

# Glossary

## **ABC transporter protein**

A large family of membrane transport proteins that use the energy of ATP hydrolysis to transfer peptides or small molecules across membranes. (Figure 11–7)

## **acetyl (–COCH<sub>3</sub>)**

Chemical group derived from acetic acid (CH<sub>3</sub>COOH). Acetyl groups are important in metabolism and are also added covalently to some proteins as a post-translational modification.

## **acetyl CoA**

Small water-soluble activated carrier molecule. Consists of an acetyl group linked to coenzyme A (CoA) by an easily hydrolyzable thioester bond. (Figure 2–62)

## **acetylcholine (ACh)**

Neurotransmitter that functions at cholinergic synapses. Found in the brain and peripheral nervous system. The neurotransmitter at vertebrate neuromuscular junctions. (Figure 15–9)

## **acetylcholine receptor (AChR)**

Membrane protein that responds to binding of acetylcholine (ACh). The nicotinic AChR is a transmitter-gated ion channel that opens in response to ACh. The muscarinic AChR is not an ion channel, but a G-protein-coupled cell-surface receptor.

## **acid**

A proton donor. Substance that releases protons (H<sup>+</sup>) when dissolved in water, forming hydronium ions (H<sub>3</sub>O<sup>+</sup>) and lowering the pH. (Panel 2–2, pp. 108–109)

## **acrosomal vesicle**

Region at the head end of a sperm cell that contains a sac of hydrolytic enzymes used to digest the protective coating of the egg. When a sperm starts to enter an egg, the contents of the vesicle are released (the acrosome reaction), helping the sperm penetrate the zona pellucida. (Figures 21–33 and 21–27)

## **actin**

Abundant protein that forms actin filaments in all eucaryotic cells. The monomeric form is sometimes called globular or G-actin; the polymeric form is filamentous or F-actin. (Panel 16–1, p. 968, and Figure 16–12)

## **actin-binding protein**

Protein that associates with either actin monomers or actin filaments in cells and modifies their properties. Examples include myosin,  $\alpha$ -actinin, and profilin. (Panel 16–3, pp. 994–995)

## **actin filament (microfilament)**

Helical protein filament formed by polymerization of globular actin molecules. A major constituent of the cytoskeleton of all eucaryotic cells and part of the contractile apparatus of skeletal muscle. (Panel 16–1, p. 968)

## **action potential**

Rapid, transient, self-propagating electrical excitation in the plasma membrane of a cell such as a neuron or muscle cell.

Action potentials, or nerve impulses, make possible long-distance signaling in the nervous system. (Figure 11–30)

## **activated carrier**

Small diffusible molecule that stores easily exchangeable energy in the form of one or more energy-rich covalent bonds. Examples are ATP, acetyl CoA, FADH<sub>2</sub>, NADH, and NADPH. (Figure 2–55)

## **activation energy**

Extra energy that must be acquired by atoms or molecules in addition to their ground-state energy in order to reach a transition state and undergo a particular chemical reaction. (Figure 2–44)

## **activator (gene activator protein, transcriptional activator)**

Gene regulatory protein that when bound to its regulatory sequence in DNA activates transcription.

## **active site**

Region of an enzyme surface to which a substrate molecule binds in order to undergo a catalyzed reaction. (Figure 1–7)

## **active transport**

Movement of a molecule across a membrane or other barrier driven by energy other than that stored in the electrochemical or concentration gradient of the transported molecule.

## **acyl group (–CO–R)**

Functional group derived from a carboxylic acid (R–C $\begin{matrix} \text{=O} \\ \diagup \\ \text{OH} \end{matrix}$ ).

## **adaptation**

(1) adaptation (desensitization): Adjustment of sensitivity following repeated stimulation. The mechanism that allows a cell to react to small changes in stimuli even against a high background level of stimulation. (2) evolutionary adaptation: an evolved trait.

## **adaptive immune response**

Response of the vertebrate adaptive immune system to a specific antigen that typically generates immunological memory. (Figures 25–1 and 25–2)

## **adaptor protein**

General term for a protein that functions solely to link two or more different proteins together in an intracellular signaling pathway or protein complex. (Figure 15–22)

## **adenomatous polyposis coli (APC) protein**

Tumor suppressor protein that forms part of a protein complex in the canonical Wnt signaling pathway that recruits free cytoplasmic  $\beta$ -catenin and degrades it.

## **adenosine triphosphate—see ATP**

## **adenylyl cyclase (adenylate cyclase)**

Membrane-bound enzyme that catalyzes the formation of cyclic AMP from ATP. An important component of some intracellular signaling pathways.

## **adherens junction**

Cell junction in which the cytoplasmic face of the plasma

membrane is attached to actin filaments. Examples include adhesion belts linking adjacent epithelial cells and focal contacts on the lower surface of cultured fibroblasts.

**ADP (adenosine 5'-diphosphate)**

Nucleotide produced by hydrolysis of the terminal phosphate of ATP. Regenerates ATP when phosphorylated by an energy-generating process such as oxidative phosphorylation. (Figure 2–57)

**adrenaline (epinephrine)**

Hormone released by adrenal gland chromaffin cells, especially in response to stress, that binds to specific GPCRs. It can initiate and coordinate a “fight or flight” response, which includes an increase in heart rate and blood sugar levels. It is also a catecholamine neurotransmitter.

**aerobic**

Occurring in, or requiring, the presence of molecular oxygen (O<sub>2</sub>).

**affinity**

The strength of binding of a molecule to its ligand at a single binding site.

**affinity chromatography**

Type of chromatography in which the protein mixture to be purified is passed over a matrix to which specific ligands for the required protein are attached, so that the protein is retained on the matrix. (Figure 8–13)

**affinity constant (association constant) (K<sub>a</sub>)**

Measure of the strength of binding of the components in a complex. For components A and B and a binding equilibrium  $A + B = AB$ , the association constant is given by  $[AB]/[A][B]$ , and is larger the tighter the binding between A and B. (Figure 3–43)

**affinity maturation**

Progressive increase in the affinity of antibodies for the immunizing antigen with the passage of time after immunization.

**Akt (protein kinase B, PKB)**

Serine/threonine protein kinase that acts in the PI 3-kinase/Akt intracellular signaling pathway involved especially in signaling cells to grow and survive. Also called protein kinase B (PKB). (Figure 15–64)

**aldehyde**

Organic compound that contains the  $\left[ -\overset{\text{O}}{\parallel}{\text{C}}-\text{H} \right]$  group. Example: glyceraldehyde. Can be oxidized to an acid or reduced to an alcohol. (Panel 2–1, p. 107)

**alga (plural algae)**

Informal term used to describe a wide range of simple unicellular and multicellular eucaryotic photosynthetic organisms. Examples include *Nitella*, *Volvox*, and *Fucus*.

**alkaline—see basic**

**alkyl group (C<sub>n</sub>H<sub>2n+1</sub>)**

General term for a group of covalently linked carbon and hydrogen atoms such as methyl (–CH<sub>3</sub>) or ethyl (–CH<sub>2</sub>CH<sub>3</sub>) groups. Usually exist as part of larger organic molecules. On their own they form extremely reactive free radicals.

**allele**

One of several alternative forms of a gene. In a diploid cell each gene will typically have two alleles, occupying the corresponding position (locus) on homologous chromosomes.

**allelic exclusion**

The expression of a protein from only one of the two alleles of the gene encoding the protein in the cell, as occurs, for example, in the expression of an immunoglobulin or T cell receptor chain or an olfactory receptor.

**allostery (adjective allosteric)**

Change in a protein's conformation brought about by the binding of a regulatory ligand (at a site other than the protein's catalytic site), or by covalent modification. The change

in conformation alters the activity of the protein and can form the basis of directed movement. (Figures 3–58 and 16–61)

**alpha helix (α helix)**

Common folding pattern in proteins, in which a linear sequence of amino acids folds into a right-handed helix stabilized by internal hydrogen bonding between backbone atoms. (Figure 3–7)

**alternative RNA splicing**

Production of different RNAs from the same gene by splicing the transcript in different ways. (Figure 7–94)

**alveoli (singular alveolus)**

Small dilated outpocketings of an epithelium, especially the epithelium of the lung, where they form millions of air-filled sacs. Similar structures are found in the milk-secreting glandular epithelium of the breast.

**amide**

Molecule containing a carbonyl group linked to an amine. (Panel 2–1, p. 107)

**amine**

Chemical group containing nitrogen and hydrogen. Becomes positively charged in water. (Panel 2–1, p. 107)

**amino acid**

Organic molecule containing both an amino group and a carboxyl group. Those that serve as building blocks of proteins are alpha amino acids, having both the amino and carboxyl groups linked to the same carbon atom. (NH<sub>2</sub>CHR<sub>2</sub>COOH, Panel 3–1, pp. 128–129)

**aminoacyl-tRNA synthetase**

Enzyme that attaches the correct amino acid to a tRNA molecule to form an aminoacyl-tRNA. (Figure 6–57)

**amino group (–NH<sub>2</sub>)**

Weakly basic functional group derived from ammonia (NH<sub>3</sub>) in which one or more hydrogen atoms are replaced by another atom. In aqueous solution it can accept a proton and carry a positive charge (–NH<sub>3</sub><sup>+</sup>).

**amino terminus—see N terminus**

**amoeba (plural amoebae)**

Carnivorous unicellular protozoan that crawls using pseudopodia.

**AMP (adenosine 5'-monophosphate)**

One of the four nucleotides in an RNA molecule. Two phosphates are added to AMP to form ATP. (Panel 2–6, pp. 116–117)

**amphipathic**

Having both hydrophobic and hydrophilic regions, as in a phospholipid or a detergent molecule.

**anabolism (biosynthesis)**

Formation of complex molecules from simple substances by living cells. (Figure 2–36)

**anaerobic**

Requiring, or occurring in, the *absence* of molecular oxygen (O<sub>2</sub>).

