. Petersburg, building it into one of the premier research institutions in the world. Vavilov traveled widely to collect and observe crop plants and their wild relatives. By analyzing the diversity of plants in different regions, and combining this information with archaeological and other evidence, Vavilov formulated his theory of crop plant origins. He believed that regions in which the domesticated varieties of a crop plant were most diverse were most likely the regions in which that crop had first been cultivated by humans. He postulated there were eight "centers of origin," an idea that led to much further research and the eventual refinement and modification of Vavilov's theory. Through the 1930s, however, under Stalin, genetic science became suspect because of its associations with the West, and Vavilov was attacked by Trofim Lysenko, who had Stalin's trust. In 1940, Vavilov was arrested and imprisoned. He died in jail three years later.

Richard Robinson

Vesalius, Andreas

Belgian anatomist
1514–1564

Andreas Vesalius was the founder of modern human anatomy. Before his time, medical illustrations served more to decorate a page than to teach human structure. Humans were often shown in squatty froglike postures with only crude representations of the locations and relationships of the internal organs. Often the figures were surrounded by signs of the zodiac, as astrologers thought each constellation influenced a particular body organ. Medical professors taught from an elevated chair, the cathedra, reading dryly in Latin from such ancient authorities as Roman physician Galen, while a low-ranking barber-surgeon removed organs from a rotting corpse and held them up for the medical students to see. Neither **embalming** nor cadaver refrigeration were yet known to Western medicine, and the professors considered it beneath their dignity to touch the foul cadaver.

embalming treating a dead body to protect it from decay

Vesalius revolutionized the teaching of medicine. A native of Brussels, educated at Paris and Padua, he taught medicine at the University of Padua in Italy. Vesalius broke with tradition and personally dissected cadavers with his students. He soon learned that the anatomy described by Galen was highly inaccurate, and he commissioned artists from the studio of Italian painter Titian to render more accurate illustrations. When other anatomists began plagiarizing these illustrations, Vesalius had them published in a seven-volume work, *De Humani Corporis Fabrica (On the Structure of the Human Body)*, in 1543. This was the first accurate atlas of human structure, and ushered in the era of modern human anatomy.

After the publication of the *Fabrica*, Vesalius enjoyed an illustrious career as a physician to, among others, Charles V, emperor of the Holy Roman Empire, and his son, Philip II. In 1564, Vesalius died in a shipwreck on the way home from a voyage to the Holy Land.

Twenty-first-century anatomical atlases, such as Frank Netter's *Atlas of Human Anatomy*, Carmine Clemente's *Anatomy*, and Anne Agur's *Grant's*

Atlas of Anatomy, and even the standard college textbooks of human anatomy owe a great debt to the tradition begun by Vesalius. SEE ALSO HISTORY OF MEDICINE

Kenneth S. Saladin

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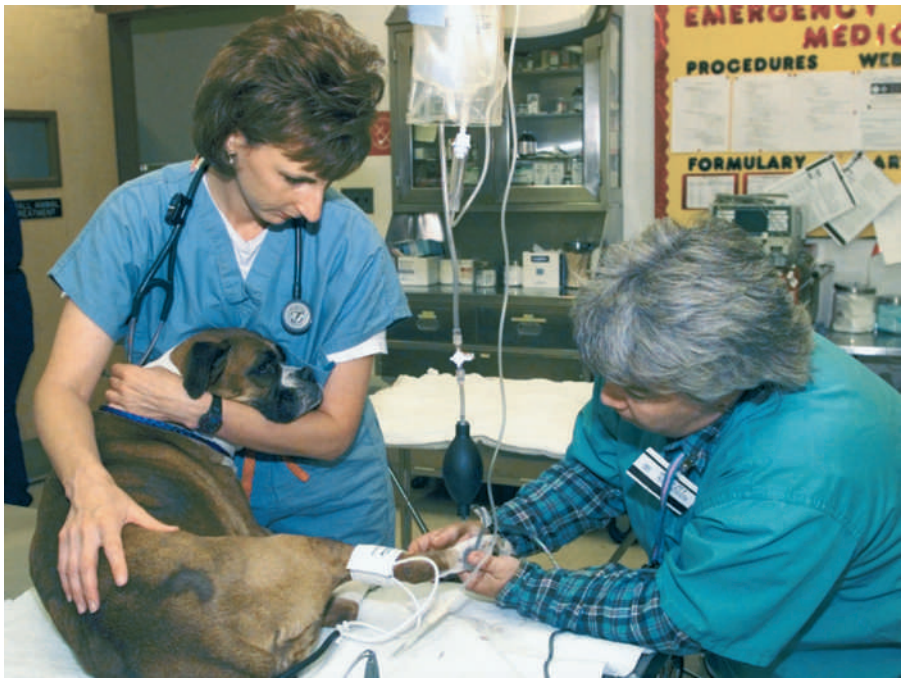
Veterinarian

Becoming a veterinarian is a challenging yet rewarding process. A veterinarian is someone who has earned a Doctor of Veterinary Medicine (DVM) or a Veterinary Medical Doctor (VMD) degree from an accredited college or university. The veterinary program consists of four years of a combination of lecture classes, practical laboratory work, and clinical experience. Many veterinary programs allow students to choose an area of emphasis (usually small animals, equine, food animals, exotic animals, or mixed), although this varies among programs. While an undergraduate degree is not required to enter a veterinary program, the great majority of veterinary students have a degree, usually a Bachelor of Science in a biological science, and many may also have a Master of Science degree. Every veterinary program's entry requirements are different, but most include undergraduate courses in biology, chemistry, physics, mathematics, biochemistry, animal science, and animal nutrition. The high school student interested in pursuing a veterinary degree would be wise to take as many science and math courses as possible. Experience in handling animals is also a necessity for admission to a veterinary program, whether in a paid position or on a vol-



A veterinary technician checks a dog's blood pressure.

unteer basis. Excellent grades are necessary: entrance into a veterinary program is very competitive because of the small number of veterinary programs in the United States.

The great majority of veterinarians are employed in private practice, but this is not the only employment opportunity. Veterinarians are needed in government to serve on medical and agricultural committees, to inspect meat and meat products, and to work in laboratories. Colleges and universities hire veterinarians to teach undergraduate and graduate courses and to conduct research. Overseas veterinary mission and Peace Corps work is available. Large research and pharmaceutical companies often have veterinarians on their staffs. A veterinary degree is extremely versatile and useful, particularly when combined with an undergraduate degree in a biological science.

Amy L. Massengill

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Viral Diseases

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

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

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

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

enzyme protein that controls a reaction in a cell

secretion material released from the cell

interferons signaling molecules of the immune system

In order to understand viral infections, one must understand a little about how a virus functions. All viruses are **obligate parasites**; that is, they depend on a "host" to survive and reproduce. In the case of a virus, the host is the cell of a living organism. Outside of a host cell, viruses are inert molecules, waiting to attach to a victim cell. Although viruses contain genetic material (either deoxyribonucleic acid [DNA] or ribonucleic acid [RNA]), they lack the internal machinery (organelles) to produce **proteins** from the information contained in their own **genetic code**. The simplest virus contains only three genes.

A viral infection begins when a virus inserts its genetic material into a host cell. First, the virus attaches to a specific structure on the cell's surface via an attachment protein. Depending on the virus, either the genetic material diffuses into the host cell or the entire virus enters the cell. The poliomyelitis virus may have over one million copies of its basic genetic information (RNA) inside a single, infected human intestinal mucosal cell.

One or more of the genes on the viral genetic material code for **enzymes** that essentially "hijack" the host cell, causing it to produce only viral parts, which are then assembled into copies of the virus within the host cell. These viral copies are released, leaving the cell either by a process called "budding" (where just one or a few viruses leave the cell at a time) or by a process called lysis (where the cellular membrane ruptures and releases all of the virus particles at once). Both processes usually kill the host cell. The new viruses then infect surrounding cells, continuing the process. Examples of diseases that are viral in origin are influenza (swine flu), some types of pneumonia, poliomyelitis, cold sores and shingles, and AIDS (acquired immunodeficiency syndrome).

Of course, host cells have several defenses against the viral attacks. For example, in animals (including humans), viral infection leads to the synthesis and **secretion** of proteins called **interferons**, which "interfere" with vi-

ral replication by helping adjacent uninfected cells become resistant to infection. Often, this is not enough to stop the spread of infection, and the body's immune system can cause fever, achiness, tiredness, and other defenses, making the person feel "sick" but acting to help the body fight off the attack. Eventually, the virus is completely removed, and the symptoms subside.

HIV (human immunodeficiency virus) is an exception to this situation because HIV infects cells of the immune system that are necessary to kill the infected cells. So, although HIV does not itself directly cause the condition known as AIDS, the eventual death of immune cells allows other infections to spread (called secondary infections).

So far, no agents have been identified that are secreted by a cell that actually kills a virus. Although antibiotics are effective against bacteria, they do not kill viruses. Recently, there have been agents called antivirals designed in the laboratory and isolated from natural sources that are being used to fight certain viral infections. For example, protease inhibitors are used to inhibit the replication of HIV. SEE ALSO AIDS; DISEASE; DNA VIRUSES; RETROVIRUS; SEXUALLY TRANSMITTED DISEASES; VIRUS

Carl J. Shuster

The first outbreaks of the paralyzing poliomyelitis (polio) virus in the United States occurred in the early nineteenth century. It reached its peak in 1952 when more than 21,000 people were infected. Due to the effective use of vaccines, the incidence of polio declined rapidly; the last documented transmission of the virus in the United States was 1979.

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Virus

Viruses are not cells and are metabolically inert outside of living cells. They can infect organisms consisting of just one cell, such as a single bacterial cell, or the individual cells of multicellular organisms such as humans. They are small compared to the cells they infect and as such must live as **intracellular parasites**. They absolutely require cells to reproduce. Within the appropriate cell, viruses are able to program the cell to replicate themselves by hijacking the normal cellular systems. The extracellular form of a virus, also known as a virion, is stable enough to survive the conditions required for transmission from one cell to another. The virion is composed of a set of **genes** (encoded by ribonucleic acid [RNA] or deoxyribonucleic acid [DNA]), which is protected by a **protein**-containing coat. The coat is often characterized by regularity and symmetry in its structure and is capable of binding to and invading cells. On invasion of a susceptible cell the virion is disassembled to release the viral **genome**. Once the viral genome is released, viral genes are expressed to reprogram the **biosynthetic** activities of the cell so that large numbers of **progeny** virions may be produced by the cell. These virions are then released by the infected cell to invade other cells so that the process can be repeated. SEE ALSO BACTERIAL VIRUSES; DNA VIRUSES; RETROVIRUS

Richard Longnecker

intracellular within a cell

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

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

genome total genetic material in a cell or organism

biosynthetic forming a complex molecule from simpler ones

progeny offspring

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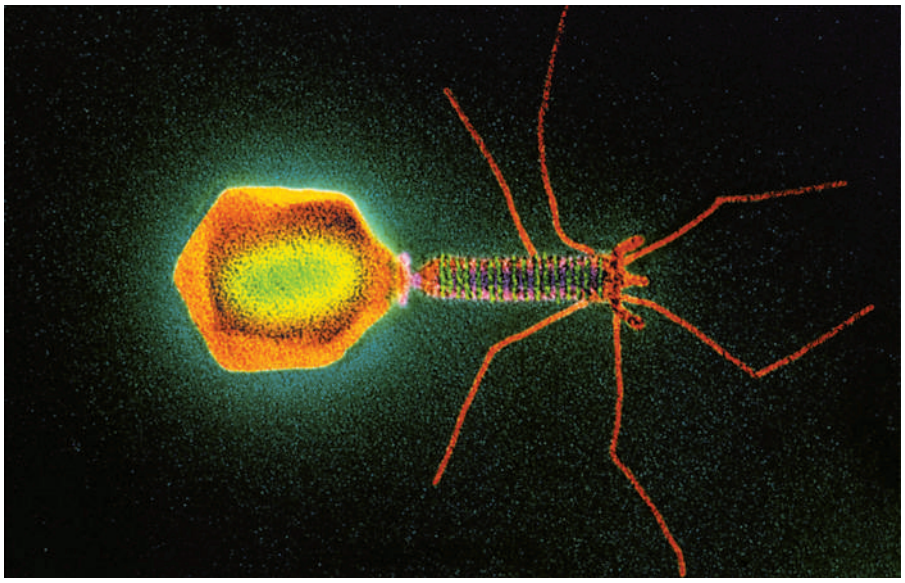

A colored transmission electron micrograph of a T4 bacteriophage virus.

Vision

The eyes are the windows on the world. Vision is found widely in many different classes of animals and may have evolved independently at different times. Vision, which involves perception of light and dark, is distinct from simple light sensitivity, such as that displayed by germinating plant sprouts that respond to the sun's direction.

Eyecups

The complexity of eyes varies markedly in different groups of animals. Nonfocusing eyecups are found in the planarians, the medusas (jellyfish) of cnidarians, some snails, and some other invertebrates. Light enters a depression lined with pigment-containing, light-sensitive cells. **Neurons** connected to these cells carry messages to the rest of the nervous system. Because there is no focusing system, the general direction and intensity of light can be detected, but there can be no perception of form or image.

neuron nerve cell

Compound Eyes

Most adult insects and crustaceans, as well as the horseshoe crab and the extinct trilobite, have compound eyes, constructed of as few as one (in some ants) to as many as thirty thousand (in some dragonflies) individual units called ommatidia. Each ommatidium is covered with a cornea, formed from the insect **exoskeleton**, and has its own crystalline cone within. Both structures focus light on the retinula (light-sensitive) cells at the base. The amount of light entering the ommatidium may be controlled by increasing or decreasing the amount of screening pigments within. The individual ommatidia do not usually cast clear images on the retinula cells, rather just a spot of color. The individual retinula cells then send this information into the brain, which puts all of the spots together to form a mental image.

exoskeleton external skeleton

Although the details of insect visual processing are unknown, there appear to be multiple levels of processing, as there are in vertebrate visual sys-

tems. Finally, insects usually have three ocelli, non-image-forming simple eyes, on the tops of their heads. These seem to awaken insects for their daily activities.

Camera Eyes

Vertebrates (including humans) and cephalopods (such as the octopus) have so-called camera eyes. Camera eyes have muscular rings called irises to control the amount of light that can hit the light-sensitive cells in the back of the eye. The ability to control the amount of light is called visual adaptation. Human eyes have a cornea on the outer surface that provides about 70 percent of the eye's focusing power, and they have an adjustable lens that provides the rest of the focusing power and allows accommodation, or change, of focus for near or far objects. Light entering the eye passes first through the cornea, then past the iris, through the lens, then the vitreous humor, which is a clear jellylike substance that gives the eye its shape. Light is absorbed by the retina, the layer of light-sensitive cells lining the back of the eye.

Light Transduction

Despite the differences in structure, eyes generally use the same set of biochemical tools to **transduce** light into a **neural** signal. A carotenoid compound (such as the chemical relatives of vitamin A), linked to a **protein** in the retinal cell membrane, captures the light energy. The light alters a chemical bond in the carotenoid, which then changes its shape, causing the membrane to alter its electrical state. The change in electrical state then will cause the retinal cell to release a chemical (called a neurotransmitter) which will excite an adjacent nerve cell. The carotenoid plus an associated protein is referred to as the visual pigment. (Interestingly, carotenes are also used by plants to help them capture the energy of the sun in photosynthesis.)

Image Processing

The visual image detected by the retina is not recorded whole and passed unchanged to the brain. Instead, the image is processed, with highlighting and integration of some features along the way. The degree of image processing varies among different types of animals. For example, toads have a "worm detector." When the optic nerves send signals to the visual-processing area of the brains to form a linear pattern, the brain says "worm" and the toad aligns to the worm and snaps it up.

The eyes of some animals have fields of vision with little or no overlap between the two eyes, giving them a 360-degree view of the world. Such wide fields of view are seen often in prey animals, allowing higher vigilance against predators. Some ground birds, for example, have eyes that have absolutely no overlap. In contrast, other animals have eyes with highly overlapping fields of vision. This allows stereoscopic vision, in which an object is viewed from two different points. Integration of these images, along with information about the relative direction in which the two eyes are pointing, allows depth perception, a critical tool for predators. It is also important for monkeys and other tree-dwelling primates, for instance, in order to know how far that next branch is so that they do not fall out of their trees!

A scanning electron micrograph of the compound eye of a fruit fly (*Drosophilia melanogaster*).

transduce to convert a signal of one type into another type

neural related to nerve cells or the nervous system

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

Ultraviolet and Polarized Light

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

The visual spectrum of all animals goes from around 350 **nanometers** (ultraviolet) through all the colors most humans see to the infrared, around 800 nanometers (one nanometer equals one-billionth of a meter). In the vertebrates, elaborate color vision is found in the primates (including humans), birds, lizards, and fish. Most other mammals lack the ability to see red or other colors (including bulls).

Insects are less well able to see the red than humans can, but they do see colors, and some insects can detect ultraviolet light. Bees can see the hidden ultraviolet color patterns of black-eyed susans and other flowers, for instance, allowing them to hone in on these flowers more easily.

Another unusual light quality that insects can detect is the plane of light polarization. Light polarization means that all of the rays arriving at the retinal cells are vibrating in the same plane; light typically becomes polarized when it is reflected off surfaces. Insects' retinas are arranged so that they detect changes in polarization. This makes it possible for honeybees to determine the direction of the sun even on cloudy days. The sun's direction in the sky is a critical piece of information communicated in the bee dance that a scout bee will do to communicate the location of nectar or pollen sources to other bees in the hive. SEE ALSO EYE

David L. Evans

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Vitamins and Coenzymes

Vitamins are chemical compounds that are vital to life and indispensable to body functions. They often exist as provitamins, inactive forms that must be converted into active vitamins before they can perform metabolic tasks in the body's cells. There are thirteen individual vitamins required by the human body for growth and maintenance of good health.

Vitamins are grouped on the basis of their ability to dissolve in water or fat. The fat-soluble Vitamins A, D, E, and K generally are found together in the fats and oils of foods. Once absorbed, they can be stored indefinitely in the liver and fatty tissues of the body. This capacity for storage can lead to unwanted toxic buildup of certain vitamins, A, D, and K in particular, that can cause great harm. Deficiencies of any vitamin can also be harmful. The National Academy of Sciences publishes recommended intake values for all thirteen vitamins.

Each of the fat-soluble vitamins performs unique functions in the body. The three active forms of Vitamin A are required for night and color vision, reproduction, and cell maturation and differentiation, the process by which precursor cells develop into a specific cell type. Vitamin A also plays

a role in fighting infections and in the development and maintenance of bone. Beta-carotene and other provitamin forms of vitamin A known as carotenoids are **antioxidants**, chemicals that block the harmful cancer-causing effects of oxidizing agents (oxygenlike molecules) on cells. This antioxidant property may also play a role in vitamin A's prevention of heart disease.

antioxidant substance that prevents damage from oxidation

The provitamin form of vitamin D is made by skin cells using sunlight and a derivative of cholesterol. It is then converted to its active form in the kidneys and liver. Vitamin D plays a role in the differentiation of cells in the intestines, skin, immune system, and bones. It also regulates blood calcium levels, which are important in maintaining proper bone density.

Vitamin E's major function in the body is as an antioxidant. It inserts itself into cell membranes and protects substances inside the cells, such as deoxyribonucleic acid (DNA), from being chemically modified by oxygenlike molecules.

Vitamin K is involved in synthesizing **proteins** that help blood clot. It is also necessary for making a key protein important in bone formation. In addition to dietary sources of vitamin K, the body can use vitamin K manufactured by bacteria that live in the intestines.

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

The water-soluble vitamins include vitamin C and the group of eight vitamins known collectively as Vitamin B. They are not readily stored and are **excreted** in urine when consumed in excess of the body's needs. Vitamin C's roles include assisting in the production and maintenance of collagen, a protein found in bones, skin, teeth, and tendons. Vitamin C also plays roles in supporting the immune system and producing thyroxine, the **hormone** that regulates body temperature and **metabolism**.

excrete deposit outside of

hormone molecule released by one cell to influence another

metabolism chemical reactions within a cell

The B vitamins act as part of coenzymes, small molecules that combine with an **enzyme** to make it active. Enzymes are proteins responsible for catalyzing most chemical reactions in the body, such as digesting food and synthesizing new compounds. The B vitamins riboflavin, thiamin, niacin, pantothenic acid, and biotin help the body use protein, fat, and carbohydrate to produce energy for the body's cells.

enzyme protein that controls a reaction in a cell

Vitamin B_6 assists in the synthesis of new proteins in the cell by assembling protein building blocks called **amino acids**. Folate and Vitamin B_{12} are required for cell multiplication. In particular, folate is involved in synthesizing DNA for the dividing cells. Vitamin B_{12} helps folate enter cells. B_{12} also maintains the protective sheaths that surround nerve fibers. SEE ALSO ENZYMES; NUCLEOTIDES

amino acid a building block of protein

Michele D. Blum

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von Humboldt, Alexander

German explorer and scientist
1769–1859

Alexander von Humboldt was a scientist and explorer who founded the field of plant biogeography, the analysis of the distribution of plants throughout the world. Humboldt was born in Germany and apprenticed with several leading German botanists as a young man. He also became trained as a geologist and worked for a time at the German Ministry of Mines.

wanderlust strong desire to travel

By 1797, however, Humboldt had developed a **wanderlust** and thirst for adventure, and in 1799 he set out for South America to find out, as he put it, "how the geographic environment influences plant and animal life." While there, and despite many hardships, Humboldt made significant studies of the botany, zoology, geography, and climate of the region. He was probably the first European to recognize the rich diversity of the tropical flora.

Humboldt discovered that the distribution of plant groups could be correlated with changes in temperature and rainfall, laying the intellectual groundwork for developments in plant ecology that would come a century later. After leaving South America, Humboldt visited the United States and met with Thomas Jefferson, whose own thinking about scientific expeditions in America was probably influenced by these conversations. Humboldt's memory is honored in the names of rivers, mountains, and counties in the western United States. SEE ALSO BIOGEOGRAPHY; BUFFON, COUNT

Richard Robinson

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Water

Water (H_2O) is vital for all living organisms, and it is no exaggeration to say that life could not occur without it. The central feature of the water molecule is the bond between the strong electron attractor oxygen and the weak attractor hydrogen. This creates a **polar covalent** bond, with a weak positive charge on each hydrogen and a weak negative charge on the oxygen. The **polar** water molecule dissolves **ions** (such as sodium, essential for membrane transport) and polar molecules (including sugars) while excluding large nonpolar molecules such as fats. This selective **solvation** forms the basis of cell structure and function, in which large insoluble membranes enclose **aqueous** solutions of nutrients and other small molecules.

polar covalent bond in which electrons are unevenly shared

polar partially charged, and usually soluble in water

ion an electrically charged particle

solvation the process of dissolving

aqueous watery or water-based

Water is liquid between 0 and 100 degrees Celsius (32 to 212 degrees Fahrenheit), a temperature range that is high enough to promote random mixing in aqueous solutions (necessary for biochemical reactions) but low

enough to prevent random breaking of most covalent bonds, which would make stable life forms impossible. Most organisms must live in the low end of this range. Finally, its high heat capacity moderates temperature changes, especially in organisms with large bodies. SEE ALSO LIPIDS; MEMBRANE STRUCTURE

Richard Robinson

Water Cycle

The water, or hydrologic, cycle refers to the global scale continuous movement of water between the oceans, the atmosphere, and the continents. Water exists on Earth in three states: liquid water, solid (ice or snow), and gas (water vapor). Liquid water covers about 70 percent of Earth's surface, primarily in oceans that store 96 percent of Earth's total water volume (1460×10^6 km^3). The remaining water is mostly contained in the polar ice caps, glaciers, and groundwater, while only small amounts occur in rivers, lakes, soils, and the atmosphere. Freshwater lakes, rivers, and groundwaters comprise only a tiny fraction of Earth's water.

Evaporation and precipitation are the major exchange processes for water between the atmosphere and Earth's surface. Water, evaporated from land, surface waters, and the oceans and transpired by vegetation, is returned to the atmosphere as water vapor. Water molecules cycle rapidly in the atmosphere, with an average residence time of only eleven days. Falling as precipitation on land, water can enter the groundwater, later emerging in lakes and rivers; run off as surface flow into rivers and lakes and, eventually, the ocean; or evaporate back to the atmosphere. The residence time of water in rivers and lakes is extremely variable (from a few weeks for rivers to over one hundred years for the deepest lakes), but is fast compared to 20,000 years in deep groundwater layers and 39,000 years in the ocean.

Although the amount of water stored is small and the residence times short, atmospheric water, rivers, and lakes are extremely important for maintenance of the world's **ecosystems**. Global patterns of precipitation and evaporation determine the distribution and character of biological habitats from deserts to rain forests. Water transports **minerals**, sediments, nutrients, and pollutants across the landscape, and over long distances in the atmosphere. Because of close links with global energy and carbon and nitrogen cycles, the water cycle is vitally important to Earth's ecology. SEE ALSO BIOGEOCHEMICAL CYCLES; ECOSYSTEM; LAKES AND PONDS; LIMNOLOGIST

ecosystem an ecological community and its environment

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

Katherine E. Webster

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Water Movement in Plants

Long-distance water movement is crucial to the survival of land plants. Although plants vary considerably in their tolerance of water deficits, they all

A drop of guttation, water extruded by a plant's root pressure, on a blade of grass.

have their limits, beyond which survival is no longer possible. About 85 percent of the fresh weight of leaves can be water. On a dry, warm, sunny day, a leaf can evaporate 100 percent of its water weight in just an hour. Water loss from the leaves must be compensated for by the uptake of water from the soil. Water transport is also important for the uptake of essential mineral nutrients from the soil. Shortages of mineral nutrients such as nitrogen, potassium, and phosphorus are often limiting to plant growth, which is why fertilizers are often added to the soil to improve plant productivity and appearance.

The Cohesion-Tension Theory

The major mechanism for long-distance water transport is described by the cohesion-tension theory, whereby the driving force of transport is transpiration, that is, the evaporation of water from the leaf surfaces. Water molecules cohere (stick together), and are pulled up the plant by the tension, or pulling force, exerted by evaporation at the leaf surface.

Water will always move toward a site with lower water potential, which is a measure of the chemical free energy of water. By definition, pure water has a water potential of 0 MegaPascals (MPa). In contrast, at 20 percent relative humidity, the water potential of the atmosphere is -500 MPa. This difference signifies that water will tend to evaporate into the atmosphere. The water within plants also has a negative potential, indicating water will tend to evaporate into the air from the leaf. The leaves of crop plants often function at -1 MPa, and some desert plants can tolerate leaf water potentials as low as -10 MPa. The water in plants can exist at such low water potentials due to the cohesive forces of water molecules. The chemical structure of water molecules is such that they cohere very strongly. By the cohesion-tension theory, when sunlight strikes a leaf, the resultant evaporation first causes a drop in leaf water potential. This causes water to move from stem to leaf, lowering the water potential in the stem, which in turn causes water to move from root to stem, and soil to root. This serves to pull water up through the **xylem** tissue of the plant.

xylem water-transporting system in plants

From Root to Leaf

Plants have root hairs and often mycorrhizal fungi at the root surface, both of which serve to filter the soil water as it enters the plant. **Mycorrhizae** are symbiotic associations between plant roots and fungi. The root cells and mycorrhizal fungi both actively uptake certain mineral nutrients. Mycorrhizae can be particularly important for the uptake of phosphate. The active uptake of **minerals** by living cells of the root and the subsequent transfer of minerals to the xylem can result in positive root pressures, with water potentials above 0 MPa. This occurs only under certain conditions, such as at night or during rainstorms, when water loss from the leaves is minimal. Such positive root pressures disappear with the onset of leaf transpiration.

mycorrhizae symbiosis between soil fungus and plant root to maximize absorption

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

Water molecules move from the soil into living cells of the root, and eventually into the transport cells of the xylem, known as tracheids and vessels. These xylem cells are dead and hollow, allowing rapid water transport. They also have hardened cell walls to help them resist the tendency to collapse as water is sucked through them. Both tracheids and vessels

have pits on the sides of their walls, which include porous areas for side-to-side transport. Unlike tracheids, a vessel is composed of many cells stacked end to end, with perforations between cells, allowing for more efficient transport.

The long-distance transport of the water molecule occurs first within the xylem cells of the root, then the xylem of the stem and branch, and then into the xylem of a leaf midrib and vein. Driven by transpiration, the water molecule is pulled from the nonliving tracheids and vessels of the xylem in the living cells of the leaf mesophyll (middle layer) and to the surface of mesophyll cell walls. The water molecule then evaporates into a leaf intercellular air space and finally out of a **stomatal** pore and into the atmosphere. Though photosynthetic action consumes some water, only a small fraction of the water that travels through the plant is used directly for the photosynthetic reaction, which occurs in leaf mesophyll cells. Instead, most water is lost by transpiration through the stomates.

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

The Role of Stomates

Leaves of land plants are covered with a waxy cuticle that prevents water loss and gas exchange. The stomates at the leaf surface have **guard cells** that open and close the stomate to regulate the uptake of carbon dioxide and release of oxygen, as required for photosynthesis. They also serve to regulate water loss from transpiration. During the day, the stomates normally open up in response to sunlight, allowing for photosynthetic gas exchange, but also allowing for transpiration. At night, the stomates normally close, preventing unnecessary water loss. When excessive water loss occurs during the day, drops in leaf water potential can cause stomates to close. Were it not for stomate closure in response to water stress, the leaves would suffer excessive water loss, the leaf cell membranes and photosynthetic apparatus would be destroyed, and "cavitation" would occur in the xylem cells. Cavitation, which is a break in the water column, occurs when air is pulled into the xylem vessel or tracheid. This can make the xylem cell unable to conduct water. Plants vary considerably in their vulnerability to cavitation, but for most plants, stomate closure can prevent cavitation from occurring.

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

The transpirational water loss allows for uptake of mineral nutrients from the soil. However, much of the water loss that land plants exhibit can be viewed as a "necessary evil." The stomates must open up to allow for photosynthesis to occur, and during the process of letting carbon dioxide into the leaf, water vapor is lost to the atmosphere. When the stomates close to prevent excess water loss, photosynthesis is compromised. SEE ALSO ANATOMY OF PLANTS; LEAVES; MYCORRHIZAE; ROOTS; SHOOTS; WATER

Frank Ewers

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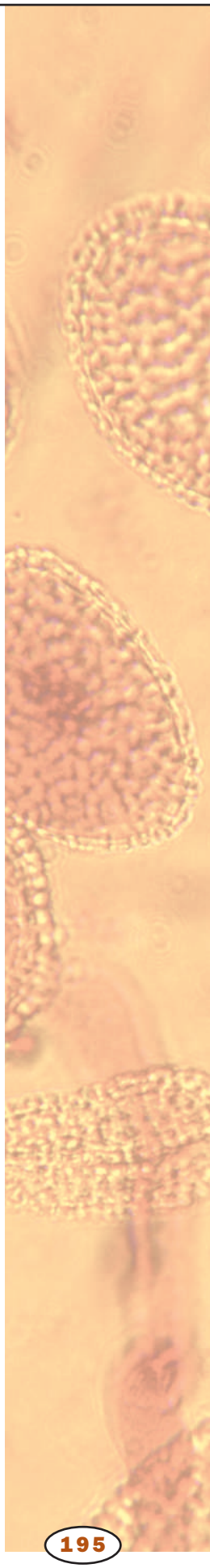

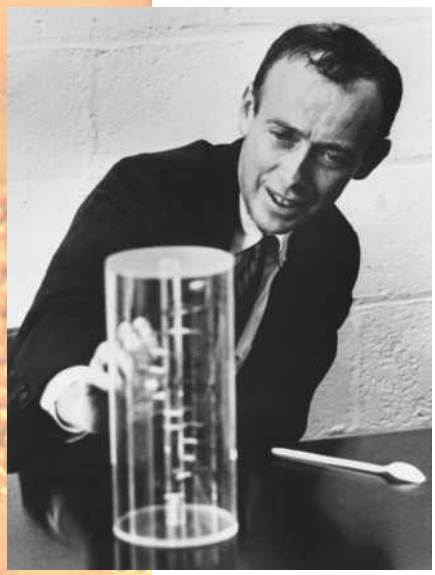

James Watson.