**anaphase**

(1) Stage of mitosis during which sister chromatids separate and move away from each other. Composed of anaphase A (chromosomes move toward the two spindle poles) and anaphase B (spindle poles move apart). (2) Anaphase I and II: stages of meiosis during which chromosome homolog pairs separate (I), and then sister chromatids separate (II). (Panel 17–1, pp. 1072–1073)

**anaphase-promoting complex (APC/C) (cyclosome)**

Ubiquitin ligase that catalyzes the ubiquitylation and destruction of securin and M- and S-cyclins, initiating the separation of sister chromatids in the metaphase-to-anaphase transition during mitosis.

**anchorage dependence**

Dependence of cell growth, proliferation, and survival on attachment to a substratum.

**anchoring junction**

Cell junction that attaches cells to neighboring cells or to the extracellular matrix. (Figure 19–2, and Table 19–1, p. 1133)

**angiogenesis**

Growth of new blood vessels by sprouting from existing ones.

**Ångstrom (Å)**

Unit of length used to measure atoms and molecules. Equal to  $10^{-10}$  meter or 0.1 nanometer (nm).

**animal pole**

In yolk eggs, the end opposite the yolk. Cells derived from the animal region will envelop those derived from the yolk (vegetal) region. (Figure 22–68)

**anion**

Negatively charged ion.

**antenna complex**

Part of a photosystem that captures light energy and channels it into the photochemical reaction center. It consists of protein complexes that bind large numbers of chlorophyll molecules and other pigments.

**antibiotic**

Substance such as penicillin or streptomycin that is toxic to microorganisms. Often a product of a particular microorganism or plant.

**antibody (immunoglobulin, Ig)**

Protein produced by B cells in response to a foreign molecule or invading microorganism. Binds tightly to the foreign molecule or cell, inactivating it or marking it for destruction by phagocytosis or complement-induced lysis.

**anticodon**

Sequence of three nucleotides in a transfer RNA (tRNA) molecule that is complementary to a three-nucleotide codon in a messenger RNA (mRNA) molecule.

**antigen**

A molecule that can induce an adaptive immune response or that can bind to an antibody or T cell receptor.

**antigenic determinant (epitope)**

Specific region of an antigen that binds to an antibody or a T cell receptor.

**antigenic variation**

Ability to change the antigens displayed on the cell surface; a property of some pathogenic microorganisms that enables them to evade attack by the adaptive immune system.

**antigen-presenting cell**

Cell that displays foreign antigen complexed with an MHC protein on the cell surface for presentation to T lymphocytes.

**antiparallel**

Describes the relative orientation of the two strands in a DNA double helix or two paired regions of a polypeptide chain; the polarity of one strand is oriented in the opposite direction to that of the other.

**antiporter**

Carrier protein that transports two different ions or small molecules across a membrane in opposite directions, either simultaneously or in sequence. (Figure 11–8)

**antisense RNA**

RNA complementary to an RNA transcript of a gene. Can hybridize to the specific RNA and block its function.

**APC—see adenomatous polyposis coli****APC/C—see anaphase-promoting complex****apical**

Referring to the tip of a cell, a structure, or an organ. The apical

surface of an epithelial cell is the exposed free surface, opposite to the basal surface. The basal surface rests on the basal lamina that separates the epithelium from other tissue.

**apical meristem**

The growing tip of a plant shoot or root, composed of dividing undifferentiated cells. (Panel 22–1, p. 1401)

**apoptosis**

Form of programmed cell death, in which a “suicide” program is activated within an animal cell, leading to rapid cell death mediated by intracellular proteolytic enzymes called caspases.

**aqueous**

Pertaining to water, as in an aqueous solution.

***Arabidopsis thaliana* (common Thale cress)**

Small flowering weed related to mustard. Model organism for flowering plants and the primary model for studies of plant molecular genetics.

**archaeon (plural arch[a]ea) (archaebacterium).**

Single-celled organism without a nucleus, superficially similar to bacteria. At a molecular level, more closely related to bacteria in metabolic machinery, but more similar to eucaryotes in genetic machinery. Archaea and Bacteria together make up the Procaryotes. (Figure 1–21)

**ARF (ADP-ribosylation factor, ARF protein)**

Monomeric GTPase in the Ras superfamily responsible for regulating both COPI coat assembly and clathrin coat assembly at Golgi membranes. (Table 15–5, p. 926)

**aromatic**

Molecule that contains carbon atoms in a ring drawn as having alternating single and double bonds. Often a molecule related to benzene.

**ARP (actin-related protein) complex (ARP2/3 complex)**

Complex of proteins that nucleates actin filament growth from the minus end.

**ARS—see autonomously replicating sequence****asexual reproduction**

Any type of reproduction (such as budding in *Hydra*, binary fission in bacteria, or mitotic division in eucaryotic microorganisms) that does not involve the mixing of two different genomes. Produces individuals that are genetically identical to the parent.

**association constant—see affinity constant****aster**

Star-shaped system of microtubules emanating from a centrosome or from a pole of a mitotic spindle.

**astral microtubule**

In the mitotic spindle, any of the microtubules radiating from the aster which are not attached to a kinetochore of a chromosome.

**ATM (ataxia telangiectasia mutated protein)**

Protein kinase activated by double-strand DNA breaks. If breaks are not repaired, ATM initiates a signal cascade that culminates in cell cycle arrest. Related to ATR.

**ATP (adenosine 5'-triphosphate)**

Nucleoside triphosphate composed of adenine, ribose, and three phosphate groups. The principal carrier of chemical energy in cells. The terminal phosphate groups are highly reactive in the sense that their hydrolysis, or transfer to another molecule, takes place with the release of a large amount of free energy. (Figure 2–26)

**ATPase**

Enzyme that catalyzes the hydrolysis of ATP. Many proteins have ATPase activity.

**ATP synthase ( $F_0F_1$  ATPase)**

Transmembrane enzyme complex in the inner membrane of



mitochondria and the thylakoid membrane of chloroplasts. Catalyzes the formation of ATP from ADP and inorganic phosphate during oxidative phosphorylation and photosynthesis, respectively. Also present in the plasma membrane of bacteria.

**ATR (ataxia telangiectasia and Rad3 related protein)**

Protein kinase activated by DNA damage. If damage remains unrepaired, ATR helps initiate a signal cascade that culminates in cell cycle arrest. Related to ATM.

**atypical protein kinase (aPKC)**

An atypical form of protein kinase C (PKC) that does not require both  $\text{Ca}^{2+}$  and phosphatidylserine for activation. One such aPKC is involved in the specification of polarity in some individual animal cells.

**auditory hair cell (sensory hair cell)**

Sensory cells in the inner ear, responsible for detecting sound by converting a mechanical stimulus (the vibrations caused by sound waves) into a release of neurotransmitter. (Figures 23–13 to 23–15)

**autocrine signaling**

Where a cell secretes signal molecules that act back on itself.

**autoimmune disease, autoimmune response**

Pathological state in which the body mounts a disabling adaptive immune response against one or more of its own molecules.

**autonomously replicating sequence (ARS)**

Origin of replication in yeast DNA.

**autophagy**

Digestion of worn-out organelles by the cell's own lysosomes.

**autoradiography**

Technique in which a radioactive object produces an image of itself on a photographic film or emulsion.

**autosome**

Any chromosome other than a sex chromosome.

**auxin**

Plant hormone, commonly indole-3-acetic acid, with numerous roles in plant growth and development.

**avidity**

Total binding strength of a polyvalent antibody with a polyvalent antigen.

**axon**

Long nerve cell projection that can rapidly conduct nerve impulses over long distances so as to deliver signals to other cells.

**axonal transport**

Directed intracellular transport of organelles and molecules along a nerve cell axon. Can be anterograde (outward from the cell body) or retrograde (back toward the cell body).

**axoneme**

Bundle of microtubules and associated proteins that forms the core of a cilium or a flagellum in eucaryotic cells and is responsible for their movements.

**BAC—see bacterial artificial chromosome**

**bacterium (plural bacteria) (eubacterium)**

Member of the domain Bacteria, one of the three main branches of the tree of life (Archaea, Bacteria, and Eucaryotes). Bacteria and Archaea both lack a distinct nuclear compartment, and together comprise the Procaryotes. (Figure 1–21)

**bacterial artificial chromosome (BAC)**

Cloning vector that can accommodate large pieces of DNA up to 1 million base pairs.

**bacteriophage (phage)**

Any virus that infects bacteria. Phages were the first organ-

isms used to analyse the molecular basis of genetics, and are now widely used as cloning vectors. *See also* bacteriophage lambda.

**bacteriophage lambda (bacteriophage  $\lambda$ , lambda)**

Virus that infects *E. coli*. Widely used as a DNA cloning vector.

**bacteriorhodopsin**

Pigmented protein found in the plasma membrane of a salt-loving archaean, *Halobacterium salinarium* (*Halobacterium halobium*). Pumps protons out of the cell in response to light. (Figure 10–33)

**basal**

Situated near the base. Opposite the apical surface.

**basal body**

Short cylindrical array of microtubules and their associated proteins found at the base of a eucaryotic cell cilium or flagellum. Serves as a nucleation site for growth of the axoneme. Closely similar in structure to a centriole.

**basal lamina (plural basal laminae)**

Thin mat of extracellular matrix that separates epithelial sheets, and many other types of cells such as muscle or fat cells, from connective tissue. Sometimes called basement membrane. (Figure 19–40)

**base**

A substance that can reduce the number of protons in solution, either by accepting  $\text{H}^+$  ions directly, or by releasing  $\text{OH}^-$  ions, which then combine with  $\text{H}^+$  to form  $\text{H}_2\text{O}$ . The purines and pyrimidines in DNA and RNA are organic nitrogenous bases and are often referred to simply as bases. (Panel 2–2, pp. 108–109)

**base excision repair**

DNA repair pathway in which single faulty bases are removed from the DNA helix and replaced. *Compare* nucleotide excision repair. (Figure 5–48)

**basement membrane—see basal lamina**

**base pair**

Two nucleotides in an RNA or DNA molecule that are held together by hydrogen bonds—for example, G paired with C, and A paired with T or U.

**basic (alkaline)**

Having the properties of a base.

**B cell (B lymphocyte)**

Type of lymphocyte that makes antibodies.

**Bcl2 family**

Family of intracellular proteins that either promote or inhibit apoptosis by regulating the release of cytochrome *c* and other mitochondrial proteins from the intermembrane space into the cytosol.

**benign**

Of tumors: self-limiting in growth, and noninvasive.

**beta-catenin ( $\beta$ -catenin)**

Multifunctional cytoplasmic protein involved in cadherin-mediated cell–cell adhesion, linking cadherins to the actin cytoskeleton. Can also act independently as a gene regulatory protein. Has an important role in animal development as part of a Wnt signaling pathway.

**beta sheet ( $\beta$  sheet)**

Common structural motif in proteins in which different sections of the polypeptide chain run alongside each other, joined together by hydrogen bonding between atoms of the polypeptide backbone. Also known as a  $\beta$ -pleated sheet. (Figure 3–7)

**binding site**

Region on the surface of one molecule (usually a protein or nucleic acid) that can interact with another molecule through noncovalent bonding.

**bi-orientation**

The attachment of sister chromatids to opposite poles of the mitotic spindle, so that they move to opposite ends of the cell when they separate in anaphase.

**biosphere**

All of the living organisms on Earth.

**biosynthesis—see anabolism****biotin**

Low-molecular-weight compound used as a coenzyme. Also useful technically as a covalent label for proteins, allowing them to be detected by the egg protein avidin, which binds extremely tightly to biotin. (Figure 2–63)

**bivalent**

A four-chromatid structure formed during meiosis, consisting of a duplicated chromosome tightly paired with its homologous duplicated chromosome.

**blastomere**

One of the many cells formed by the cleavage of a fertilized egg. (Figure 22–69)

**blastula**

Early stage of an animal embryo, usually consisting of a hollow ball of epithelial cells surrounding a fluid-filled cavity, before gastrulation begins.

**blotting**

Biochemical technique in which macromolecules separated on a gel are transferred to a nylon membrane or sheet of paper, thereby immobilizing them for further analysis. [See Northern, Southern, and Western (immuno-) blotting.] (Figure 8–38)

**B lymphocyte—see B cell****bond energy**

Strength of the chemical linkage between two atoms, measured by the energy in kilocalories or kilojoules needed to break it.

**bright-field microscope**

Normal light microscope in which the image is obtained by simple transmission of light through the object being viewed.

**brush border**

Dense covering of microvilli on the apical surface of epithelial cells in the intestine and kidney.

**budding yeast**

Common name given to the baker's yeast *Saccharomyces cerevisiae*, a model experimental organism, which divides by budding off a smaller cell.

**buffer**

Solution of weak acid or weak base that resists pH change when small quantities of acid or base are added, or when solution is diluted.

**Ca<sup>2+</sup>/calmodulin-dependent protein kinase—see (CaM-kinase)****cadherin**

Member of the large cadherin superfamily of transmembrane adhesion proteins. Mediates homophilic Ca<sup>2+</sup>-dependent cell–cell adhesion in animal tissues. (Figure 19–4, and Table 19–2, p. 1135)

***Caenorhabditis elegans***

A small (~1mm) nematode worm used extensively in molecular and developmental biology as a model organism.

**caged molecule**

Organic molecule designed to change into an active form when irradiated with light of a specific wavelength. Example: caged ATP.

**CAK—see Cdk-activating kinase****calcium pump—see Ca<sup>2+</sup> pump****calmodulin**

Ubiquitous intracellular Ca<sup>2+</sup>-binding protein that undergoes a large conformation change when it binds Ca<sup>2+</sup>, allowing it to regulate the activity of many target proteins. In its activated (Ca<sup>2+</sup>-bound) form, it is called Ca<sup>2+</sup>/calmodulin. (Figure 15–43)

**calorie**

Unit of heat energy, equal to 4.2 joules. One calorie (small “c”) is the amount of heat needed to raise the temperature of 1 gram of water by 1°C. A kilocalorie (1000 calories) is the unit used to describe the energy content of foods.

**Calvin cycle—see carbon-fixation cycle****CAM (cell adhesion molecule)**

Protein on the surface of an animal cell that mediates cell–cell binding or cell–matrix binding.

**CaM-kinase**

Serine/threonine protein kinase that is activated by Ca<sup>2+</sup>/calmodulin. Indirectly mediates the effects of an increase in cytosolic Ca<sup>2+</sup> by phosphorylating specific target proteins. (Figure 15–43)

**CaM-kinase II**

Multifunctional Ca<sup>2+</sup>/calmodulin-dependent protein kinase that phosphorylates itself and various target proteins when activated. Found in most animal cells but is especially abundant at synapses in the brain, and is involved in some forms of synaptic plasticity in vertebrates. (Figure 15–44)

**cAMP—see cyclic AMP****cAMP-dependent protein kinase—see protein kinase A****cancer**

Disease featuring abnormal and improperly controlled cell division resulting in invasive growths, or tumors, that may spread throughout the body. (Figure 20–37)

**capsid**

Protein coat of a virus, formed by the self-assembly of one or more types of protein subunit into a geometrically regular structure. (Figure 3–30)

**Ca<sup>2+</sup> pump (calcium pump, Ca<sup>2+</sup> ATPase)**

Transport protein in the membrane of sarcoplasmic reticulum of muscle cells (and elsewhere). Pumps Ca<sup>2+</sup> out of the cytoplasm into the sarcoplasmic reticulum using the energy of ATP hydrolysis.

**carbohydrate**

General term for sugars and related compounds containing carbon, hydrogen, and oxygen, usually with the empirical formula (CH<sub>2</sub>O)<sub>n</sub>.

**carbon fixation reaction**

Process by which inorganic carbon (as atmospheric CO<sub>2</sub>) is incorporated into organic molecules. The second stage of photosynthesis. (Figure 14–39)

**carbon-fixation cycle (Calvin cycle)**

Major metabolic pathway in photosynthetic organisms by which CO<sub>2</sub> and H<sub>2</sub>O are converted into carbohydrates. Requires both ATP and NADPH. (Figure 14–40)

**carbonyl group (C=O)**

Carbon atom linked to an oxygen atom by a double bond. (Panel 2–1, p. 107)

**carboxyl group (–COOH)**

Carbon atom linked both to an oxygen atom by a double bond and to a hydroxyl group. Molecules containing a carboxyl group are weak acids—carboxylic acids. (Panel 2–1, p. 107)

**carboxyl terminus—see C terminus****carcinogen**

Any agent, such as a chemical or a form of radiation, that causes cancer.

**carcinoma**

Cancer of epithelial cells. The most common form of human cancer.

**cardiac muscle**

Specialized form of striated muscle found in the heart, consisting of individual heart muscle cells linked together by cell junctions.

**carrier protein—see transporter****cartilage**

Form of connective tissue composed of cells (chondrocytes) embedded in a matrix rich in type II collagen and chondroitin sulfate proteoglycan.

**cascade—see signaling cascade****caspase**

Intracellular protease that is involved in mediating the intracellular events of apoptosis.

**catabolism**

General term for the enzyme-catalyzed reactions in a cell by which complex molecules are degraded to simpler ones with release of energy. (Figure 2–36)

**catalyst**

Substance that can lower the activation energy of a reaction (thus increasing its rate), without itself being consumed by the reaction.

**catastroph factor**

Protein that destabilizes microtubule arrays by increasing the frequency of rapid disassembly of tubulin subunits from one end (catastrophe). (Figure 16–16)

 **$\beta$ -catenin—see beta catenin****cation**

Positively-charged ion.

**caveola (plural caveolae)**

Invaginations at the cell surface that bud off internally to form pinocytotic vesicles. Thought to form from lipid rafts, regions of membrane rich in certain lipids.

**CD4**

Co-receptor protein found on helper T cells, regulatory T cells, and macrophages. It binds to class II MHC proteins (on antigen presenting cells) outside the peptide-binding groove.

**CD8**

Co-receptor protein found on cytotoxic T cells. It binds to class I MHC proteins (on antigen-presenting cell) outside the peptide-binding groove.

**CD28**

Co-receptor protein on T cells that binds a co-stimulatory B7 protein on dendritic cells, providing an additional signal required for the activation of a naïve T cell by antigen.

**Cdc6**

Protein essential in the preparation of DNA for replication. With Cdt1 it binds to an origin recognition complex on chromosomal DNA and helps load the Mcm proteins onto the complex to form the prereplicative complex.

**Cdc20**

Activating subunit of the anaphase-promoting complex (APC/C).

**Cdc25**

Protein phosphatase that dephosphorylates Cdks and increases their activity.

**Cdc gene (cell-division-cycle gene)**

Gene whose product (a Cdc protein) controls a specific step or set of steps in the eucaryotic cell cycle. Originally identified in yeasts.

**Cdk—see cyclin-dependent kinase****Cdk-activating kinase (CAK)**

Protein kinase that phosphorylates Cdks in cyclin-Cdk complexes, activating the Cdk.

**Cdk inhibitor protein (CKI)**

Protein that binds to and inhibits cyclin-Cdk complexes, primarily involved in the control of G1 and S phases.

**cDNA**

DNA molecule made as a copy of mRNA and therefore lacking the introns that are present in genomic DNA.

**Cdt1**

Protein essential in the preparation of DNA for replication. With Cdc6 it binds to origin recognition complexes on chromosomes and helps load the Mcm proteins on to the complex, forming the prereplicative complex.

**cell adhesion molecule—see CAM****cell cortex**

Specialized layer of cytoplasm on the inner face of the plasma membrane. In animal cells it is an actin-rich layer responsible for movements of the cell surface.

**cell cycle (cell-division cycle)**

Reproductive cycle of a cell: the orderly sequence of events by which a cell duplicates its chromosomes and, usually, the other cell contents, and divides into two. (Figure 17–4)

**cell-cycle control system**

Network of regulatory proteins that governs progression of a eucaryotic cell through the cell cycle.