Watson, James

American biologist
1928–

James Dewey Watson, American biologist, won the Nobel Prize in 1962 for the discoveries he made in molecular genetics, along with Francis Crick and Maurice Wilkins.

Watson was born on April 6, 1928, in Chicago, Illinois, and was declared a child prodigy at an early age. Indeed, in his youth, he appeared on a television program called "Chicago Quiz Show."

Watson began his university studies at the age of fifteen at the University of Chicago, from which he graduated at nineteen. While in college, Watson was deeply affected by the writings of Erwin Schrodinger, who was among the first to articulate the concept of the gene. Watson received his doctoral degree in 1950 from Indiana University, after conducting research on bacterial viruses.

After receiving his Ph.D., Watson won a fellowship from the Merck Foundation and spent a year furthering his study of bacterial viruses in Copenhagen, Denmark. From Copenhagen, Watson moved on to Cambridge University, where he first met and collaborated with Frances Crick, a young British biophysicist.

In 1952, Watson and Crick began to investigate the molecular structure, and significance to genetics, of nucleic acids. The collaborators began by looking specifically at the earlier work done by Maurice Wilkins and Rosalind Franklin on **X-ray crystallography** analysis of deoxyribonucleic acid (DNA), a substance that was already considered to make genes, the fundamental units of heredity.

X-ray crystallography use of X rays to determine the structure of a molecule

Watson and Crick used Wilkins's and Franklin's data to create a three-dimensional model of the DNA molecule. Watson and Crick hoped that their model would agree with the chemical facts previously established about DNA; for example, that DNA consisted of phosphates, nitrogenous bases, and sugars. In addition, Wilkins's X-ray crystallography experiments had already determined many of the patterns by means of which such molecules were connected.

Watson and Crick tried out various ways of arranging model molecules in space, finally settling on the aptly named "double helix." Their model, afterward referred to as the Watson-Crick model, showed DNA as a two-stranded twisted "helix." The two strands consisted of **complementary** pairs of **nucleotide** units. 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

nucleotide the building block of RNA or DNA

Between 1956 and 1976, Watson ran a laboratory at Harvard University, where he also taught courses in biology. Additionally, in 1969 he was named director of the Cold Spring Harbor Laboratory in New York State. In 1991, Watson became the first director of the Human Genome Project, established by a consortium of public agencies to sequence the entire human genome, but he later resigned over the issue of patenting human genes.

Among his notable publications are *Molecular Biology of the Gene* (1965) and *The Double Helix* (1968). SEE ALSO CRICK, FRANCIS

Hanna Rose Shell

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Wetlands

"Wetlands" is the collective term for habitats that are too wet to be upland and not wet enough to be fully aquatic. They occur in areas of transition between dry upland and open water or in low areas where drainage water collects or the water table is at the ground's surface.

Wetlands are characterized by:

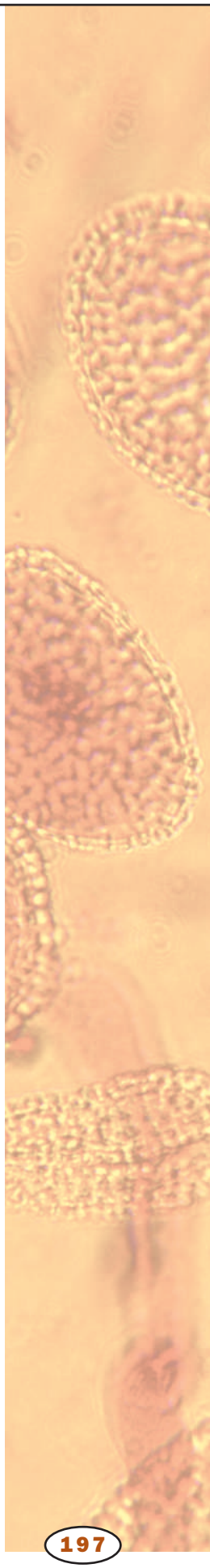
- the presence of surface water, at least part of the year
- unique soils that differ from adjacent uplands (due to the influence of waterlogging)
- plants adapted to wet soil conditions (hydrophytic vegetation)

There are many types of wetlands, differing in water chemistry, hydrology, soils, topography, climate, and vegetation. The broadest categories are coastal and inland wetlands. Coastal wetlands experience periodic flooding by saltwater or brackish water, and include estuaries (tidal marshes), mud flats, and mangrove swamps. They are nurseries for crustaceans, such as shrimp, and many fish species, and are also important habitat for birds and other wildlife. The presence of coastal wetlands can reduce inland erosion and other damage from hurricanes and winter storms.

Inland wetlands are freshwater wetlands and occur throughout the interior of a continent. These wetlands include: cattail marshes and wet meadows dominated by grasses, sedges, and herbs; swamps dominated by woody vegetation such as shrubs and trees; and peatlands (fens and bogs) that contain a buildup of peat, which forms as plants die and fall into the water and are not completely decomposed. The Florida Everglades are a vast inland wetland system.

A key factor determining what kind of soil and plant community develops in a wetland is the depth and duration of waterlogging and its effect on oxygen (O_2) in the soil. Soils that are waterlogged for any length of time become depleted of O_2 because soil microbes and plant roots use it during cellular respiration. The oxygen is not quickly replaced by O_2 from the atmosphere because O_2 diffuses very slowly through water. The anoxic (low oxygen) conditions influence soil development. Decomposition of plant litter and other **organic** matter is slowed in absence of O_2 and the wetland soils become high in organic matter. If decomposition is much slower than the production of plant matter, peat will form. Peatlands typically occur in northern climates where low average temperatures further slow decomposition.

organic composed of carbon, or derived from living organisms



Wetlands are important and valuable natural resources.

Since O_2 availability is a limiting factor for plants growing in wetlands, most wetland plants have structural adaptations that increase gas exchange. Some have spongy tissues, called aerenchyma, in their stems and roots that conduct O_2 within the plant from the aboveground shoot down to the roots. Others produce **adventitious** roots above the anoxic zone or have prop roots with pores that let in oxygen from the atmosphere.

adventitious growing from a nonstandard location

In the past, many people viewed wetlands as mosquito-infested wastelands needing to be drained. More than one-half of the original wetlands of the United States have been drained or otherwise altered. Now there is a public consciousness that wetlands are important and valuable natural resources. Wetlands improve water quality by removing and retaining nutrients from surface waters and trapping sediments. They reduce flood and storm damage, and act to control erosion of shorelines. They provide important habitat for fish, crustaceans, and other wildlife and produce natural products such as blueberries, cranberries, rice, mink, and beaver. They support hunting and fishing activities and provide other recreational and educational opportunities.

SEE ALSO Estuaries; Global Climate Change; Limnologist

Martha Phillips

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Wildlife Biologist

Wildlife biologists are scientists who study wild animals to understand how they interact with other animals and their habitat. They may also manipulate wildlife populations and their habitats (for instance, by planting food sources) in an effort to conserve these valuable resources. The job of a wildlife biologist involves a variety of outdoor activities such as observing, capturing, and measuring animals, or measuring and manipulating their habitats. An equally important part of the job involves developing management plans; collecting and analyzing data; documenting activities; and

Biologists take samples from a drugged polar bear for data about pesticides in the Hudson Bay area of Manitoba.

communicating with other professionals and the public. Private landowners occasionally hire wildlife biologists, but most are employed by federal or state fish and game agencies (e.g. Fish and Wildlife Service, Forest Service). In addition to a solid foundation in biology, a wildlife biologist needs a good background in chemistry and mathematics (especially statistics), and must be able to communicate clearly both orally and in writing. Anyone interested in a career as a wildlife biologist should earn a bachelor's degree in Wildlife Management and should also gain experience through part-time or seasonal employment in the field. Opportunities for career advancement are significantly enhanced by earning a master's degree and those individuals interested in research should consider acquiring a doctoral degree (Ph.D.). SEE ALSO BIODIVERSITY; CONSERVATION; ZOOLOGY; ZOOLOGY RESEARCHER

John H. Roese

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Wine-making, Biology of

Wine is made by fermenting fleshy fruits, principally the cultivated grape *Vitis vinifera* (family Vitaceae). Grapes are grown on farms called vineyards. Grapevines are trellised to improve air circulation and access to sunlight. When they are ripe, wine grapes are usually harvested by hand and then mechanically destemmed and crushed. The juice is then inoculated with yeast (*Saccharomyces cerevisiae*), which ferments the sugars in the grape juice to form ethyl alcohol, at a final concentration of 12 to 14 percent. White wine is made without the grape skins, whereas red wine uses the skin to give color to the wine. After fermentation, the wine is usually transferred to oak casks for finishing, or flavor development. Sparkling wines, such as champagne, are bottled before fermentation is complete, thus trapping some carbon dioxide in the bottle.

The flavor of wine is influenced by many factors, beginning with the soil and climate. Although most varieties of grapes are frost-hardy, the best wines come from regions with more moderate climates. Grapes grow well on rocky hillsides, but more level and richer soils also produce fine wines, as long as the ground drains well. The deep roots of the grapevine minimize the need for irrigation, and fertilizer is kept to a minimum to prevent overproduction of lesser-quality grapes. Weather during the growing season is critical to fruit set, grape development, and wine quality. The best harvests occur in years with plentiful rainfall early in the season, followed by a warm but not excessively hot summer and a dry harvest season. SEE ALSO AGRICULTURE; BEER-MAKING, BIOLOGY OF; COFFEE, BOTANY OF; GLYCOLYSIS AND FERMENTATION

Richard Robinson

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Wood and Wood Products

Wood and wood products have played a critical role in the evolution of humankind. From the most primitive of beginnings, humans have used wood for survival and to improve the quality of life. In the twenty-first century, people continue to use wood for many of the same purposes that their most ancient ancestors did. Fuel for heating and cooking is still the largest consumer of wood fiber. Construction of shelter and furniture is secondary as is pulp and paper production.

As a raw material, nothing else in history possesses the versatility of timber. On a volumetric basis, in the year 2000 worldwide annual consumption was between 3 and 4 billion cubic meters. To put this in perspective, if all of this wood was lashed together it could make a floating bridge 2 meters (6.54 feet) thick and 40 meters (131 feet) wide that stretches around the world at the equator. As evidence of wood's exceptional utility value, there are approximately 5,000 distinctly different types and applications of wood products in society.

As a raw material, wood has no equal peers. On a strength-to-weight ratio, wood is stronger than steel. Heavy timber has unique thermal insulating properties, which often allow it to retain structural integrity during building and warehouse fires that completely soften and deform structural steel members. While concrete has excellent structural properties, its density is so high that it is often ruled out as a building material. High shipping

A man walks across giant rollers used to crush wood pulp at the Ketchikan Pulp Company in Ketchikan, Alaska.

and handling costs associated with concrete limit its use to areas close in proximity to the raw mineral mines.

Petrochemical-based plastics offer new alternatives to wood use in construction but such plastics are not renewable. The energy requirements and pollution volumes associated with the production of each of these products is significantly higher than those levels associated with wood products conversion, often four to ten times greater. Additionally, of the materials concrete, plastic, steel, and wood, only wood is naturally renewable.

Forest to Lumber Yard

In the United States, most round wood (in the form of stems or logs) comes from managed forest land (both public and private). The growing population's demand for land, renewable raw materials, and environmental protection has pushed forest management and wood products production to become highly efficient and ecologically healthy. Most management strategies are geared toward multiple use; that is, recreation, wildlife, sporting, ecology, and other uses are included with timber production.

Both natural regeneration and manual replanting are used to restock forest land after timber harvesting. North America is rich with productive land on which to grow trees and with intellectual capital to promote the wise, efficient, and sustainable use of wood fiber. Third-party certification or "green" labeling is emerging as a means to assure wise and efficient forest management and timber conversion.

Also, approval by the International Standards Organization (ISO) is a key tool for companies involved in worldwide wood products trading. Companies that are able to gain wood certification and/or ISO approval have a distinct market advantage because consumers have assurance that the products or materials they consume have conformed to stringent manufacturing and sound environmental principles.

The techniques of timber conversion (turning trees into wood products) have been evolving for thousands of years. During the latter half of the twentieth century, conversion technology advanced exponentially. Computer power has been a key ingredient for optimizing production of wood products. Sawmilling (turning trees into lumber) has been practiced for hundreds of years. Formerly, only the biggest and best trees were cut and brought to mills, and people made decisions regarding how to cut these into lumber.

During the early 1900s, sawmill timber conversion efficiency was approximately 35 to 40 percent, meaning more than half of each trunk was wasted. In the twenty-first century, computers and automated equipment often make most of the decisions regarding how tree stems will be converted to products. The scanning and automation technology used in the forest products industry is the same as that used by the military and the automobile and aerospace industries. Development and application of such technology has allowed smaller and less valuable trees to be used for products.

Historically, the wood fiber that did not become lumber was burned or landfilled. Today, conversion efficiency can reach 70 percent. (There is always some inherent loss associated with turning round stems into rectan-

gular boards.) The residual chips and sawdust from sawmilling are turned into pulp for paper and particles for pressed wood composites. Bark is mainly used as fuel or mulch. The close alliance of these different industries can raise conversion efficiency to 100 percent.

The United Nation's Food and Agriculture Organization has reported that the world's overall forest area declined by 1.6 percent (140 million acres) between 1990 and 1995. Because of this sharp decline, there is a growing trend toward harvesting from plantation forests versus natural forests.

Wood Products

In addition to solid lumber production, there are a variety of composite wood products that have been developed. Plywood and laminated veneer lumber use thin sheets of wood veneer as lamina (layers) for panel-type and lumber-type products, respectively. The conversion efficiency associated with wood veneer production is higher than that of lumber production. Oriented strand products use thin wafers of wood as a raw material. In this case, low-grade trees are reduced to thousands of small strands, and the strands are subsequently pressed together with adhesive into panel products. When trees are reduced to strands, conversion efficiency is 90 to 95 percent. The only fraction not used for strands is the bark, which is converted to fuel or mulch.

Structural panel products like plywood and oriented strand board have revolutionized the building construction industry in the Americas and worldwide. Panel products allow rapid housing construction and provide many superior properties compared to the materials used previously. Nonstructural wood composites offer further utilization potential for wood fiber. Often using waste sawdust or shavings as raw materials, particleboard and medium-density fiber board are used extensively in the furniture and cabinet industry. These stable products are used as core materials for both low- and high-cost furniture. When used properly, each of these composite products offers advantages over traditional solid wood products. Dimensional stability, uniformity, long spans, and engineered strength enhancement are just a few such advantages.