**cell division**

Separation of a cell into two daughter cells. In eucaryotic cells it entails division of the nucleus (mitosis) closely followed by division of the cytoplasm (cytokinesis).

**cell-division-cycle gene—see Cdc gene****cell fate**

In developmental biology, describes what a particular cell at a given stage of development will normally give rise to.

**cell-free system**

Fractionated cell homogenate that retains a particular biological function of the intact cell, and in which biochemical reactions and cell processes can be more easily studied.

**cell line**

Population of cells of plant or animal origin capable of dividing indefinitely in culture.

**cell memory**

Retention by cells and their descendants of persistently altered patterns of gene expression, without any change in DNA sequence. *See also* epigenetic inheritance.

**cell plate**

Flattened membrane-bounded structure that forms by fusing vesicles in the cytoplasm of a dividing plant cell and is the precursor of the new cell wall.

**cell senescence—see replicative cell senescence****cell signaling**

The processes in which cells are stimulated or inhibited by extracellular signals, usually chemical signals produced by other cells.

**cell transformation—see transformation****cellularization**

The formation of cells around each nucleus in a multinucleate cytoplasm, transforming it into a multicellular structure.

**cellulose**

Structural polysaccharide consisting of long chains of covalently linked glucose units. Provides tensile strength in plant cell walls. (Figures 19–78 and 19–79)



**cell wall**

Mechanically strong extracellular matrix deposited by a cell outside its plasma membrane. Prominent in most plants, bacteria, archaea, algae, and fungi. Not present in most animal cells.

**central lymphoid organ (primary lymphoid organ)**

Organ in which lymphocytes are produced from precursor cells. In adult mammals, these are the thymus and bone marrow.

**centriole**

Short cylindrical array of microtubules, closely similar in structure to a basal body. A pair of centrioles is usually found at the center of a centrosome in animal cells. (Figure 16–31)

**centromere**

Constricted region of a mitotic chromosome that holds sister chromatids together. Also the site on the DNA where the kinetochore forms that captures microtubules from the mitotic spindle. (Figure 4–50)

**centrosome**

Centrally located organelle of animal cells that is the primary microtubule-organizing center (MTOC) and acts as the spindle pole during mitosis. In most animal cells it contains a pair of centrioles. (Figures 16–30 and 17–29)

**CG island**

Region of DNA with a greater than average density of CG sequences; these regions generally remain unmethylated.

**CGN—see *cis* Golgi network****channel (membrane channel)**

Transmembrane protein complex that allows inorganic ions or other small molecules to diffuse passively across the lipid bilayer. (Figures 11–3 and 11–4)

**channel-forming junction**

Cell-cell junction that links the cytoplasm of adjacent cells and provides a passageway for small molecules and ions to pass from cell to cell. In animal tissues, composed of connexin or innexin proteins. In plants, a similar function is performed by plasmodesmata. (Figure 19–2, and Table 19–1, p. 1133)

**channel protein**

Membrane transport protein that forms an aqueous pore in the membrane through which a specific solute, usually an ion, can pass. *Compare* transporter.

**chaperone (molecular chaperone)**

Protein that helps guide the proper folding of other proteins, or helps them avoid misfolding. Includes heat shock proteins (Hsp).

**checkpoint**

Point in the eucaryotic cell-division cycle where progress through the cycle can be halted until conditions are suitable for the cell to proceed.

**chelate**

To combine reversibly, usually with high affinity, with a metal ion such as iron, calcium, or magnesium.

**chemical biology**

Name given to a strategy that uses large-scale screening of hundreds of thousands of small molecules in biological assays to identify chemicals that affect a particular biological process and that can then be used to study it.

**chemical bond**

Chemical affinity between two atoms that holds them together. Types found in living cells include covalent bonds and noncovalent bonds. (*See also* ionic bond, hydrogen bond.)

**chemiosmotic coupling (chemiosmosis)**

Mechanism in which a gradient of hydrogen ions (a pH gradient, or proton gradient) across a membrane is used to drive an energy-requiring process, such as ATP production or the rotation of bacterial flagella.

**chemokine**

Chemotactic cytokine. Small secreted protein that attracts cells, such as white blood cells, to move towards its source. Important in the functioning of the immune system.

**chemotaxis**

Directed movement of a cell or organism towards or away from a diffusible chemical.

**chiasma (plural *chiasmata*)**

X-shaped connection visible between paired homologous chromosomes during meiosis. Represents a site of chromosomal crossing-over, a form of genetic recombination.

**chimera**

Whole organism formed from an aggregate of two or more genetically different populations of cells (two or more genotypes), originating from different zygotes. *Compare* mosaic.

**ChIP—see chromatin immunoprecipitation****chitin**

Abundant organic polymeric polysaccharide of *N*-acetylglucosamine. A major component of insect exoskeletons and the cell walls of fungi.

**chlorophyll**

Light-absorbing green pigment that plays a central part in photosynthesis in bacteria, plants, and algae.

**chloroplast**

Organelle in green algae and plants that contains chlorophyll and carries out photosynthesis. A specialized form of plastid.

**cholesterol**

An abundant lipid molecule with a characteristic four-ring steroid structure. An important component of the plasma membranes of animal cells. (Figure 10–4)

**chondrocyte (cartilage cell)**

Connective-tissue cell that secretes the matrix of cartilage.

**chromatid**

One of the two copies of a duplicated chromosome formed by DNA replication during S phase. The two chromatids, called sister chromatids, are joined at the centromere.

**chromatin**

Complex of DNA, histones, and nonhistone proteins found in the nucleus of a eucaryotic cell. The material of which chromosomes are made.

**chromatin immunoprecipitation (ChIP)**

Technique by which chromosomal DNA bound by a particular protein can be isolated and identified by precipitating it by means of an antibody against the bound protein. (Figure 7–32)

**chromatin remodeling complex**

Enzyme complex that alters histone-DNA configurations in eucaryotic chromosomes, changing the accessibility of the DNA to other proteins, notably those involved in transcription.

**chromatography**

Broad class of biochemical techniques in which a mixture of substances is separated by charge, size, hydrophobicity, non-covalent binding affinities, or some other property by allowing the mixture to partition between a moving phase and a stationary phase. Used to separate mixtures of proteins or nucleic acids. *See also* affinity-, DNA affinity-, and high-performance liquid chromatography. (Figures 8–13 and 8–14)

**chromosome**

Structure composed of a very long DNA molecule and associated proteins that carries part (or all) of the hereditary information of an organism. Especially evident in plant and animal cells undergoing mitosis or meiosis, during which each chromosome becomes condensed into a compact rod-like structure visible in the light microscope.

**ciliate**

Single-celled eucaryotic organism (protozoan) characterized by numerous cilia on its surface.

**cilium** (plural **cilia**)

Hairlike extension of a eucaryotic cell containing a core bundle of microtubules. Many cells contain a single non-motile cilium, while others contain large numbers that perform repeated beating movements. *Compare* flagellum.

**circadian clock** (**circadian rhythm**)

Internal cyclical process that produces a particular change in a cell or organism with a period of around 24 hours, for example the sleep-wakefulness cycle in humans.

**cis**

On the same or near side.

**cisterna** (plural **cisternae**)

Flattened membrane-bounded compartment, as found in the endoplasmic reticulum or Golgi apparatus. (Figures 13–3 and 13–25)

**citric acid cycle** (**tricarboxylic acid (TCA) cycle**, **Krebs cycle**)

Central metabolic pathway found in aerobic organisms. Oxidizes acetyl groups derived from food molecules, generating the activated carriers NADH and FADH<sub>2</sub>, some GTP, and waste CO<sub>2</sub>. In eucaryotic cells it occurs in the mitochondria. (Panel 2–9, pp. 122–123)

**CKI**—*see* **Cdk inhibitor protein****class I MHC protein**

One of two classes of MHC protein. Found on the surface of almost all vertebrate cell types, where it can present peptides derived from an infecting intracellular microbe (such as a virus) to cytotoxic T cells. (Figure 25–50)

**class II MHC protein**

One of two classes of MHC protein. Found on the surface of various antigen-presenting cells, where it presents foreign peptides to helper T cells. (Figure 25–50)

**class switch**

Change from making one class of immunoglobulin (for example, IgM) to making another class (for example, IgG) that many B cells undergo during the course of an adaptive immune response. Involves DNA rearrangement called class-switch recombination. (Figure 25–41)

**clathrin**

Protein that assembles into a polyhedral cage on the cytosolic side of a membrane so as to form a clathrin-coated pit, which buds off by endocytosis to form an intracellular clathrin-coated vesicle. (Figure 13–6)

**cleavage**

(1) Physical splitting of a cell into two. (2) Specialized type of cell division seen in many early embryos whereby a large cell becomes subdivided into many smaller cells without growth.

**clonal selection theory**

Theory that explains how the adaptive immune system can respond to millions of different antigens in a highly specific way. From a population of lymphocytes with a vast repertoire of randomly generated antigen-specific receptors, a given foreign antigen activates (selects) only those lymphocyte clones that display a receptor that fits the antigen. (Figure 25–8)

**clone**

Population of identical individuals (cells or organisms) formed by repeated (asexual) division from a common ancestor. Also used as a verb: “to clone a gene” means to create multiple copies of a gene by growing a clone of carrier cells (such as *E. coli*) into which the gene has been introduced, and from which it can be recovered, by recombinant DNA techniques.

**cloning vector**

Small DNA molecule, usually derived from a bacteriophage or plasmid, which is used to carry the fragment of DNA to be cloned into the recipient cell, and which enables the DNA fragment to be replicated. (Figure 8–39)

**coactivator**

Protein that does not itself bind DNA but assembles on other DNA-bound gene regulatory proteins to activate transcription of a gene. (Figure 7–51)

**coated vesicle**

Small membrane-bounded organelle with a cage of proteins (the coat) on its cytosolic surface. Formed by the pinching off of a coated region of membrane (coated pit). Some coats are made of clathrin, others are made from other proteins.

**codon**

Sequence of three nucleotides in a DNA or mRNA molecule that represents the instruction for incorporation of a specific amino acid into a growing polypeptide chain.

**coenzyme**

Small molecule tightly associated with an enzyme that participates in the reaction that the enzyme catalyzes, often by forming a covalent bond to the substrate. Examples include biotin, NAD<sup>+</sup>, and coenzyme A.

**coenzyme A (CoA)**

Small molecule used in the enzymatic transfer of acyl groups. *See also* acetyl CoA, and Figure 2–62.

**cofactor**

Inorganic ion or coenzyme required for an enzyme's activity.

**cohesin, cohesin complex**

Complex of proteins that holds sister chromatids together along their length before their separation. (Figure 17–24)

**coiled-coil**

Especially stable rodlike protein structure formed by two or more alpha helices coiled around each other. (Figure 3–9)

**co-immunoprecipitation (co-IP)**

Method of isolating proteins that form a complex with each other by using an antibody specific for one of the partners.

**collagen**

Fibrous protein rich in glycine and proline that is a major component of the extracellular matrix in animals, conferring tensile strength. Exists in many forms: type I, the most common, is found in skin, tendon, and bone; type II is found in cartilage; type IV is present in basal laminae. (Figures 3–23 and 19–66)

**colony-stimulating factor (CSF)**

General name for numerous signal molecules that control differentiation of blood cells.

**complement system**

System of serum proteins activated by antibody-antigen complexes or by microorganisms. Helps eliminate pathogenic microorganisms by directly causing their lysis or by promoting their phagocytosis.

**complementary**

(1) Of nucleic acid sequences: capable of forming a perfect base-paired duplex with each other. (Figure 4–4) (2) Of other interacting molecules, such as an enzyme and its substrate: having biochemical or structural features that marry up, so that noncovalent bonding is facilitated. (Figure 2–16)

**complementary DNA**—*see* **cDNA****complementation** (**genetic complementation**)

Phenomenon in which the mating of two individuals, each showing an abnormal phenotype, results in offspring in which the normal (wild-type) phenotype has been restored. Basis of a test of whether two mutations are in the same or different genes. (Panel 8–1, pp. 554–555)

**complex trait**

Heritable characteristic whose transmission to progeny does not obey simple Mendelian laws. Such traits are due to the interaction of multiple genes and/or gene-environment interactions.



**condensation reaction (dehydration reaction)**

Chemical reaction in which two molecules are covalently linked through  $-OH$  groups with the removal of a molecule of water.

**condensin (condensin complex)**

Complex of proteins involved in chromosome condensation prior to mitosis. Target for M-Cdk. (Figure 17–27)

**conditional mutation**

Mutation that changes a protein or RNA molecule so that its function is altered only under some conditions, such as at an unusually high or unusually low temperature. (Panel 8–1, pp. 554–555)

**confocal microscope**

Type of light microscope that produces a clear image of a given plane within a solid object. It uses a laser beam as a pinpoint source of illumination and scans across the plane to produce a two-dimensional “optical section.”

**connective tissue**

Any supporting tissue that lies between other tissues and consists of cells embedded in a relatively large amount of extracellular matrix. Includes bone, cartilage, and loose connective tissue.

**connexin**

Protein component of gap junctions, a four-pass transmembrane protein. Six connexins assemble in the plasma membrane to form a connexon, or ‘hemichannel.’ (Figure 19–34)

**connexon**

Water-filled pore in the plasma membrane formed by a ring of six connexin protein subunits. Half of a gap junction: connexons from two adjoining cells join to form a continuous channel through which ions and small molecules can pass. (Figure 19–34)

**consensus sequence**

Average or most typical form of a sequence that is reproduced with minor variations in a group of related DNA, RNA, or protein sequences. Indicates the nucleotide or amino acid most often found at each position. Preservation of a sequence implies that it is functionally important. (Figure 6–12)

**constitutive**

Occurring steadily, regardless of circumstances; opposite of regulated.

**constitutive secretory pathway (default pathway)**

Pathway present in all cells by which molecules such as plasma membrane proteins are continually delivered to the plasma membrane from the Golgi apparatus in vesicles that fuse with the plasma membrane. The default route to the plasma membrane if no other sorting signals are present. (Figure 13–63)

**contractile ring**

Ring containing actin and myosin that forms under the surface of animal cells undergoing cell division. Contracts to pinch the two daughter cells apart. (Figure 17–50)

**convergent extension**

Rearrangement of cells within a tissue that causes it to extend in one dimension and shrink in another. (Figure 22–76)

**cooperativity**

Phenomenon in which the binding of one ligand molecule to a target molecule promotes the binding of successive ligand molecules. Seen in the assembly of large complexes, as well as in enzymes and receptors composed of multiple allosteric subunits, where it sharpens the response to a ligand. (Figure 15–25)

**co-receptor**

In immunology: receptor on B cells or T cells that does not bind antigen but binds to other molecules and helps the antigen-binding receptors activate the lymphocyte. (Figure 25–57) More generally: a receptor that collaborates with

another conventional cell-surface receptor, helping the cell respond to secreted signal proteins. Examples are LRP (in the Wnt/ $\beta$ -catenin signaling pathway) and cell-surface proteoglycans. (Figure 15–77)

**co-repressor**

Protein that does not itself bind DNA but assembles on other DNA-bound gene regulatory proteins to inhibit the expression of a gene. (Figure 7–51)

**cortical granule**

Specialized secretory vesicle present under the plasma membrane of unfertilized eggs, including those of mammals. The contents of the cortical granules, released by exocytosis after fertilization, alter the egg coat so as to prevent the entry of further sperm.

**co-translational**

Occurring as translation proceeds. Examples include the import of a protein into the endoplasmic reticulum before the polypeptide chain is completely synthesized (co-translational translocation, Figure 12–35), and the folding of a nascent protein into its secondary and tertiary structure as it emerges from a ribosome. (Figure 6–84)

**co-transport (coupled transport)**

Membrane transport process in which the transfer of one molecule depends on the simultaneous or sequential transfer of a second molecule. (Figure 11–8)

**coupled reaction**

Linked pair of chemical reactions in which the free energy released by one serves to drive the other. (Figure 2–51)

**covalent bond**

Stable chemical link between two atoms produced by sharing one or more pairs of electrons. (Figure 2–5 and Panel 2–1, pp. 106–107)

**Cre/lox**

Site-specific recombination system used to produce conditional mutants in which the target gene can be excised in a specific tissue or at a specific time. A site-specific recombinase (Cre) is introduced under the control of a promoter that will activate it as required. The gene to be disrupted is flanked by introduced lox sequences, at which the activated Cre operates to excise the gene. (Figure 5–79)

**crista (plural cristae)**

Invagination of the inner mitochondrial membrane.

**critical concentration**

Concentration of a protein monomer, such as actin or tubulin, that is in equilibrium with the assembled form of the protein (i.e., assembled into actin filaments or microtubules, respectively). (Panel 16–2, pp. 978–979)

**crossover (chiasma)**

In meiotic recombination, a site on the paired chromosomes where a segment of a maternal chromatid is exchanged for a corresponding segment of a homologous paternal chromatid (Figures 21–6 and 21–10)

**cross-strand exchange—see Holliday junction****cryptochrome**

Flavoprotein responsive to blue light, found in both plants and animals. In animals, it is involved in circadian rhythms.

**C terminus (carboxyl terminus)**

The end of a polypeptide chain that carries a free carboxyl ( $-COOH$ ) group. (Figure 3–1)

**cut-and-paste transposition**

Type of movement of a transposable element in which the element is cut out of the DNA and inserted into a new site by a special transposase enzyme. (Figure 5–69)

**cyclic AMP (cAMP)**

Nucleotide that is generated from ATP by adenylyl cyclase in response to various extracellular signals. It acts as small