The quest to develop stronger, straighter, and more efficient renewable products is ongoing. In an effort to better utilize agricultural byproducts, materials such as wheat straw, kenaf, cotton gin trash, and bagasse are being researched as supplemental fiber sources in wood-based composites. Advanced **hybrid** composites between wood and materials such as carbon fiber, plastics, and fiberglass have been investigated and are becoming more common in highly specialized structural materials. The level of information-sharing currently available through technology continues to foster the research and development of amazing products at a record pace. SEE ALSO Conifers; Forester

hybrid combination of two different types

Rubin Shmulsky

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Zoology

Zoology is a branch of biology that concentrates on the study of animals. The term comes from two Greek words: "zoon," which means "animal," and "logos," which means "the word about." Although the Greek philosopher Aristotle is sometimes called "the father of zoology," humans have always been interested in learning about animals, so it is difficult to say when zoology originated.

Because the animal kingdom is by far the largest and most varied of all the kingdoms, zoology is an extremely broad discipline. It includes such topics as the anatomy, physiology, **embryology**, genetics, and ecology of animals. It was natural, therefore, that this topic became subdivided as human knowledge increased. An early partition distinguished vertebrate zoology from invertebrate zoology, but because about 97 percent of all animals are invertebrates (spineless), that was not an appropriate distinction. While classical zoologists of the 1800s and 1900s were concerned largely with discovering new kinds of animals and describing their structure and their evolutionary relationships, twenty-first-century zoology focuses on understanding how different animals solve the common problems of survival (such as obtaining energy, coping with temperature changes, and coordinating behavior), a field known as comparative animal physiology. SEE ALSO ANIMALIA; BIOLOGY.

embryology development of the embryo

Margaret Simpson

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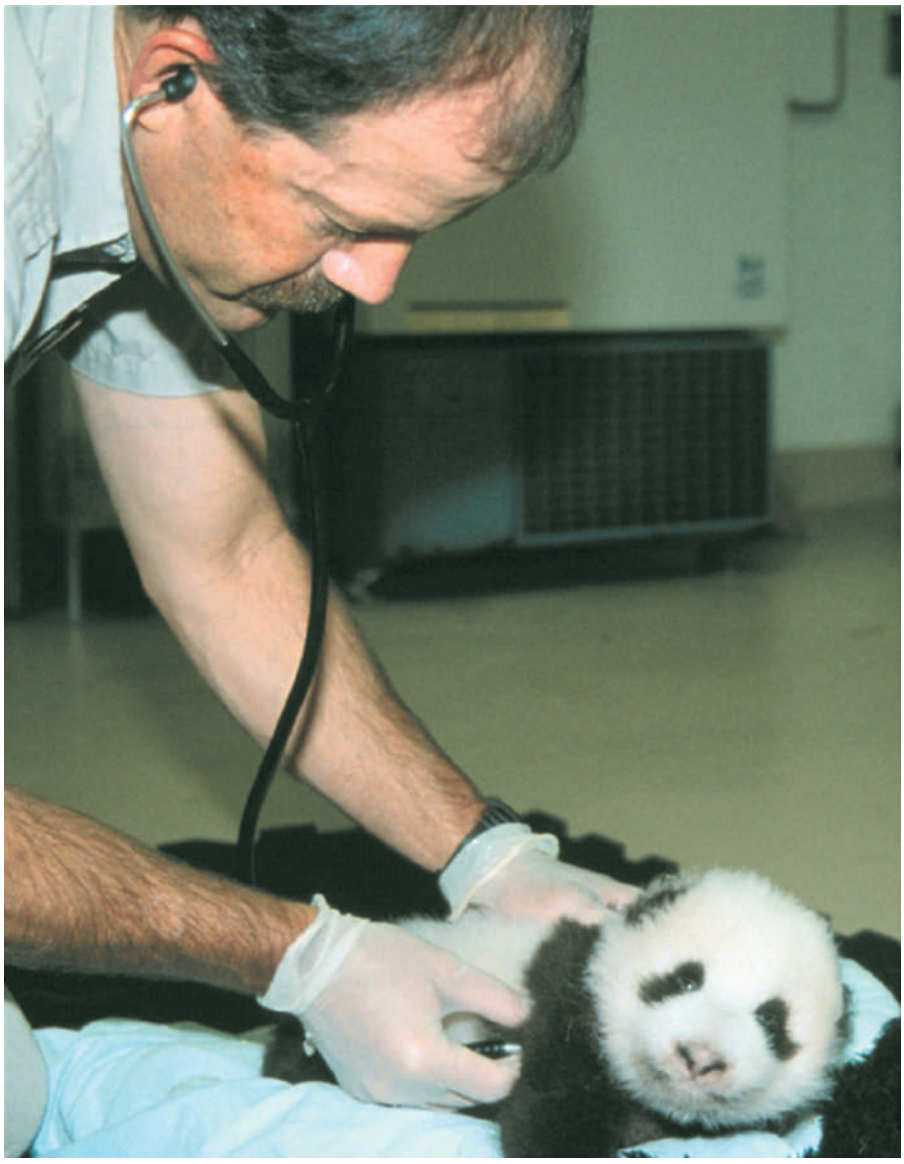
Zoology Researcher

A zoologist is a scientist who studies animals, whether slugs or spiders, rattlesnakes or ravens. Most zoologists work at universities where often they also teach biology. Others work as government biologists for the Forest Service or the U. S. Fish and Wildlife Service, for example. Others work for nonprofit environmental organizations or private companies that do environmental impact reports. A few write about science for the public.

Zoologists may study animals in a laboratory or in the wild. For example, a zoologist might go to Africa several times a year to study the social behavior of hyenas. The zoologist catches individual hyenas and puts collars on them that carry radio transmitters. Each transmitter emits a different signal, so the zoologist always knows where each hyena is. This not only allows the researcher to map the movements of each animal, but to find the animal when necessary.

Zoologists also breed animals in captivity. In captivity, animals rarely behave the same way that they do in the wild, but it is easier to do experiments under controlled conditions. Whether in the lab or in the field, zoologists study the behavior, evolution, ecology, and physiology of animals. Many zoologists study how one species interacts with another or how plants and animals "coevolve." Zoologists who study behavior or physiology often study animals mainly in a laboratory.



A zoo veterinarian examines the San Diego Zoo's female giant panda cub in October 1999.

Almost all zoologists have at least a bachelor's degree in biology, zoology, ecology, or a similar field. Many zoologists have a master of arts (M.A.) or a master of science (M.S.) degree. University and college professors almost always have a doctor of philosophy (Ph.D.). Often, zoologists who work for the government must pass an exam in a field such as wildlife biology. High school students interested in a career in zoology should take math classes, through calculus, and explore nearby natural areas, learning the names of the plants and animals. SEE ALSO BEHAVIOR PATTERNS; ENDANGERED SPECIES; FIELD STUDIES IN ANIMAL BEHAVIOR

Jennie Dusheck

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Volume 1

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photograph. © The Purcell Team/Corbis; **p. 81** Red-tailed hawk perched on stump, photograph by Robert J. Huffman/Field Mark Publications; **p. 83** Beaulieu, Emile-Etienne, holding handful of the RU-486 abortion drug/pills, which he invented, photograph. AP/Wide World Photos; **p. 90** Red and white blood cells flowing through saphenous vein, scanning electron micrograph. © Image Shop/Phototake; **p. 94** Cancellous bone tissue affected by osteoporosis, false-color scanning electron micrograph. © Professor P. Motta/Dept. of Anatomy/University of La Sapienza, Rome/Science Photo Library, Photo Researchers, Inc.; **p. 97** Axial section of human brain showing metastatic tumor, MRI by Simon Fraser. © Simon Fraser/Science Photo Library, Photo Researchers, Inc.; **p. 101** Human brain with hypothalamus highlighted, green dot, MRI scan by Scott Camazine & Sue Trainor; © Scott Camazine & Sue Trainor/Photo Researchers, Inc.; **p. 105** Liverwort, plant with leaf-like structures covered with tiny capsules, photograph. JLM Visuals; **p. 109** Marine life from Cambrian Period, photograph by Robert J. Huffman/Field Mark Publications; **p. 110** Human breast cancer cells growing in culture, photograph by Cecil Fox. © Cecil Fox/Photo Researchers, Inc; **p. 111** Human abdomen showing cancer of the ascending colon, colored barium enema X ray. © Science Photo Library/Photo Researchers, Inc.; **p. 116** Electronic image of human heart undergoing angiography; indicates massive aneurism of aortal arch, photograph. © CNRI/Phototake; **p. 119** Listeria monocytogenes, scanning electron micrograph image. © CNRI/Phototake; **p. 137** Tobacco leaf chloroplast, micrograph, photograph. © Dr. Jeremy Burgess/Science Photo Library, National Audubon Society Collection/ Photo Researchers, Inc. Reproduced with permission; **p. 141** Human chromosomes showing male mutation on gene 7, which determines cystic fibrosis, photomicrograph by Jean Claude Revy. © Jean Claude Revy/Phototake; **p. 142** Digital image of multipolar and bipolar spindles from T84 colonic cancer cell cultures, photograph. © Albert Tousson/Phototake; **p. 144** Mitosis metaphase of an animal cell, immunofluorescence photomicrograph. © CNRI/Phototake; **p. 146** Human male chromosomes, XY karyotype, with G banding, karotype. © CNRI/Phototake; **p. 153** Micro injection introducing foreign genes into animal cells, photograph by M. Baret. © M. Baret/Rapho, Photo Researchers, Inc; **p. 158** Second growth birch forest, photograph. © Richard P. Jacobs/JLM Visuals; **p. 161** Ground finch with dark feathers and bill, photograph by Tim Davis. Photo Researchers, Inc; **p. 163** Pine cones, photograph. JLM Visuals; **p. 167** People along polluted Swazambhunath River, in Kathmandu, Nepal, photograph. © Charlie Crangle/JLM Visuals; **p. 182** Sand skink on top of shiny dark green leaf, 1985, Florida, photograph by Joseph T. Collins/ Photo Researchers, Inc.; **p. 184** Stretch of the great coral reef, between Cairns and Townsville, photograph. © Yann Arthus-Bertrand/Corbis; **p. 187** Crick, Francis, photograph. The Library of Congress; **p. 189** Horseshoe crab, photograph. © John M. Burnley/The National Audubon Society Collection/Photo Researchers, Inc; **p. 192** Breast cancer cell dividing, colored scanning electron micrograph. © Quest/Science Photo Library, Photo Researchers, Inc.; **p. 198** Darwin, Charles, photograph. Popperfoto/Archive Photos. © Archive Photos, Inc.; **p. 202** Shadows form on the El Oued dunes, The Algerian Sahara Desert, Algeria, photograph. © Adam Woolfitt/Corbis; **p. 203** High desert oasis, photograph. © Richard P. Jacobs/JLM Visuals; **p. 205** Human embryo, 8-cell stage, day 3, scanning electron micrograph, SEM, scan by Dr. Yorgos Nikas. © Dr. Yorgos Nikas/ Phototake; **p. 209** Frog embryos complete their metamorphoses inside their eggs, photograph. Michael & Patricia Fogden/Corbis; **p. 224** Human DNA fingerprint taken from blood to match donor and patient in organ transplantation, photograph. © Index Stock/ Phototake; **p. 227** Herpes simplex virus, HSV6, scanning electronic micrograph. © Dr. Dennis Kunkel/Phototake; **p. 230** Surgeon looking at CAT scans, photograph. © Steve Chenn/Corbis; **p. 233** Lab technician Li Zhang performing a density test from urine samples at the Australian Sports Drug Testing Laboratory, photograph. AP/Wide World Photos.

Volume 2

p. 6 Professor Ernst Haeckel, the German naturalist and philosopher, poses as if in a jungle scene, photograph. © Hulton-Deutsch Collection/Corbis; **p. 9** Lush growth, mossy tree, temperate rain forest, photograph by Robert J. Huffman/Field Mark Publications; **p. 12** Scientist sitting at scanning transmission electron microscope, STEM, photograph by Sinclair Stammers/Science Photo Library/Photo Researchers, Inc.; **p. 14** Gloved hands holding a sheet/culture, electrophoresis gel, photograph. © Eurelios/Phototake; **p. 17** White tiger in the zoo, photograph. © Shawn Gerrits/JLM Visuals; **p. 21** Scintigram of normal human thyroid, front view, photograph. © CNRI/Phototake; **p. 23** Phagocytosis, color enhanced transmission electron micrograph. © Biophoto Associates/Science Source/Photo Researchers, Inc; **p. 27** Entomologist Elidia Fernandez sorts an insect collection for the Institute for Biodiversity, photograph. © Gary Braasch/Corbis; **p. 39** Ravenglass Estuary curving to the sea, Cumbria, England, photograph. Corbis/Genevieve Leaper; **p. 41** Chlamydia pneumonia, photograph by Dr. Kari Lounatmaa. Custom Medical Stock Photo; **p. 42** Escherichia Coli, photograph by Kari Lounatmaa. Photo Researchers; **p. 44** Bumble bee, photograph. © Lloyd R. Brockus III/JLM Visuals; **p. 46** Darwin's Large Cactus Finch, © Breck P. Kent/ JLM Visuals; **p. 50** Antibiotic Staphylococcus aureus, photograph by Hank Morgan. © Hank Morgan/Science Photo Library, Photo Researchers, Inc.; **p. 53** Fossil fish, photograph. © Richard P. Jacobs/ JLM Visuals; **p. 58** Ginkgo tree, photograph. JLM Visuals; **p. 60** X ray, color enhanced normal intravenous pyelogram. © Biophoto Associates/Science Source/Photo Researchers, Inc; **p. 65** Dinosaur skeleton on display at the Royal Terrell Museum, photograph. © Paul A. Souders/Corbis; **p. 67** Carolina parakeets lie in bags with tags, photograph. © Jonathan Blair/Corbis; **p. 73** Rod cells in the retina of the human eye, colored scanning electron micrograph. © Quest/Science Photo Library, Photo Researchers, Inc.; **p. 77** Normal human uterus and fallopian tubes, hysterosalpinograph. © GCA/CNRI/Phototake; **p. 83** Human fetus, 10 weeks old, inside amniotic sac, photograph. © CNRI/Phototake; **p. 86** Gray wolves exhibiting submissive behaviors, photograph. © Mary Ann McDonald/Corbis; **p. 88** Agronomists place a plastic greenhouse over crops, photograph. © Ted Spiegel/ Corbis; **p. 90** Despain, Don, measures Lodgepole Pine Seedlings, photograph. © Raymond Gehman/Corbis; **p. 94** Snapdragons in flower, photograph by Eric Kamp. © Eric Kamp/Phototake; **p. 95** Lab Agent Kathy Dressel works on DNA evidence in the murder of JonBenet Ramsey at the Colorado Bureau of Investigation, Boulder, Colorado, photograph. AP/Wide World Photos; **p. 98** Boreal forest, evergreen trees, Michigan, photograph. JLM Visuals; **p. 100** Oak/hickory trees in autumn, photograph by Robert J. Huffman/Field Mark Publications; **p. 102** Moss-covered lianas in the Daintree National Park, Queensland, Australia, photograph. © Paul A. Souders/Corbis; **p. 103** Agile gibbon hanging from tree branch with baby at waist, photograph. © Breck P. Kent/JLM Visuals; **p. 105** Strawberry plants with fruit and blossoms, photograph. © Ed Young/Corbis; **p. 111** Dark yellow Witches' Butter jelly fungus, photograph. © Richard P. Jacobs/JLM Visuals; **p. 113** Detail that shows the gills of a mushroom, photograph. © Laura Sivell; Papilio/Corbis; **p. 114** Salmon gills showing the filaments of the gills, photograph. © Ron Boardman; Frank Lane Picture Agency/Corbis; **p. 124** Cancer cells infected with bioengineered adenovirus, photograph by Jean Claude Revy. © Jean Claude Revy/Phototake; **p. 132** Chicken embryo, 96-hours old, photograph. © Richard P. Jacobs/JLM Visuals; **p. 142** Man using computer to design complex proteins, photograph by Richard Nowitz. © Richard Nowitz/Phototake; **p. 147** Mexico City, photograph. Reuters/Archive Photos; **p. 154** Piles of wheat during harvest, Polouse Valley, Washington, photograph. © Vince Streano/Corbis; **p. 157** Grassland, photograph. © Richard P. Jacobs/JLM Visuals; **p. 159** Baby smiling, photograph. © Simon Dearden/Corbis; **p. 160** Hand development of a 2, 6, and 19 year old male, computer color enhanced X ray by Scott Camazine. © Scott Camazine, Photo Researchers, Inc.; **p. 162** Cycad, photograph. JLM Visuals;