- intracellular signaling molecule, mainly by activating cAMP-dependent protein kinase (PKA). It is hydrolyzed to AMP by a phosphodiesterase. (Figure 15–34)
- cyclic AMP-dependent protein kinase (protein kinase A, PKA)**  
Enzyme that phosphorylates target proteins in response to a rise in intracellular cyclic AMP. (Figure 15–35)
- cyclic GMP (cGMP)**  
Nucleotide that is generated from GTP by guanylyl cyclase in response to various extracellular signals.
- cyclin**  
Protein that periodically rises and falls in concentration in step with the eucaryotic cell cycle. Cyclins activate crucial protein kinases (called cyclin-dependent protein kinases, or Cdk) and thereby help control progression from one stage of the cell cycle to the next.
- cyclin-Cdk complex**  
Protein complex formed periodically during the eucaryotic cell cycle as the level of a particular cyclin increases. A cyclin-dependent kinase (Cdk) then becomes partially activated. (Figures 17–15 and 17–16, and Table 17–1, p. 1063)
- cyclin-dependent kinase (Cdk)**  
Protein kinase that has to be complexed with a cyclin protein in order to act. Different Cdk-cyclin complexes trigger different steps in the cell-division cycle by phosphorylating specific target proteins. (Figure 17–15)
- cyclosome—see anaphase-promoting complex**
- cytochrome**  
Colored heme-containing protein that transfers electrons during respiration and photosynthesis.
- cytochrome *b-c<sub>1</sub>* complex**  
Second of the three electron-driven proton pumps in the respiratory chain. Accepts electrons from ubiquinone. (Figure 14–26)
- cytochrome *c***  
Soluble component of the mitochondrial electron-transport chain. Its release into the cytosol from the mitochondrial intermembrane space also initiates apoptosis. (Figure 14–26)
- cytochrome oxidase complex**  
Third of the three electron-driven proton pumps in the respiratory chain. It accepts electrons from cytochrome *c* and generates water using molecular oxygen as an electron acceptor. (Figure 14–26)
- cytokine**  
Extracellular signal protein or peptide that acts as a local mediator in cell–cell communication.
- cytokine receptor**  
Cell-surface receptor that binds a specific cytokine or hormone and acts through the Jak–STAT signaling pathway. (Figure 15–68)
- cytokinesis**  
Division of the cytoplasm of a plant or animal cell into two, as distinct from the associated division of its nucleus (which is mitosis). Part of M phase. (Panel 17–1, pp. 1072–1073)
- cytoplasm**  
Contents of a cell that are contained within its plasma membrane but, in the case of eucaryotic cells, outside the nucleus.
- cytoplasmic tyrosine kinase**  
Enzymes activated by certain cell-surface receptors (tyrosine-kinase-associated receptors) that transmit the receptor signal onwards by phosphorylating target cytoplasmic proteins on tyrosine side chains.
- cytoskeleton**  
System of protein filaments in the cytoplasm of a eucaryotic cell that gives the cell shape and the capacity for directed movement. Its most abundant components are actin filaments, microtubules, and intermediate filaments.
- cytosol**  
Contents of the main compartment of the cytoplasm, excluding membrane-bounded organelles such as endoplasmic reticulum and mitochondria.
- cytotoxic T cell (killer T cell)**  
Type of T cell responsible for killing host cells infected with a virus or another type of intracellular pathogen.
- DAG—see diacylglycerol**
- dalton**  
Unit of molecular mass. Approximately equal to the mass of a hydrogen atom ( $1.66 \times 10^{-24}$  g).
- death receptor**  
Transmembrane receptor protein that can signal the cell to undergo apoptosis when it binds its extracellular ligand. (Figure 18–6)
- default secretory pathway—see constitutive secretory pathway**
- degenerate**  
Not a moral judgment but an adjective describing multiple states that amount to the same thing: different triplet combinations of nucleotide bases (codons) that code for the same amino acid, for example.
- dehydration reaction—see condensation reaction**
- dehydrogenase**  
Enzyme that removes a hydride ion ( $H^-$ ), equivalent to a proton plus two electrons from a substrate molecule.
- delta *G*—see free-energy change**
- delta *G*<sup>o</sup>—see standard free-energy change**
- denaturation**  
Dramatic change in conformation of a protein or nucleic acid caused by heating or by exposure to chemicals. Usually results in the loss of biological function.
- dendrite**  
Extension of a nerve cell, often elaborately branched, that receives stimuli from other nerve cells.
- dendritic cell**  
The most potent type of antigen-presenting cell, which takes up antigen and processes it for presentation to T cells.
- deoxyribonucleic acid—see DNA**
- deoxyribose**  
The five-carbon monosaccharide component of DNA. Differs from ribose in having H at the 2-carbon position rather than OH.  $C_5H_{10}O_4$ . Compare ribose.
- depolarization**  
Shift in a cell's membrane potential to a less negative value inside.
- dermis**  
Thick underlying layer of connective tissue in the skin, beneath the epidermis. Rich in collagen.
- desensitization—see adaptation**
- desmosome**  
Anchoring cell–cell junction, usually formed between two epithelial cells. Characterized by dense plaques of protein into which intermediate filaments in the two adjoining cells insert. (Figure 19–3)
- determination**  
In developmental biology, an embryonic cell is said to be determined if it has become committed to a particular specialized path of development. Determination reflects a change in the internal character of the cell, and it precedes the much more readily detected process of cell differentiation.
- diacylglycerol (DAG)**  
Lipid produced by the cleavage of inositol phospholipids in response to extracellular signals. Composed of two fatty acid

chains linked to glycerol, it serves as a small signaling molecule to help activate protein kinase C (PKC). (Figure 15–38)

#### **dideoxy method**

The standard enzymatic method of DNA sequencing. (Figure 8–50)

#### **differential-interference-contrast microscope**

Type of light microscope that exploits the interference effects that occur when light passes through parts of a cell of different refractive indexes. Used to view unstained living cells.

#### **differentiation**

Process by which a cell undergoes a change to an overtly specialized cell type.

#### **diffusion**

Net drift of molecules in the direction of lower concentration due to random thermal movement.

#### **diploid**

Containing a double genome (two sets of homologous chromosomes and hence two copies of each gene or genetic locus). *Compare* haploid.

#### **dissociation constant ( $K_d$ )**

Measure of the tendency of a complex to dissociate. For components A and B and the binding equilibrium  $A + B \rightleftharpoons AB$ , the dissociation constant is given by  $[A][B]/[AB]$ , and it is smaller the tighter the binding between A and B. The dissociation constant ( $K_d$ ) is the reciprocal of  $K_a$ . *See also* affinity constant, equilibrium constant. (Figure 3–43)

#### **disulfide bond (–S–S–)**

Covalent linkage formed between two sulfhydryl groups on cysteines. For extracellular proteins, a common way of joining two proteins together or linking different parts of the same protein. Formed in the endoplasmic reticulum of eucaryotic cells. (Panel 2–1, p. 107, and Figure 3–28)

#### **DNA (deoxyribonucleic acid)**

Polynucleotide formed from covalently linked deoxyribonucleotide units. The store of hereditary information within a cell and the carrier of this information from generation to generation. (Figure 4–3 and Panel 2–6, pp. 116–117)

#### **DNA affinity chromatography**

Technique for purifying sequence-specific DNA-binding proteins by their binding to a matrix to which the appropriate DNA fragments are attached. (Figure 7–28)

#### **DNA footprinting**

Technique for determining the DNA sequence to which a DNA-binding protein binds. (Figure 7–29)

#### **DNA helicase**

Enzyme that is involved in opening the DNA helix into its single strands for DNA replication.

#### **DNA library**

Collection of cloned DNA molecules, representing either an entire genome (genomic library) or complementary DNA copies of the mRNA produced by a cell (cDNA library).

#### **DNA ligase**

Enzyme that joins the ends of two strands of DNA together with a covalent bond to make a continuous DNA strand.

#### **DNA methylation**

Addition of methyl groups to DNA. Extensive methylation of the cytosine base in CG sequences is used in vertebrates to keep genes in an inactive state.

#### **DNA microarray**

A large array of short DNA molecules (each of known sequence) bound to a glass microscope slide or other suitable support. Used to monitor expression of thousands of genes simultaneously: mRNA isolated from test cells is converted to cDNA, which in turn is hybridized to the microarray. (Figure 8–73)

#### **DNA-only transposon**

Transposable element that exists as DNA throughout its life cycle. Many move by cut-and-paste transposition. *See also* transposon.

#### **DNA polymerase**

Enzyme that synthesizes DNA by joining nucleotides together using a DNA template as a guide.

#### **DNA primase**

Enzyme that synthesizes a short strand of RNA on a DNA template, producing a primer for DNA synthesis. (Figure 5–11)

#### **DNA replication**

Process by which a copy of a DNA molecule is made.

#### **DNA tumor virus**

General term for a variety of different DNA viruses that can cause tumors. (Figure 20–43)

#### **domain (protein domain)**

Portion of a protein that has a tertiary structure of its own. Larger proteins are generally composed of several domains, each connected to the next by short flexible regions of polypeptide chain. Homologous domains are recognized in many different proteins.

#### **dominant**

In genetics, the member of a pair of alleles that is expressed in the phenotype of an organism while the other allele is not, even though both alleles are present. Opposite of recessive. (Panel 8–1, pp. 554–555)

#### **dominant negative mutation**

Mutation that dominantly affects the phenotype, blocking gene activity and causing a loss-of-function phenotype even in the presence of a normal copy of the gene. (Panel 8–1, pp. 554–555)

#### **double helix**

The three-dimensional structure of DNA, in which two antiparallel DNA chains, held together by hydrogen bonding between the bases, are wound into a helix. (Figure 4–5)

#### ***Drosophila melanogaster***

Species of small fly, commonly called a fruit fly. A model organism in molecular genetics.

#### **duplex DNA**

Double-stranded DNA.

#### **dynamic instability**

Sudden conversion from growth to shrinkage, and vice versa, in a protein filament such as a microtubule or actin filament. (Panel 16–2, pp. 978–979)

#### **dynamamin**

Cytosolic GTPase that binds to the neck of a clathrin-coated vesicle in the process of budding from the membrane, and which is involved in completing vesicle formation.

#### **dynein**

Large motor protein that undergoes ATP-dependent movement along microtubules.

#### ***E. coli*—see *Escherichia coli***

#### **ectoderm**

Embryonic epithelial tissue that is the precursor of the epidermis and nervous system.

#### **effector cell**

Cell that carries out the final response or function in a particular process. The main effector cells of the immune system, for example, are activated lymphocytes and phagocytes that help eliminate pathogens.

#### **E2F protein**

Gene regulatory protein that switches on many genes that encode proteins required for entry into the S-phase of the cell cycle.



**eIF**—*see* eucaryotic initiation factor

**elastic fiber**

Extensible fiber formed by the protein elastin in many animal connective tissues, such as in skin, blood vessels, and lungs, which gives them their stretchability and resilience.

**elastin**

Extracellular protein that forms extensible fibers (elastic fibers) in connective tissues.

**electrochemical gradient**

Combined influence of a difference in the concentration of an ion on two sides of a membrane and the electrical charge difference across the membrane (membrane potential). Ions or charged molecules can move passively only down their electrochemical gradient.

**electron**

Negatively charged subatomic particle that orbits the nucleus in an atom. (Figure 2–1)

**electron acceptor**

Atom or molecule that takes up electrons readily, thereby gaining an electron and becoming reduced.

**electron carrier**

Molecule such as cytochrome *c*, NADH, NADPH, and FADH<sub>2</sub> which carries electrons and transfers them from donor molecules to acceptor molecules. *See also* electron transport chain, and Figure 2–60.

**electron donor**

Molecule that easily gives up an electron, becoming oxidized in the process.

**electron microscope**

Microscope that uses a beam of electrons to create the image.

**electron-microscope tomography (EM tomography)**

Technique for viewing three-dimensional specimens in the electron microscope in which multiple views are taken from different directions by tilting the specimen holder. The views are combined computationally to give a three-dimensional image.