p. 166 Harvey, William, photograph. U.S. National Library of Science; **p. 167** Bicyclist sitting under a shade tree, photograph by Robert J. Huffman/Field Mark Publications; **p. 170** Hearing, human system, diagram by Hans & Cassidy. Gale Group; **p. 173** Heart, diagram by Hans & Cassidy. Gale Group. **p. 178** Close-up of branch with very long thorns, photograph. © Richard P. Jacobs/JLM Visuals; p. 181 Close-up of genetically manipulated corn, photograph. © Carolina Biological Supply Company/Phototake; **p. 183** Buchner, Eduard, photograph. Hulton-Deutsch Collection/Corbis; **p. 186** Microscope used by Robert Hooke, 17th century, photograph. © Bettmann/Corbis; **p. 189** Young girl on her father's shoulders, photograph. © Raoul Minsart/Corbis; **p. 193** Cuvier, Georges Leopold, photograph. The Library of Congress; **p. 199** Hales, Stephen, engraving. The Library of Congress; **p. 209** Beginnings of Civilization, map by XNR Productions Inc. Gale Research; **p. 213** Female researcher loading an automated DNA sequencer at the Joint Genome Institute, photograph. Photo Researchers; **p. 215** Computer print-out of sequence of DNA, placed below multi-well sample tray, upper left, and automated pipettes, lower right, illustration by © James King-Holmes/Science Photo Library. Photo Researchers; **p. 217** Ingredients that should make up the bulk of a healthy diet, including fruits, vegetables, whole grains, photograph. © Nathan Benn/Corbis; **p. 221** Tomatoes ripen on vine for market, photograph. © Ed Young/Corbis.

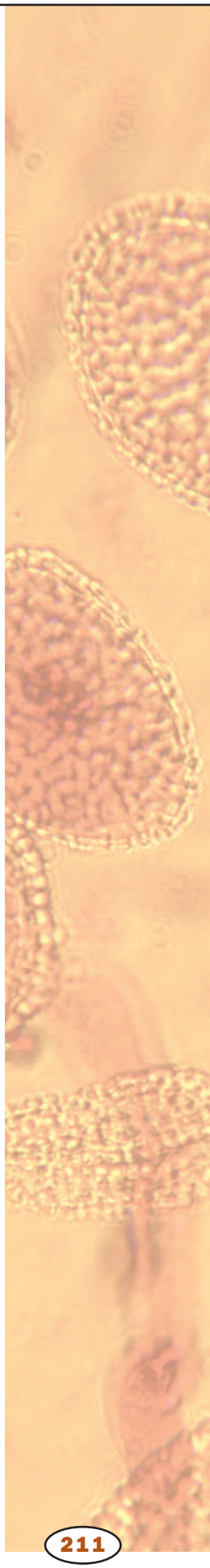
Volume 3

p. 2 Human brain, cervical spine, and spinal marrow, magnetic resonance imaging (MRI). © GCA/CNRI/Phototake; **p. 6** Cancer cell attacked by tumor infiltrating lymphocytes, scanning electron micrograph by Jean Claude Revy. © Jean Claude Revy/Phototake; **p. 8** Katydid on human hand, photograph. JLM Visuals; **p. 11** House and hill overgrown with kudzu, photograph. JLM Visuals; **p. 22** Canadian Rockies, Ben My Chreem, Yukon, photograph. © Lowell R. Laudon/JLM Visuals; **p. 26** Leakey, Dr. L.S.B and Mary, photograph. AP/Wide World Photos, Inc; **p. 27** Young girl fits blocks of different shapes through similarly shaped holes in a red box, photograph. © Robert Kozma/Corbis; **p. 30** Spine of Cleistocactus, close-up, photograph. © Peggy Morsch/JLM Visuals; **p. 32** Golden lichen, photograph. © Don Blegen/JLM Visuals; **p. 33** Grandmother holding her grandson, Philadelphia, PA, photograph. © Ed Eckstein/Corbis; **p. 36** Spawning sockeye salmon run the Fraser River from Shushwap Lake to Adams River, photograph. © Stuart Westmorland/Corbis; **p. 38** Chicken embryo, 56-hours old, photograph. © Richard P. Jacobs/JLM Visuals; **p. 40** Microscope, parts labeled, photograph. Carolina Biological Supply Company/Phototake; **p. 52** Two Ceratium tripos, photomicrograph by Eric Grave. © Eric Grave/Phototake; **p. 53** Lymphangiography, diagram of man's body, illustration. Electronic Illustrators Group; **p. 57** Human testis showing spermatogenesis, photomicrograph by Ken Wagner. © Ken Wagner/Phototake; **p. 61** Marine biologist in diving suit inspecting coral reef damaged by illegal fishing practices, photograph. AP/Wide World Photos**;** **p. 63** Male frigatebird with its red throat pouch inflated, photograph. © Wolfgang Kaehler/Corbis; **p. 64** McClintock, Barbara, photograph. UPI/Corbis-Bettmann; **p. 70** Transmission Electron Micrograph, TEM, image of Golgi apparatus, photograph. © Dr. Dennis Kunkel/Phototake; **p. 80** Mendel, Gregor, photograph. Archive Photos, Inc; **p. 86** Two lysomes that contain digestive enzymes which destroy damaged molecules; in an intestinal epithelial cell, colored high resolution scanning electron micrograph. P. Motta & T. Naguro/Science Photo Library/Photo Researchers, Inc; **p. 89** Fat cells that make up adipose connective tissue, colored scanning electron micrograph. © Quest/Science Photo Library, Photo Researchers, Inc; **p. 90** Quality control microbiologist Kim Egger inspects a bacteria culture from ground meat processed at Excel Corporation's slaughterhouse, photograph. AP/Wide World Photos; **p. 93** Spring tide of surfbirds surge from the mud flats of Alaska's Copper River delta, photograph. © Jonathan Blair/Corbis; **p. 94** Indian leaf butterfly, photograph. © Richard P. Jacobs/JLM Visuals; **p.**

99 Mitosis of an animal cell, early prophase, photograph. © CNRI/Phototake; **p. 100** Mitosis of an animal cell, early metaphase, photograph. © CNRI/Phototake; mitosis of an animal cell, immunofluorescence photomicrograph. © CNRI/Phototake; mitosis telophase of an animal cell, photograph. © CNRI/Phototake; **p. 101** Fruit fly head, magnified 200 times, scanning electron micrograph. © Dr. Dennis Kunkel, Phototake; **p. 104** Hands holding lab mouse, photograph. © Mario Beauregard/Corbis; **p. 107** Eastern prairie fringed orchid, photograph. U.S. Fish and Wildlife Service; **p. 114** Human knee joint with patella, X ray. © CNRI/Phototake; **p. 116** White American alligator shows a genetic mutation known as ieucism, Miami Zoo, photograph. © W. Perry Conway/Corbis; **p. 118** African clawed frog, Xenopus laevis, mutated, with three hind legs, photograph by Mark Smith. © Mark Smith/Science Source/Photo Researchers, Inc.; **p. 120** Endotrophic mycorrhizae in orchid root, magnified 100x, photograph. © Carolina Biological Supply Company/Phototake; **p. 122** Eggs and spiderlings of Uloborid Spider, photograph. © J. C. Cokendolpher/JLM Visuals; **p. 130** Human brain with Parkinson's Disease showing atrophy, Computerized Axial Tomography, CAT, scan. © GJLP/CNRI/Phototake; **p. 134** Two types of neurons; top of image shows a bipolar neuron, bottom of image is a developing neuron, scanning electron micrograph. © Dr. Dennis Kunkel/Phototake; **p. 137** Nitrogen fixation, bacteria, plants, photograph. © Adam Hart-Davis, National Audubon Society Collection/Photo Researchers, Inc.; **p. 139** Macrophage engulfing a Leishmania sp. parasite, colored scanning electron micrograph. © Juergen Berger, Max-Planck Institute/Science Photo Library, Photo Researchers, Inc.; **p. 142** Single mammalian tissue culture cell, color transmission electron micrograph. Dr. Gopal Murti/Science Photo Library/Photo Researchers, Inc.; **p. 149** Loh, Dan, photograph. AP/Wide World Photos; **p. 151** Anemone, Tunicate, Oyster, and Sponge, photograph. © Stephen Frink/Corbis; **p. 152** Bottlenosed dolphin playing, photograph. © Stephen Frink/Corbis; **p. 155** Blood smear showing leukemia cells, photomicrograph. © Margaret Cubberly/Phototake; **p. 160** Hand wearing glove, holding worms, compost sits below, photograph by Robert J. Huffman/Field Mark Publications; **p. 164** Meteorite ALH84001, from Mars, 4.5 billion years old, photograph. National Aeronautics and Space Administration (NASA); **p. 172** Larson, Peter, running fingers over teeth of a Tyrannosaurus rex skeleton, photograph. AP/Wide World Photos; **p. 175** Dog hookworms in small intestines, photograph. © Michael L. Wolmack/JLM Visuals; **p. 178** Young native boy with blonde hair trait, Lubaria Island, Solomon Islands, photograph. © Wolfgang Kaehler/Corbis; **p. 183** Micrograph comparing healthy red blood cells with a sickle cell, photograph by Dr. Gopal Murti. National Audubon Society Collection/Photo Researchers, Inc.; **p. 190** Diagram showing the central and peripheral nervous systems, left, and the autonomic nervous system, right, illustration by Frank Forney; **p. 192** Scientist performing pharmacological research, photograph. © Bob Krist/Corbis; **p. 194** Cecropia moth, photograph. Robert J. Huffman/Field Mark Publications; **p. 203** Dromedary camel, photograph. © Leonard Lee Rue, III/The National Audubon Society Collection/Photo Researchers, Inc.; **p. 206** Marine Plankton, green organisms with orange spots, 1960-1995, photograph by Douglas P. Wilson. Corbis/Dougals P. Wilson; Frank Lane Picture Agency; **p. 226** Digitalis, photograph. © Ken Wagner/Phototake; **p. 227** Release of pollen from anther of a black walnut, photograph. © Yoav Levy/Phototake; **p. 230** Closed General Electric plant in Pittsfield, Massachusetts, on the Housatonic River, photograph. AP/Wide World Photos; **p. 237** Cheetah, photograph. Robert J. Huffman/Field Mark Publications.

Volume 4

p. 2 Peregrine falcon with wings outstretched, photograph by Tim Davis. Photo Researchers, Inc.; **p. 3** School of fish swimming above blue and green coral reef, Indian Ocean, off Pemba Island, 1991, photograph by Stephen Frink. Corbis/Stephen Frink; **p. 21** Dinoflagellate gambierdiscus toxicus, scanning electron micrograph by Dr. Dennis



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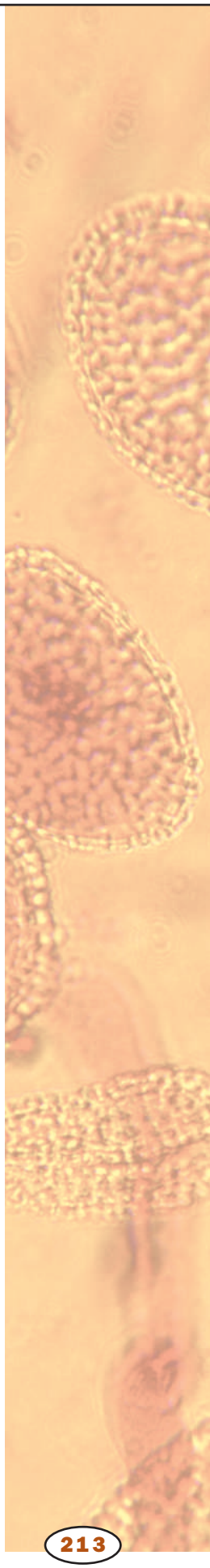
AP/Wide World Photos; **p. 188** T4 bacteriophage virus, colored transmission electron micrograph. © Department of Microbiology, Biozentrum/Science Photo Library/Photo Researchers, Inc.; **p. 189** Compound eye of a fruit fly, scanning electron micrograph, SEM. © Dr. Dennis Kunkel; **p. 194** Drop of guttation, water extruded by a plant's root pressure, on a blade of grass. Alpine Lakes Wilderness Area, Washington, photograph. © Pat O'Hara/Corbis; **p. 196** Watson, Dr. James Dewey, with DNA model, 1962, photograph. UPI/Corbis-Bettmann; **p. 198** Dead tree trunks, stumps in deep blue water, golden leaves, photograph by Robert J. Huffman/Field Mark Publications; **p. 199** Biologists take samples from drugged polar bears for data about pesticides, photograph. © Galen Rowell/Corbis; **p. 201** Man walks across giant rollers used to crush wood pulp at the Ketchikan Pulp Company, photograph. © Kevin Fleming/Corbis; **p. 205** Zoo veterinarian Don Janssen examining the San Diego Zoo's 2-week old giant panda cub, photograph. AP/Wide World Photos.