**electron-transport chain**

Series of reactions in which electron carrier molecules pass electrons ‘down the chain’ from a higher to successively lower energy levels, to a final acceptor molecule. The energy released during electron movement can be used to power various processes. Electron-transport chains present in the inner mitochondrial membrane (called the respiratory chain) and in the thylakoid membrane of chloroplasts generate a proton gradient across the membrane that is used to drive ATP synthesis. *See especially* Figures 14–3 and 14–10.

**electrophoresis**

Technique for separating molecules (typically proteins or nucleic acids) on the basis of their speed of migration through a porous medium when subjected to a strong electric field.

**electroporation**

Method for introducing DNA into cells, especially bacteria, in which a brief electric shock makes the cell membrane temporarily permeable to the foreign DNA.

**elongation factor (EF)**

Nomenclature used in both transcription and translation. In transcription, elongation factors associate with RNA polymerase and allow it to transcribe long stretches of DNA without dissociating. In translation, elongation factors bind to the ribosome and, by hybridizing GTP, drive the addition of amino acids to the growing polypeptide chain.

**EM tomography**—*see* electron-microscope tomography

**embryonic stem cell (ES cell)**

Cell derived from the inner cell mass of the early mammalian

embryo. Capable of giving rise to all the cells in the body. Can be grown in culture, genetically modified, and inserted into a blastocyst to develop a transgenic animal.

**endocrine**

Relating to hormones or the glands that secrete them.

**endocrine cell**

Specialized animal cell that secretes a hormone into the blood. Usually part of a gland, such as the thyroid or pituitary gland.

**endocrine signaling**

Signaling via hormones released by endocrine glands into the bloodstream and carried to distant target cells that have receptors that bind the specific hormone. (Figures 15–4 and 15–5)

**endocytosis**

Uptake of material into a cell by an invagination of the plasma membrane and its internalization in a membrane-bounded vesicle. *See also* pinocytosis and phagocytosis.

**endoderm**

Embryonic tissue that is the precursor of the gut and associated organs.

**endonuclease**

Enzyme that cleaves nucleic acids *within* the polynucleotide chain. *Compare* exonuclease.

**endoplasmic reticulum (ER)**

Labyrinthine membrane-bounded compartment in the cytoplasm of eucaryotic cells, where lipids are synthesized and membrane-bound proteins and secretory proteins are made. (Figure 12–36)

**endosome**

Membrane-bounded organelle in animal cells that carries materials newly ingested by endocytosis and passes many of them on to lysosomes for degradation.

**endothelial cell**

Flattened cell type that forms a sheet (the endothelium) lining all blood and lymphatic vessels.

**enhancer**

Regulatory DNA sequence to which gene regulatory proteins bind, increasing the rate of transcription of a structural gene that can be many thousands of base pairs away.

**entropy (S)**

Thermodynamic quantity that measures the degree of disorder or randomness in a system; the higher the entropy, the greater the disorder. (Panel 2–7, pp. 118–119)

**enveloped virus**

Virus with a capsid surrounded by a lipid bilayer membrane (the envelope), which is derived from the host cell plasma membrane when the virus buds from the cell. (Figure 24–15)

**enzyme**

Protein that catalyzes a specific chemical reaction.

**enzyme-coupled receptor**

A major type of cell-surface receptor that has a cytoplasmic domain that either has enzymatic activity or is associated with an intracellular enzyme. In either case, the enzymatic activity is stimulated by an extracellular ligand binding to the receptor. (Figure 15–16)

**Eph receptor**

The most numerous type of receptor tyrosine kinase (RTK) that recognizes Ephrins. (Figure 15–52)

**Ephrin**

One of a family of membrane-bound protein ligands for the Eph receptor tyrosine kinases (RTKs) that, among many other functions, stimulate repulsion or attraction responses that guide the migration of cells and nerve cell axons during animal development.

**epidermis**

Epithelial layer covering the outer surface of the body. Has different structures in different animal groups. The outer layer of plant tissue is also called the epidermis.

**epigenetic inheritance**

Inheritance of phenotypic changes in a cell or organism that do not result from changes in the nucleotide sequence of DNA. Can be due to positive feedback loops of gene regulatory proteins or to heritable modifications in chromatin such as DNA methylation or histone modifications causing heterochromatin formation. (Figures 4–35 and 7–86)

**epinephrine—see adrenaline****epistatic**

Describes a mutation in one gene that masks the effect of a mutation in another gene when both mutations are present in the same organism or cell.

**epithelium (plural epithelia)**

Sheet of cells covering the outer surface of a structure or lining a cavity.

**epitope—see antigenic determinant****equilibrium constant ( $K$ )**

Ratio of forward and reverse rate constants for a reaction. Equal to the association or affinity constant ( $K_a$ ) for a simple binding reaction ( $A + B \rightleftharpoons AB$ ). See also affinity constant, dissociation constant. (Figure 3–43)

**ER—see endoplasmic reticulum****ER lumen**

Space enclosed by the membrane of the endoplasmic reticulum (ER).

**ER resident protein**

Protein that remains in the endoplasmic reticulum (ER) or its membranes and carries out its function there, as opposed to proteins that are present in the ER only in transit.

**ER retention signal**

Short amino acid sequence on a protein that prevents it from moving out of the endoplasmic reticulum (ER). Found on proteins that are resident in the ER and function there.

**ER signal sequence**

N-terminal signal sequence that directs proteins to enter the endoplasmic reticulum (ER). Cleaved off by signal peptidase after entry.

**erythrocyte (red blood cell)**

Small hemoglobin-containing blood cell of vertebrates that transports oxygen to, and carbon dioxide from, tissues. (Figure 11–40)

**erythropoietin**

A hormone produced by the kidney that stimulates the production of red blood cells in bone marrow.

**ES cell—see embryonic stem cell*****Escherichia coli* (*E. coli*)**

Rodlike bacterium normally found in the colon of humans and other mammals and widely used in biomedical research.

**ester**

Molecule formed by the condensation reaction of an alcohol group with an acidic group. Phosphate groups usually form esters when linked to a second molecule. (Panel 2–1, pp. 106–107)

**eubacteria**

True bacteria, in contradistinction to archaea (archaeobacteria). (Figure 1–21)

**eucaryote (eukaryote)**

Organism composed of one or more cells that have a distinct nucleus. Member of one of the three main divisions of the living world, the other two being Bacteria and Archaea. (Figure 1–21)

**eucaryotic initiation factor (eIF)**

Protein that helps load initiator tRNA on to the ribosome, thus initiating translation.

**euchromatin**

Region of an interphase chromosome that stains diffusely; “normal” chromatin, as opposed to the more condensed heterochromatin.

**excision repair—see base excision repair****exocytosis**

Process by which most molecules are secreted from a eucaryotic cell. These molecules are packaged into membrane-bounded vesicles that fuse with the plasma membrane and release their contents to the outside.

**exon**

Segment of a eucaryotic gene that consists of a sequence of nucleotides that will be represented in mRNA or in the final transfer, ribosomal, or other mature RNA molecule. In protein-coding genes, exons encode the amino acids in the protein. An exon is usually adjacent to a noncoding DNA segment called an intron. (Figure 4–15)

**exonuclease**

Enzyme that cleaves nucleotides one at a time from the ends of polynucleotides. Compare endonuclease.

**expression vector**

A virus or plasmid that carries a DNA sequence into a suitable host cell and there directs the synthesis of the protein encoded by the sequence. (Figure 8–48)

**extracellular matrix**

Complex network of polysaccharides (such as glycosaminoglycans or cellulose) and proteins (such as collagen) secreted by cells, and in which the cells are embedded.

**extracellular signal molecule**

Any secreted or cell-surface chemical signal that binds to receptors and regulates the activity of the cell expressing the receptor.

**facilitated diffusion—see passive transport****FAD/FADH<sub>2</sub> (flavin adenine dinucleotide/reduced flavin adenine dinucleotide)**

Electron carrier system that functions in the citric acid cycle. One molecule of FAD gains two electrons plus two protons in becoming the activated carrier FADH<sub>2</sub>. (Figure 2–83)

**FAK—see focal adhesion kinase****Fas (Fas protein, Fas death receptor)**

Transmembrane death receptor that initiates apoptosis when it binds its extracellular ligand (Fas ligand). (Figure 18–6)

**fat**

Energy-storage lipid in cells. Composed of triglycerides—fatty acids esterified with glycerol.

**fatty acid**

Carboxylic acid with a long hydrocarbon tail. A major source of energy during metabolism and a starting point for the synthesis of phospholipids. (Panel 2–5, pp. 114–115)

**Fc receptor**

One of a family of cell-surface receptors that bind the tail region (Fc region) of an antibody (immunoglobulin) molecule. Different Fc receptors are specific for different classes of antibodies such as IgG, IgA, or IgE.

**feedback inhibition**

The process in which a product of a reaction feeds back to inhibit a previous reaction in the same pathway. (Figures 3–56 and 3–57)

**fermentation**

Anaerobic energy-yielding metabolic pathway. In anaerobic glycolysis, for instance, pyruvate is converted into lactate or ethanol, with the conversion of NADH to NAD<sup>+</sup>. (Figure 2–71)

**fertilization**

Fusion of a male and a female gamete (both haploid) to form a diploid zygote, which develops into a new individual.

**F<sub>0</sub>F<sub>1</sub> ATPase—see ATP synthase****fibroblast**

Common cell type found in connective tissue. Secretes an extracellular matrix rich in collagen and other extracellular matrix macromolecules. Migrates and proliferates readily in wounded tissue and in tissue culture.

**fibronectin**

Extracellular matrix protein involved in adhesion of cells to the matrix and guidance of migrating cells during embryogenesis. Integrins on the cell surface are receptors for fibronectin.

**filopodium (plural filopodia) (microspike)**

Thin, spike-like protrusion with an actin filament core, generated on the leading edge of a crawling animal cell. (Figure 16–47)

**FISH—see fluorescence *in situ* hybridization****fission yeast**

Common name for the yeast model organism *Schizosaccharomyces pombe*. It divides to give two equal-sized cells.