Glossary

abiotic nonliving

abscission shedding of leaves; falling off

acetylation addition of an acetyl group, CH_3-CHOO-

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

acinus one of the small divisions of a fruit such as a raspberry

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

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

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

adhesion attachment; sticking to the surface of

ADP adenosine diphosphate, the low-energy form of ATP

adventitious growing from a nonstandard location

aerobe organism that needs oxygen

aerobic with oxygen, or requiring it

aestivating remaining dormant for the summer

affinity attraction

aflatoxin toxic compound produced by a mold fungus

agar gel derived from algae

agnosia "not knowing"; loss of ability to recognize familiar objects

agroecosystem agricultural ecosystem

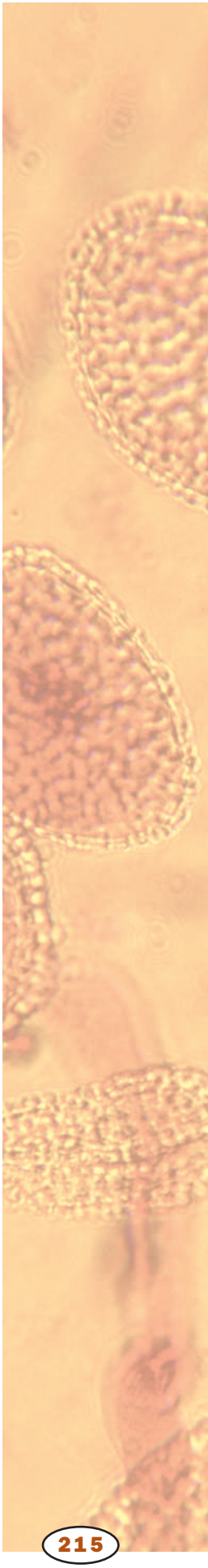
alkaline chemically basic, with an excess of OH- ions

allele a particular form of a gene

allelopathy inhibition of one plant's growth by another plant

amino acid a building block of protein

amoeba a single-celled protist that moves by crawling



amoeboid like an amoeba, especially in movement via extension of portions of the membrane

AMP adenosine monophosphate, form of ATP after removal of two phosphate groups

amphipathic having both polar and nonpolar regions

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

anadromous describes fish that return to the rivers where they were born in order to breed

anaerobe organism not needing oxygen

anaerobic without oxygen, or not requiring oxygen

anemia lack of oxygen-carrying capacity in the blood

aneurysm bulging of the wall of a blood vessel

antagonism working against

antagonist muscle muscle that works against the action undertaken

anterior toward the front

anterograde forward

anthocyanins colored compounds made by plants

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

antibody immune system protein that binds to foreign molecules

antigen foreign substance that provokes an immune response

antioxidant substance that prevents damage from oxidation

antitoxin molecule used to inactivate a toxin

aphasia loss of the ability to form ideas into words

apical at the tip

apical meristem growing tip from which all plant tissues arise

appendage attached organ or structure

aqueous watery or water-based

areolar related to a small space within a tissue

aromatic compound including a double-bonded carbon ring

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

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

asymptomatic without symptoms

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

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

attenuation lessening over time

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

autonomic independent; regulating involuntary actions

autonomic nervous system one of the branches of the motor system, controlling involuntary muscles and glands

autosomal dominant pattern of inheritance in which inheritance of a single allele from either parent results in expression of the trait

avian concerning birds

axon long extension of a nerve cell down which information flows

B lymphocyte white blood cell that makes antibodies

B.C.E. before the Common Era, equivalent to B.C.

basal lowest level

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

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

bilaterally symmetric symmetric, or similar, across a central line

bilayer composed of two layers

bioaccumulate build up within organisms

bioluminescence production of light by biochemical reactions

biopharmaceuticals drugs produced by and harvested from living organisms

biosynthetic forming a complex molecule from simpler ones

biotic living

bolting sudden spurt of growth

boreal of, relating to, or located in northern regions

brood parasite organism of one species that lays its eggs in the nest of another species

C4 and CAM plants plants that employ accessory systems for trapping carbon for photosynthesis

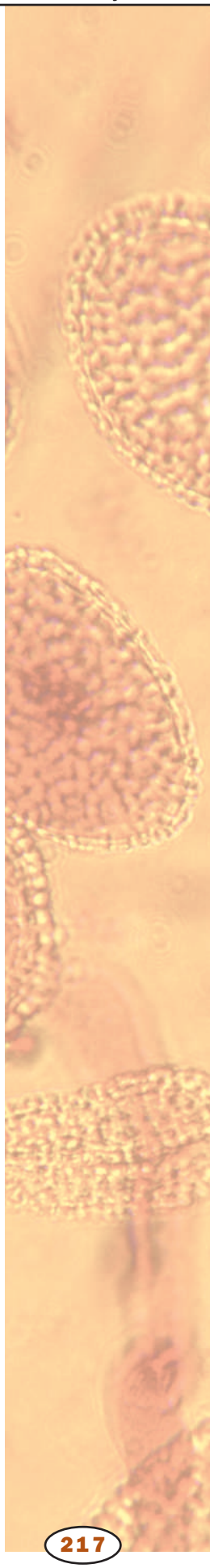
cadherins family of calcium-dependent adhesion proteins

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

cardiomyopathy heart muscle disease

catalysis aiding in the reaction of

catalyst substance that aids in a reaction without being used up



catalyze aid in the reaction of

caudate toward the tail

C.E. Common Era; equivalent to AD

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

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

central nervous system brain and spinal cord

centromere region of the chromosome linking chromatids

cerebral cortex outermost wrinkled portion of the brain

chemiosmosis use of proton gradients to make ATP

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

chromatid a replicated chromosome before separation from its copy

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

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

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

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

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

circadian related to a day or daylength

clavicle collar bone

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

codon sequence of three mRNA nucleotides coding for one amino acid

cognition mental processes of thought and awareness

cognitive related to thought or awareness

communicable transmissible from person to person

complementary matching opposite

complex carbohydrate molecules formed by linking simpler carbohydrates such as sugars

condensation compaction of chromosome strands into a tight structure

conformation three-dimensional shape

congenital present at birth; inherited

conjunctiva eye membrane that helps seal the eye socket

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

consanguineous descended from the same ancestor

constitutive at a constant rate or continually

contiguous adjacent to or touching

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

coralloid resembling coral

coronary artery artery supplying blood to the heart

cortical related to the cortex, or outer portion

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

cranial related to the cranium, or brain cavity

cryptobiosis when a plant or animal becomes so inactive that its life processes nearly come to a stop

cutaneous related to the skin

cutaneous respiration gas exchange through the skin

cytology study of cells

cytoplasm material in a cell, excluding the nucleus

cytoskeleton internal scaffolding in a cell, composed of protein

cytosol fluid portion of a cell, not including the organelles

Darwinian fitness capacity to survive and reproduce

deciduous trees that shed their leaves in the fall

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

dementia neurological illness characterized by impaired thought or awareness

desiccation drying out

desynchronized not happening at the same time

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

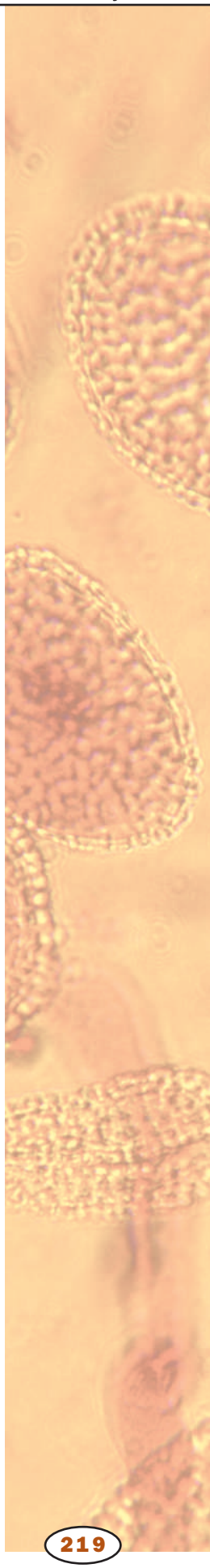
dialysis cleansing by partial filtration

dicot plant having two cotyledons, or seed leaves

dikaryotic cell cell with a pair of nuclei

dilation expansion or swelling

dimer polymer formed from two molecules of a simple compound



dimerizes forms a pair

diploid having pairs of chromosomes in the nucleus

dissociate break apart

distal away from

diurnal active during the daytime

dorsal to the back of

ecosystem an ecological community and its environment

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

efferent conducting outward or directing away from

electrolytes ions in body fluids

electromagnetic radiation light, X rays, and other forms of radiant energy

electron transport system membrane-bound system of proteins that extracts energy from high-energy electrons, found in mitochondria and chloroplasts

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

electrophoresis gel porous medium through which molecules can be separated using an electric current

embalming treating a dead body to protect it from decay

embryology development of the embryo

emulsify suspend in solution through interaction with soap or similar molecules

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

endogenous caused by factors inside the organism

endometriosis disorder of the endometrium, the lining of the uterus

endoplasmic reticulum network of membranes within the cell

endosperm nutritive tissue within a seed

endosymbiosis symbiosis in which one partner lives within the other

endothermic characterized by regulation of body temperature through metabolic activity

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

enzymatic related to the function of an enzyme

enzyme protein that controls a reaction in a cell

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

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

epithelium one of four tissue types found in the body, characterized by thin sheets and usually serving a protective or secretory function

esophagus tube connecting the throat to the stomach

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

eukaryotic cell a cell with a nucleus

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

evapotranspiration loss of water from a plant by evaporation within the leaf

evidentiary DNA profile analyzed DNA from a sample used as evidence

excrete deposit outside of

exocrine gland gland that secretes substances to an external or internal surface rather than into the bloodstream

exoskeleton external skeleton

extensibility ability to expand or grow larger

fallopian tubes tubes through which eggs pass to the uterus

fecundity ability to reproduce

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

fertilization union of sperm and egg

fibroblast undifferentiated cell normally giving rise to connective tissue cells

filtrate material passing through a filter

focal at a point

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

food web set of feeding relations in an ecosystem

forb broad-leaved herbaceous plant

forensic related to legal proceedings

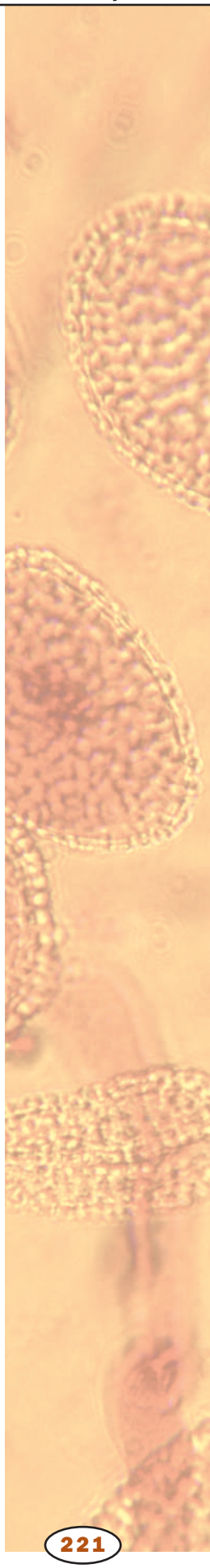
fulcrum pivot point of a lever

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

gamete reproductive cell, such as sperm or egg

gametophyte a haploid plant that makes gametes by mitosis

ganglia cluster of nerve cell bodies



gastroenteritis inflammation of the gastrointestinal tract, often from infection

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

gene expression use of a gene to create the corresponding protein

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

genitalia reproductive organs

genome total genetic material in a cell or organism

germ line cells creating eggs or sperm

gestation period of fetal development within the mother

glial supporting tissue of the elements of nervous tissue, including the brain, spinal cord, and ganglia

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

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

glycolysis initial stages of sugar breakdown in a cell

gradient difference in concentration between two places

grafting attachment and fusing of parts from different plants

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

gymnosperms "naked seed" plants, including conifers

hallucination altered sensory experience resulting in the perception of objects that are not real

haploid having single, nonpaired chromosomes in the nucleus

hectare 10,000 square meters (2.47 acres)

heme the deep red, iron containing, nonprotein portion of hemoglobin and myglobin

hemicellulose complex carbohydrate related to cellulose and found in cell walls of plants and some other organisms

hemoglobin oxygen-carrying protein complex in red blood cells

herbarium a collection of dried plant specimens systematically arranged for reference

hermaphrodite organism possessing both male and female reproductive structures

heterodimer complex molecule composed of two different parts

heterogeneous composed of, or containing, different parts or types

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

hexamer a structure composed of six parts

histogenesis origin or production of tissues

histology study of tissues

histone protein around which DNA wraps to form chromosomes

homologous similar in structure

homologous chromosomes chromosomes carrying similar genetic information

homologous recombination exchange of DNA segments between chromosomes

homozygous containing two identical copies of a particular gene

hormone molecule released by one cell to influence another

hybrid combination of two different types

hydrocarbon molecule or group composed only of C and H

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

hydrolyze to split apart using water

hydrophilic "water loving"

hydrophobic "water hating," such as oils

hydroponics growing of plants without soil

hydroxyl chemical group consisting of -OH

hypersalinity very high level of salt

hypersecretion excess secretion

hypersensitivity reaction immune reaction characterized by rapid and severe response, often with swelling of airways

hyphae threadlike part of the vegetative portion of the fungus

hyposecretion lack of secretion

hypothermia subnormal temperature of the body

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

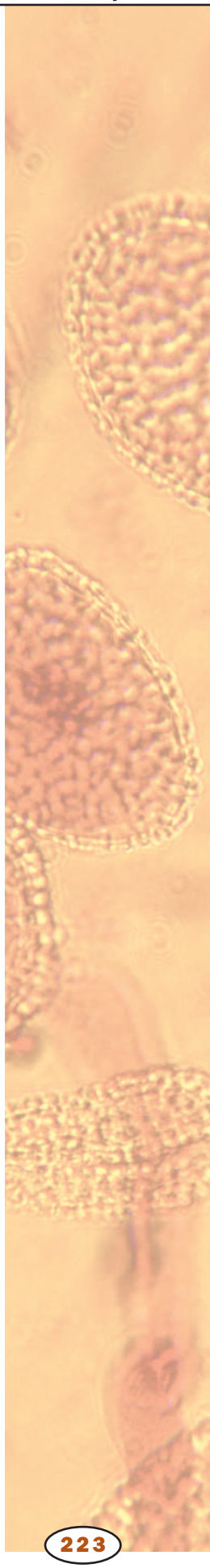
immunoglobulin an immune protein, also called an antibody

immunosuppressant inhibition of the immune response

in utero inside the uterus

in vitro "in glass"; in lab apparatus, rather than within a living organism

inbred repeatedly bred with close relatives, creating organisms with very little genetic variation



inducible able to be switched on

inflorescence characteristic arrangement of flowers on a stalk

infrastructure roads, phone lines, and other utilities that allow commerce

inorganic not bonded to carbon

insectivorous insect-eating

integrins a family of transmembrane linking proteins

interferons signaling molecules of the immune system

intermediate filament protein one type of cytoskeleton protein

interspecific between different species

interstitial space space between cells in a tissue

intracellular within a cell

intraocular within the eyeball

intrinsic to intimate part of; within

intron untranslated portion of a gene that interrupts coding regions

ion an electrically charged particle

ionic based on or functioning by means of ions

ionizing radiation high-energy radiation that destroys chemical bonds

isometric relating to contraction without movement

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

keratin a major structural protein

kilobase one thousand DNA bases; a measure of size of a piece of DNA

kilobasepair one thousand DNA base pairs; a measure of size of a piece of DNA

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

Krebs cycle central metabolic pathway in mitochondria

lactation production of milk by the mammary glands

laparoscopic surgery surgery in which an instrument is inserted through a very small incision, usually guided by some type of imaging technique

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

lateral side-to-side

lethargy lack of excitability; torpor

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

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

lineage ancestral line

lipid fat or waxlike molecule, insoluble in water

lipoprotein combination of protein and lipid, or fatlike molecule

locus site on a chromosome (plural, loci)

lotic of, relating to, or living in actively moving water

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

lymphatic system network of tubes that permeates the body for transport of lymph and combat of infection

lymphocyte white blood cell found in lymph nodes

lyse break apart

lysine an amino acid

lysing disintegration or dissolution of cells

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

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

materialism the belief that life is due entirely to biochemical interactions, without the intervention of supernatural forces

matrix a network, usually of threadlike fibers

medium nutrient source

meiosis cell division that forms eggs or sperm

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

metabolism chemical reactions within a cell

metabolite molecule involved in a metabolic pathway

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

metaphase intermediate stage in cell division, in which chromosomes line up before separating

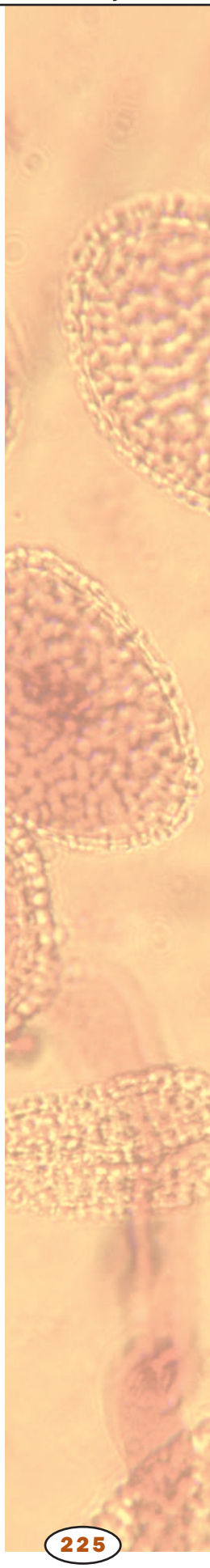
metastasis breaking away of cancer cells from a solid tumor to travel elsewhere in the body

metazoans animals other than sponges

methylation addition of the methyl group CH_3

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

mid-dorsal middle of the back



middle lamella layer of material between two plant cells that holds them together

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

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

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

mitogen substance that stimulates mitosis

mitosis separation of replicated chromosomes

molecular hybridization base-pairing among DNAs or RNAs of different origins

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

monoculture cultivation of a single type of crop in a large area

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

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

montane mountainous region

morphology related to shape and form

motile able to move

motor neuron nerve cell that controls a muscle or gland

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

multimer composed of many similar parts

multinucleate having many nuclei within a single cell membrane

muscle tone low level, constant muscle contraction

mutualism symbiosis between two organisms in which both benefit

mycorrhizae symbiosis between soil fungus and plant root to maximize absorption

myxedema thyroid disorder characterized by dry skin, swelling in the face, and mental deterioration

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

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

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

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

neritic zone near the shore

neural related to nerve cells or the nervous system

neurologist doctor who treats brain disorders

neuron nerve cell

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

niche the habitat supplying the right environment for a particular species

nm nanometer; one-billionth of a meter

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

nondisjunction failure of separation of homologous chromosomes during meiosis

nuclear envelope double membrane surrounding the cell nucleus

nucleated having a nucleus

nucleotide the building block of RNA or DNA

nucleus membrane-bound portion of cell containing the chromosomes

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

octomer composed of eight parts

oligosaccharide chain of several sugar molecules

oncogene gene that causes cancer

oocyte unfertilized egg

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

organelle membrane-bound cell compartment

organic composed of carbon, or derived from living organisms; also, a type of agriculture stressing soil fertility and avoidance of synthetic pesticides and fertilizers

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

osseous related to bone

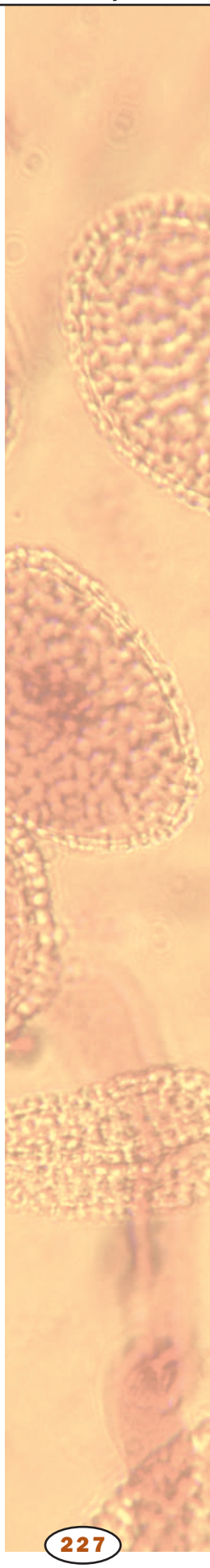
outcross fertilization between two different plants

ovipary production of eggs that hatch outside the body

ovovivipary production of eggs that hatch within the female's body

ovule multicellular structure that develops into a seed after fertilization

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



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

oxidative characterized by oxidation, or loss of electrons

oxidative phosphorylation use of oxygen to make ATP

oxidize to react or make react with oxygen

palatine bone bone of the hard palate at the roof of the mouth

paleoanthropology study of ancient humans

palindromic reading the same forward and backward

pandemic disease spread throughout an entire population

papillate small, nipplelike projection

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

parasitology study of parasites

parasympathetic nervous system branch of the nervous system promoting nutrient absorption and other maintenance activities

pathogen disease-causing organism

pathogenesis pathway leading to disease

pathologic related to disease

pectin carbohydrate in plants that forms crosslinks to stabilize cell walls

peptide bond bond between two amino acids

peptidoglycans polymer that is composed of polysaccharides and peptic chains

perianth combined sepals and petals

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

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

phage short for bacteriophage

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

pharynx throat

phase-contrast microscopy technique that manipulates passage of light through transparent specimens to reveal internal features

phenotype observable characteristics of an organism

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

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

phosphodiester the link between two nucleotides in DNA or RNA

phosphorylate add a phosphate group to

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

phyletic gradualism the belief that evolutionary change is slow and steady

phylogenetic related to phylogeny, the evolutionary development of a species

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

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

phytoplankton microscopic floating creatures that photosynthesize

pinnate featherlike

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

pipette lab instrument for precise measurement and transfer of small volumes of liquids

pistil female reproductive organ of a flower

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

plankton microscopic floating organisms

plant hybridization creation of offspring by union of two different types of plants, such as wheat and rye

plasmid small ring of DNA found in many bacteria

plasticity change form

plate tectonics the movement of large plates of Earth's crust

polar partially charged, and usually soluble in water

polar covalent bond in which electrons are unevenly shared

polymer molecule composed of many similar parts

polymerase enzyme complex that synthesizes DNA or RNA from individual nucleotides

polymerization linking together of similar parts to form a polymer

polypeptide chain of amino acids

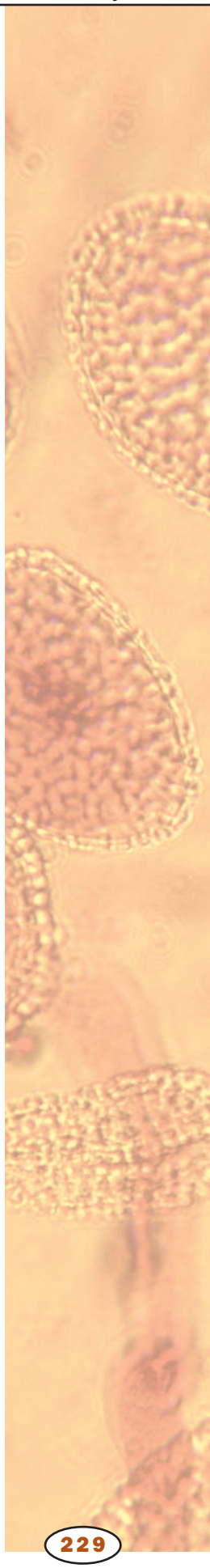
polysaccharide carbohydrate composed of many individual units of sugar

posterior toward the back

postmortem after death

prebiotic before the origin of life

Precambrian before the Cambrian era; before 600 million years ago



primer short nucleotide sequence that helps begin DNA replication

progeny offspring

prokaryote single-celled organism without a nucleus

promoter DNA sequence to which RNA polymerase binds to begin transcription

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

prostrate face downward

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

proteolysis breakdown of proteins

protoecology early ecology

protoplasm fluid portion of a plant cell within the cell wall

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

protozoa any of a phylum of minute protoplasmic animals present in almost every kind of habitat, some of which pose serious threats to humans and animals

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

psychosis severe mental disorder characterized by diminished connection with reality

psychotropic affecting consciousness, thought, or emotion

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

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

quarternary fourth level

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

reproductive isolation isolation of a population from other populations of the same species due to inability to successfully reproduce; an early stage in species formation

respire use oxygen to burn cellular fuel

restriction enzyme enzyme that cuts DNA at a particular sequence

restriction fragments fragments of DNA created by restriction enzymes

reticular netlike

retrograde backward

reverse transcriptase enzyme that copies RNA into DNA

reverse transcription creation of DNA from an RNA template

ribonucleoprotein combination of RNA and protein

ribosome protein-RNA complex in cells that synthesizes protein

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

RNA polymerase enzyme complex that creates RNA from DNA template

saline of, or relating to, salt

saprophyte plant that feeds on decaying parts of other plants

savanna open grassland with sparse trees

sclerophyll small, tough evergreen leaves

secretion material released from the cell

secretory pathway series of events within a cell by which molecules are brought to the plasma membrane for release from the cell

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

serotinous developing late in the season

serotype identity of an organism or virus based on reaction to an antibody

sessile attached and remaining in one place

silviculture cultivation of forest trees

sleep apnea difficulty breathing while asleep

solenoid cylindrical coiled structure

solute dissolved substance

solvation the process of dissolving

somatic nonreproductive; not an egg or sperm

somatostatin hormone produced by the hypothalamus that influences growth

spasticity of, or relating to, spasms

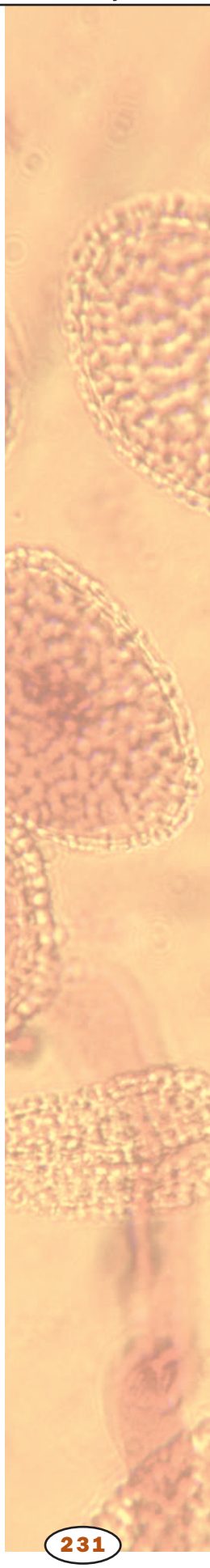
spectroscopy process using light or other emitted radiation to determine properties of a sample

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

spontaneous generation the theory that life began from nonliving matter

stasis state of no change

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



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

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

strong bond high-energy arrangement between two atoms involving electron-sharing; strong bonds require more energy to break than weak bonds

subcutaneous below the skin

substrate the molecule acted on by an enzyme; also a surface for attachment

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

superficial on the surface; not deep

symbiont organism living in close association with another organism

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

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

synaptic transmission passage of chemicals between nerve cells to send messages or alter neuron firing

synchronously at the same time

synergism working together to create a larger product rather than a simple sum

systemic throughout the body

T cell white blood cell that controls the immune response

taxon a level of classification, such as kingdom or phylum

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

template master copy

teratogens substances that cause birth defects

tertiary third level

thermoregulation temperature regulation

transcribe creation of an RNA copy of a DNA gene

transcription messenger RNA formation from a DNA sequence

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

transduction conversion of a signal of one type into another type

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

translation synthesis of protein using mRNA code

translocation movement of sugars and other nutrients throughout a plant

transverse situated or lying across

trimer a structure composed of three parts

triploid possessing three sets of chromosomes

trophic related to feeding

trophic level feeding level in an ecosystem

true breeding giving only offspring identical to the parents

turgor internal pressure

ubiquitous found everywhere

ultrasonography use of sound waves to produce an image

ungulate hoofed mammals such as cattle

uninucleate possessing one nucleus

vas deferens tube through which sperm travel from testes to urethra

vector carrier

ventral to toward the belly side

ventricle fluid-filled chamber

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

vesicle membrane-bound sac

vestigial no longer functional

visceral related to the viscera, or internal organs

viscous thick

vivipary production of live young

volatile easily vaporized

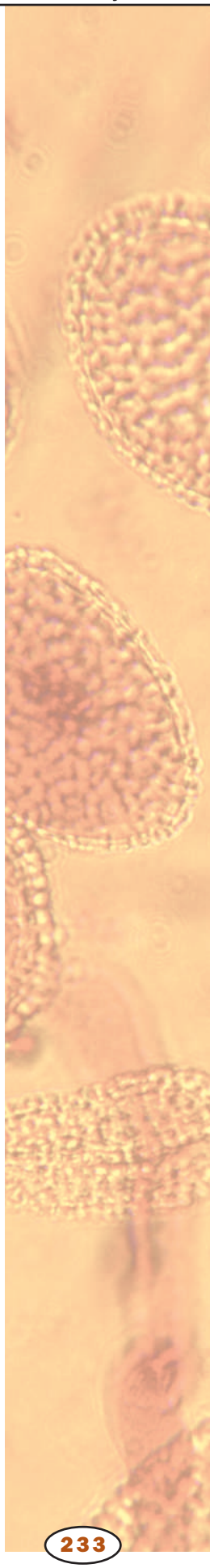
vulva external female genitalia

weak bond low-energy arrangement between two atoms involving electron-sharing; weak bonds require less energy to break than strong bonds

X-ray crystallography use of X rays to determine the structure of a molecule

xylem water-transporting system in plants

zygote fertilized egg



Topic Outline

AGRICULTURE AND ECONOMIC BOTANY

Agriculture
Agronomist
Beer-making, Botany of
Coffee, Botany of
Desertification
Ethnobotany
Forester
Grain
Grasses
History of Agriculture
Horticulturist
Hybridization-Plant
Landscape Ecology
Nitrogen Cycle
Nitrogen Fixation
Organic Agriculture
Plant Pathogens and Pests
Pollution and Bioremediation
Soil
Vavilov, Nikolay
Wine-making, Botany of

ANIMAL ANATOMY AND PHYSIOLOGY

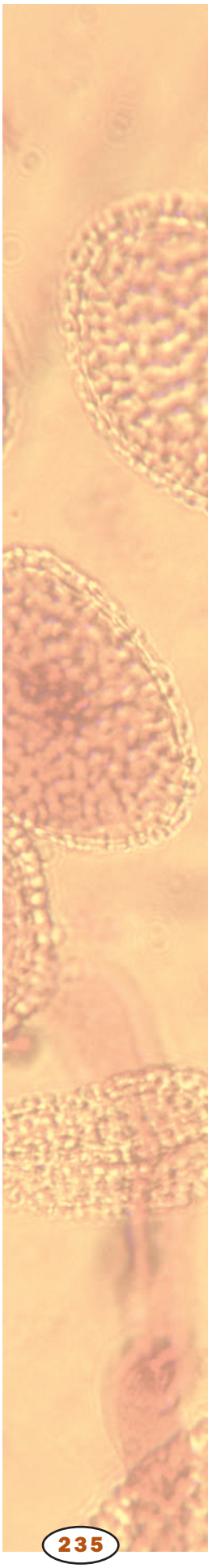
Amniote egg
Animalia
Circulatory Systems
Connective Tissue
Digestion
Epithelium
Excretory Systems
Gas Exchange
Growth
Life Cycles
Locomotion
Model Organisms in Physiology and Medicine
Muscle
Nervous Systems
Neuron
Organ
Osmoregulation
Physiological Ecology
Respiration
Scaling
Sex Determination
Skeletons
Social Behavior
Temperature Regulation
Vision
Zoology

ANIMAL BEHAVIOR

Behavior, Genetic Basis of
Behavior Patterns
Feeding Strategies
Field Studies in Animal Behavior
Migration and Animal Navigation
Mimicry, Camouflage, and Warning Coloration
Pheromone
Physiological Ecology
Population Dynamics
Predation and Defense
Sexual Selection
Symbiosis
Temperature Regulation
Wildlife Biologist

ANIMAL DIVERSITY

Amphibian
Animalia
Annelid
Arachnid
Arthropod
Biodiversity
Bird
Bony Fish
Cambrian Explosion
Cartilaginous Fish
Chordata
Cnidarian



Coral Reef
Crocodilian
Crustacean
Echinoderm
Endangered Species
Entomologist
Extinction, Mammals
Human Evolution
Insect
Mammal
Marsupial
Mollusk
Monotreme
Nematode
Parasitic Diseases
Platyhelminthes
Porifera
Primate
Reptile
Tuatara
Tunicate
Turtle
Zoology
Zoology Researcher

AQUATIC BIOLOGY

Algae
Amphibian
Bony Fish
Cartilaginous Fish
Cnidarian
Coral Reef
Crustacean
Echinoderm
Estuaries
Extreme Communities
Lakes and Ponds
Limnologist
Marine Biologist
Mollusk
Ocean Ecosystems: Hard Bottoms
Ocean Ecosystems: Open Ocean
Ocean Ecosystems: Soft Bottoms
Platyhelminthes
Porifera
Rivers and Streams
Water

BACTERIA AND ARCHAEA

Archaea
Bacterial Cell
Bacterial Diseases
Bacterial Genetics
Bacterial Viruses
Biotechnology
Cell Evolution
Cell Wall
Chloroplast
Clone
Control of Gene Expression
Cyanobacteria
Dubos, René
Ecosystem
Eubacteria
Microbiologist
Mitochondrion
Model Organisms: Cell Biology and Genetics
Plant Pathogens and Pests
Poisons
Recombinant DNA
Sexually Transmitted Diseases
Transgenic Techniques

BEHAVIOR

Behavior, Genetic Basis of
Behavior Patterns
Brain
Competition
Feeding Strategies
Field Studies in Animal Behavior
Flight
Learning
Locomotion
Migration and Animal Navigation
Mimicry, Camouflage, and Warning Coloration
Pheromone
Predation and Defense
Sexual Reproduction
Sexual Selection
Sleep
Social Behavior
Sociobiology

BIOCHEMISTRY

Amino Acid
Antibodies in Research
Biochemist
Biogeochemical Cycles
Carbohydrates
Carbon Cycle
DNA
DNA Sequencing
Drug Testing
Electrophoresis
Enzymes
Glycolysis and Fermentation
History of Biology: Biochemistry
Krebs Cycle

Lipids
Lysosomes
Membrane Proteins
Metabolism
Mitochondrion
Nitrogen Cycle
Nitrogen Fixation
Nucleotides
Origin of Life
Oxidative Phosphorylation
Pauling, Linus
Peroxisomes
Pharmacologist
Poisons
Polymerase Chain Reaction
Prion
Protein Structure
Protein Synthesis
Radionuclides
RNA
Secondary Metabolites in Plants
Separation and Purification
Structure Determination
Vitamins and Coenzymes
Water

BIOLOGY AND SOCIETY

Alcohol and Health
Anabolic Steroids
Behavior, Genetic Basis of
Biological Weapons
Biology of Race
Carson, Rachel
Creationism
Desertification
Doctor, Specialist
Dubos, René
Endangered Species
Ethnobotany
Evolution, Evidence for
Extinction, Mammals
Fire Ecology
Gene Therapy
Global Climate Change
Human Genome Project
Human Population
Invasive Species
Organic Agriculture
Pauling, Linus
Pollution and Bioremediation
Psychiatric Disorders, Biology of
Psychoactive Drugs
Recombinant DNA
Reproductive Technology
Sexually Transmitted Diseases
Smoking and Health
Sociobiology
Transgenic Techniques

BIOMES

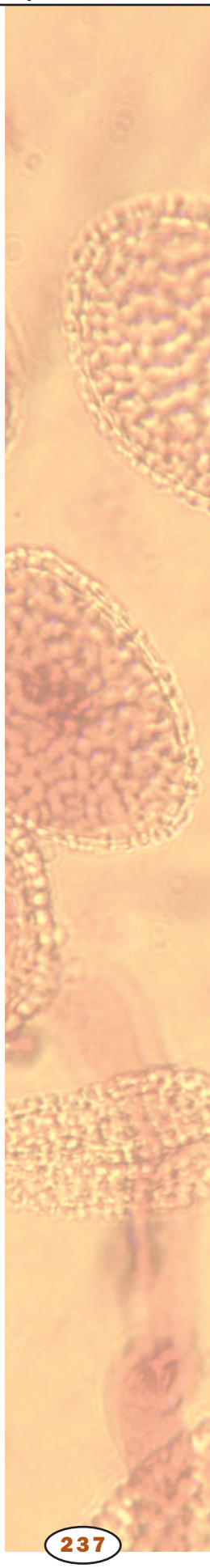
Biogeography
Biome
Coral Reef
Desert
Field Studies in Plant Ecology
Forest, Boreal
Forest, Temperate
Forest, Tropical
Global Climate Change
Grassland
Remote Sensing
Tundra

BIOTECHNOLOGY

Antibodies in Research
Antisense Nucleotides
Bacterial Genetics
Bioinformatics
Biological Weapons
Biotechnology
Clone
Electrophoresis
Forensic DNA Analysis
Genomics
Human Genome Project
Hybridization
Polymerase Chain Reaction
Recombinant DNA
Reproductive Technology
Reverse Transcriptase
Separation and Purification
Structure Determination
Transgenic Techniques

CAREERS

Agronomist
Biochemist
Botanist
College Professor
Dentist
Doctor, Family Practice
Doctor, Specialist
Emergency Medical Technician
Entomologist
Epidemiologist
Forester
Health and Safety Officer
High School Biology Teacher
Horticulturist



Laboratory Technician
Marine Biologist
Medical Assistant
Microbiologist
Microscopist
Nurse
Nurse Practitioner
Nutritionist
Pharmaceutical Sales Representative
Pharmacologist
Physician Assistant
Plant Pathologist
Psychiatrist
Public Health Careers
Science Writer
Veterinarian
Wildlife Biologist
Zoology Researcher

CELL FUNCTION

Active Transport
Cancers
Cell Cycle
Cell Motility
Control Mechanisms
Control of Gene Expression
Cytokinesis
Endocytosis
Enzymes
Exocytosis
Glycolysis and Fermentation
History of Plant Physiology
Hormones
Ion Channels
Krebs Cycle
Lysosomes
Meiosis
Membrane Proteins
Membrane Transport
Metabolism
Mitochondrion
Model Organisms: Cell Biology and Genetics
Nuclear Transport
Oxidative Phosphorylation
Peroxisomes
Protein Synthesis
Protein Targeting
Replication
Ribosome
RNA Processing
Signaling and Signal Transduction
Synaptic Transmission
Transcription

CELL STRUCTURE

Archaea
Bacterial Cell
Cell
Cell Evolution
Cell Junctions
Cell Motility
Cell Wall
Chloroplast
Connective Tissue
Cyanobacteria
Cytoskeleton
Electron Microscopy
Endoplasmic Reticulum
Epithelium
Eubacteria
Extracellular Matrix
Golgi
History of Biology: Cell Theory and Cell Structure
Ion Channels
Life, What Is
Light Microscopy
Lysosomes
Membrane Proteins
Membrane Structure
Membrane Transport
Microscopist
Mitochondrion
Model Organisms: Cell Biology and Genetics
Muscle
Neuron
Nuclear Transport
Nucleolus
Nucleus
Organelle
Origin of Life
Peroxisomes
Plasma Membrane
Porter, Keith
Ribosome
T Cells
Tissue
Vacuole

CIRCULATION AND RESPIRATION

Blood
Blood Clotting
Blood Sugar Regulation
Blood Vessels
Cardiovascular Diseases
Circulatory Systems
Gas Exchange
Harvey, William
Heart and Circulation

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

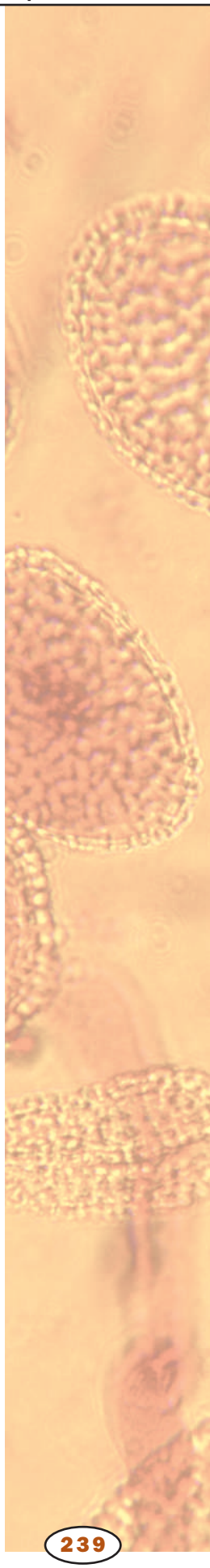
AIDS
Alcohol and Health
Anabolic Steroids
Autoimmune Disease
Bacterial Diseases
Birth Control
Blood Sugar Regulation
Cancers
Cardiovascular Diseases
Clinical Trials
Disease
Environmental Health
Female Reproductive System
Fungal Diseases
Gene Therapy
Health
Health and Safety Officer
Herbal Medicine
History of Medicine
Human Nutrition
Imaging in Medicine
Immune Response
Male Reproductive System
Model Organisms in Physiology and Medicine
Neurologic Diseases
Oncogenes and Cancer Cells
Pain
Parasitic Diseases
Poisonous Plants
Prion
Protozoan Diseases
Psychiatric Disorders, Biology of
Psychoactive Drugs
Sex Determination
Sexual Reproduction
Sexually Transmitted Diseases
Sleep
Smoking and Health
Stress Response
Transplant Medicine
Vaccines
Viral Diseases
Vitamins and Coenzymes

DNA, RNA, CHROMOSOMES

Antisense Nucleotides
Chromosome Aberrations
Chromosome, Eukaryotic
Crick, Francis
DNA
DNA Sequencing
Gene
Genome
Medical/Science Illustrator
Meiosis
Mitosis
Mutation
Nucleotides
Polymerase Chain Reaction
Recombinant DNA
Replication
Sex Chromosomes
Transfer RNA
Watson, James

ECOLOGY

Biogeochemical Cycles
Biogeography
Biome
Carbon Cycle
Community
Competition
Conservation
Coral Reef
Desert
Desertification
Ecological Research, Long-term
Ecology
Ecology, History of
Ecosystem
Endangered Species
Estuaries
Extinction, Mammals
Feeding Strategies
Field Studies in Plant Ecology
Fire Ecology
Forest, Boreal
Forest, Temperate
Forest, Tropical
Global Climate Change



Grassland
Habitat
Invasive Species
Lakes and Ponds
Landscape Ecology
Limnologist
Marine Biologist
Mimicry, Camouflage, and Warning Coloration
Nitrogen Cycle
Ocean Ecosystems: Hard Bottoms
Ocean Ecosystems: Open Ocean
Ocean Ecosystems: Soft Bottoms
Physiological Ecology
Pollution and Bioremediation
Population Dynamics
Predation and Defense
Remote Sensing
Rivers and Streams
Symbiosis
Theoretical Ecology
Tundra
Water Cycle
Wetlands

ENDOCRINE SYSTEM

Adrenal Gland
Anabolic Steroids
Birth Control
Blood Sugar Regulation
Endocrine System
Female Reproductive System
Hormones
Hypothalamus
Pancreas
Pituitary Gland
Sex Determination
Stress Response
Thyroid Gland

EVOLUTION AND ADAPTATION

Adaptation
Amniote Egg
Angiosperms
Biodiversity
Biogeography
Buffon, Count (Georges-Louis Leclerc)
Cambrian Explosion
Cell Evolution
C4 and CAM Plants
Convergent Evolution
Creationism
Darwin, Charles
Evolution
Evolution, Evidence for
Evolution of Plants
Extinction, Mammals
Extreme Communities
Hardy-Weinberg Equilibrium
Herbivory and Plant Defenses
History of Evolutionary Thought
Human Evolution
Lamarck, Jean-Baptiste
Leakey Family
Mimicry, Camouflage, and Warning Coloration
Natural Selection
Origin of Life
Osmoregulation
Paleontology
Physiological Ecology
Population Genetics
Predation and Defense
Scaling
Secondary Metabolites in Plants
Sociobiology
Speciation
Species

EXPERIMENTAL TECHNIQUES

Antibodies in Research
Antisense Nucleotides
Biochemist
Bioinformatics
Biotechnology
Cell Culture
Clinical Trials
Clone
Crick, Francis
DNA Sequencing
Drug Testing
Ecological Research, Long-term
Electron Microscopy
Electrophoresis
Field Studies in Animal Behavior
Field Studies in Plant Ecology
Forensic DNA Analysis
Gene Therapy
Genetic Analysis
Genomics
Hardy-Weinberg Equilibrium
History of Biology: Biochemistry
History of Plant Physiology
Human Genome Project
Hybridization
Imaging in Medicine
Ingenhousz, Jan
Laboratory Technician
Leeuwenhoek, Anton
Light Microscopy
Linkage and Gene Mapping

Microbiologist
Microscopist
Model Organisms: Cell Biology and Genetics
Model Organisms: Physiology and Medicine
Pasteur, Louis
Pauling, Linus
Pharmacologist
Polymerase Chain Reaction
Porter, Keith
Radiation Hybrid Mapping
Radionuclides
Recombinant DNA
Reproductive Technology
Reverse Transcriptase
Scaling
Separation and Purification
Structure Determination
Theoretical Ecology
Transgenic Techniques
Transplant Medicine
Van Helmont, J. B.
Watson, James
Zoology Researcher

FUNGI

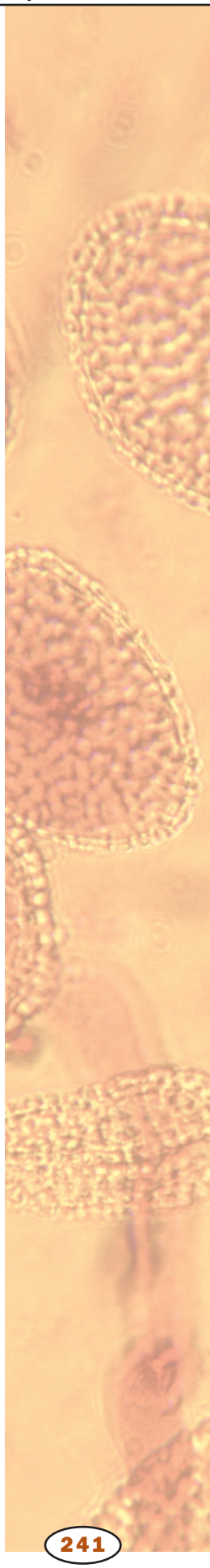
Biodiversity
Cell
Cell Wall
Fungal Diseases
Fungi
Lichen
Mycorrhizae
Plant Pathogens and Pests
Symbiosis
Taxonomy, History of

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

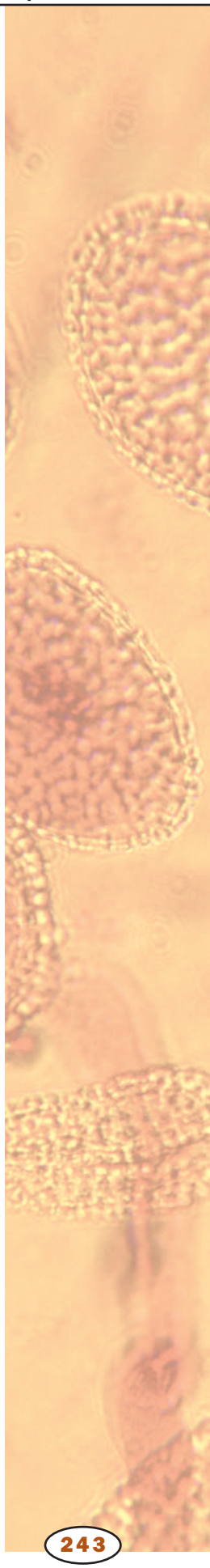
Biological Weapons
Brain
Central Nervous System
Chemoreception
Eye
Hearing
Hypothalamus
Ion Channels
Nervous Systems
Neurologic Diseases
Neuron
Pain
Peripheral Nervous System
Psychiatric Disorders, Biology of
Psychiatrist
Psychoactive Drugs
Spinal Cord
Stress Response
Synaptic Transmission
Touch
Vision

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

Cumulative Index

Boldface type indicates article titles; italics indicate illustrations; an italic f after a page number indicates figures; and an italic t after a page number indicates tables.

B

C

D

E

F

G

H

I

J

K

L

M

N

O

P

Q

R

S

T

U

V

X

Y

Z