**fixative**

Chemical reagent such as formaldehyde, glutaraldehyde, or osmium tetroxide used to preserve cells for microscopy. Samples treated with these reagents are said to be 'fixed,' and the process is called fixation.

**flagellum (plural flagella)**

Long, whiplike protrusion whose undulations drive a cell through a fluid medium. Eucaryotic flagella are longer versions of cilia. Bacterial flagella are smaller and completely different in construction and mechanism of action. *Compare* cilium.

**flavin adenine dinucleotide—see FAD/FADH<sub>2</sub>****fluorescence**

Light emission exhibited by some substances (fluorochromes) as their electrons, having been excited by absorption of light, return to their normal lower energy state. The emitted radiation is always at a lower energy (longer wavelength) than the absorbed radiation.

**fluorescence-activated cell sorter (FACS)**

Machine that sorts cells according to their fluorescence. (Figure 8–2)

**fluorescence *in situ* hybridization (FISH)**

Technique in which fluorescently labeled nucleic acid probes hybridize to specific DNA or RNA sequences *in situ*.

**fluorescence microscope**

Microscope designed to view material stained with fluorescent dyes. Similar to a light microscope but the illuminating light is passed through one set of filters before the specimen, to select those wavelengths that excite the dye, and through another set of filters before it reaches the eye, to select only those wavelengths emitted when the dye fluoresces.

**fluorescence recovery after photobleaching (FRAP)**

Technique for monitoring the kinetic parameters of a protein by analyzing how fluorescent protein molecules move into an area of the cell bleached by a beam of laser light.

**fluorescence resonance energy transfer (FRET)**

Technique for monitoring the closeness of two fluorescently labeled molecules (and thus their interaction) in cells. (Figure 8–26)

**focal adhesion, (focal contact, adhesion plaque)**

Anchoring cell junction, forming a small region on the surface of a fibroblast or other cell that is anchored to the extracellular matrix. Attachment is mediated by transmembrane proteins such as integrins, which are linked, through other proteins, to actin filaments in the cytoplasm.

**focal adhesion kinase (FAK)**

Cytoplasmic tyrosine kinase present at cell-matrix junctions (focal adhesions) in association with the cytoplasmic tails of integrins.

**follicle cell**

One of the cell types that surround a developing oocyte or egg. (Figure 21–24)

**footprinting—see DNA footprinting****FRAP—see fluorescence recovery after photobleaching****free energy (G) (Gibbs free energy)**

The energy that can be extracted from a system to drive reactions. Takes into account changes in both energy and entropy. (Panel 2–7, pp. 118–119)

**free-energy change ( $\Delta G$ )**

Change in the free energy during a reaction: the free energy of the product molecules minus the free energy of the starting molecules. A large negative value of  $\Delta G$  indicates that the reaction has a strong tendency to occur. (Panel 2–7, pp. 118–119)

**free radical**

Atom or molecule which is extremely reactive by virtue of its having at least one unpaired electron. Responsible for much intracellular DNA damage.

**free ribosome**

Ribosome that is free in the cytosol, unattached to any membrane.

**freeze-fracture electron microscopy**

Technique for studying membrane structure, in which the membrane of a frozen cell is fractured along the interior of the bilayer, separating it into the two monolayers with the interior faces exposed.

**FRET—see fluorescence resonance energy transfer****fungus (plural fungi)**

Kingdom of eucaryotic organisms that includes the yeasts, molds, and mushrooms. Many plant diseases and a relatively small number of animal diseases are caused by fungi.

**fusion protein**

Engineered protein that combines two or more normally separate polypeptides. Produced from a recombinant gene.

**G—see free energy** **$\Delta G$ —see free energy change** **$\Delta G^\circ$ —see standard free energy change****G<sub>i</sub>—see inhibitory G protein****G<sub>q</sub>**

Class of G protein that couples GPCRs to phospholipase C- $\beta$  to activate the inositol phospholipid signaling pathway.

**G<sub>s</sub>—see stimulatory G protein****GAG—see glycosaminoglycan****gain-of-function mutation**

Mutation that increases the activity of a gene, or makes it active in inappropriate circumstances. Usually dominant. (Panel 8–1, pp. 554–555)

**gamete**

Specialized haploid cell (a sperm or egg) formed from primordial germ cells by meiosis and specialized for sexual reproduction. *See also* germ cell.

**gamma-tubulin ring complex ( $\gamma$ TuRC)**

Protein complex containing  $\gamma$ -tubulin and other proteins that is an efficient nucleator of microtubules and caps their minus ends.

**ganglion (plural ganglia)**

Cluster consisting mainly of neuronal cell bodies and associated glial cells, located outside the central nervous system.



**ganglioside**

Any glycolipid having one or more sialic acid residues in its structure. Found in the plasma membrane of eucaryotic cells and especially abundant in nerve cells. (Figure 10–18)

**GAP—see GTPase-activating protein****gap gene**

In *Drosophila* development, a gene that is expressed in specific broad regions along the anteroposterior axis of the early embryo, and which helps designate the main divisions of the insect body. (Figure 22–37)

**gap junction**

Communicating channel-forming cell–cell junction present in most animal tissues that allows ions and small molecules to pass from the cytoplasm of one cell to the cytoplasm of the next.

**gastrulation**

Stage in animal embryogenesis during which the embryo is transformed from a ball of cells to a structure with a gut (a gastrula). (Figure 22–3)

**G<sub>1</sub>-Cdk**

Cyclin-Cdk complex formed in vertebrate cells by a G<sub>1</sub>-cyclin and the corresponding cyclin-dependent kinase (Cdk). (Table 17–1, p. 1063)

**G<sub>1</sub>-cyclin**

Cyclin present in the G<sub>1</sub> phase of the eucaryotic cell cycle. Forms complexes with Cdks that help govern the activity of the G<sub>1</sub>/S-cyclins, which control progression to S-phase.

**GEF—see guanine nucleotide exchange factor****gel-mobility shift assay**

Technique for detecting proteins bound to a specific DNA sequence by the fact that the bound protein slows down the migration of the DNA fragment through a gel during gel electrophoresis. (Figure 7–27)

**gel-transfer hybridization—see blotting****geminin**

Protein that prevents the formation of new prereplicative complexes during S phase and mitosis, thus ensuring that the chromosomes are replicated only once in each cell cycle.

**gene**

Region of DNA that is transcribed as a single unit and carries information for a discrete hereditary characteristic, usually corresponding to (1) a single protein (or set of related proteins generated by variant post-transcriptional processing), or (2) a single RNA (or set of closely related RNAs).

**gene activator protein—see activator****gene control region**

The set of linked DNA sequences regulating expression of a particular gene. Includes promoter and regulatory sequences required to initiate transcription of the gene and control the rate of initiation. [Figures 7–37 (prokaryotes) and 7–44 (eucaryotes)]

**gene conversion**

Process by which DNA sequence information can be transferred from one DNA helix (which remains unchanged) to another DNA helix whose sequence is altered. It often accompanies general recombination events. (Figure 5–66)

**gene expression**

Production of an observable molecular product (RNA or protein) by a gene.

**general recombination, general genetic recombination—see homologous recombination****general transcription factor**

Any of the proteins whose assembly at a promoter is required for the binding and activation of RNA polymerase and the initiation of transcription. (Table 6–3, p. 341)

**gene regulatory protein**

General name for any protein that binds to a specific DNA sequence to influence the transcription of a gene.

**gene repressor protein—see repressor****genetic code**

Set of rules specifying the correspondence between nucleotide triplets (codons) in DNA or RNA and amino acids in proteins. (Figure 6–50)

**genetic engineering (recombinant DNA technology)**

Collection of techniques by which DNA segments from different sources are combined to make a new DNA, often called a recombinant DNA. Recombinant DNAs are widely used in the cloning of genes, in the genetic modification of organisms, and in molecular biology generally.

**genetic instability**

Abnormally increased spontaneous mutation rate, such as occurs in cancer cells.

**genetic mosaic—see mosaic****genetic recombination—see recombination****genetic redundancy**

The presence of two or more similar genes with overlapping functions.

**genetics**

The study of the genes of an organism on the basis of heredity and variation.

**genetic screen**

Procedure for discovery of genes affecting specific aspects of the phenotype by surveying large numbers of mutagenized individuals.

**genome**

The totality of genetic information belonging to a cell or an organism; in particular, the DNA that carries this information.

**genomic DNA**

DNA constituting the genome of a cell or an organism. Often used in contrast to cDNA (DNA prepared by reverse transcription from mRNA). Genomic DNA clones represent DNA cloned directly from chromosomal DNA, and a collection of such clones from a given genome is a genomic DNA library.

**genomic imprinting**

Phenomenon in which a gene is either expressed or not expressed in the offspring depending on which parent it is inherited from. (Figure 7–82)

**genomics**

Study of the DNA sequences and properties of entire genomes.

**genotype**

Genetic constitution of an individual cell or organism. The particular combination of alleles found in a specific individual. (Panel 8–1, pp. 554–555)

**germ cell**

A cell in the germ line of an organism, which includes the haploid gametes and their specified diploid precursor cells. Germ cells contribute to the formation of a new generation of organisms and are distinct from somatic cells, which form the body and leave no descendants.

**germ layer**

One of the three primary tissue layers (endoderm, mesoderm, and ectoderm) of an animal embryo. (Figure 22–70)

**germ line**

The cell lineage that consists of the haploid gametes and their specified diploid precursor cells.

**GFP—see green fluorescent protein****Gibbs free energy—see free energy**

- giga-**  
Prefix denoting one billion ( $10^9$ ).
- glial cell**  
Supporting nonneural cell of the nervous system. Includes oligodendrocytes and astrocytes in the vertebrate central nervous system and Schwann cells in the peripheral nervous system.
- glucagon**  
Hormone produced in the pancreas that stimulates liver cells to convert stored glycogen to glucose, leading to a rise in blood sugar levels. Effect is opposite to that of insulin.
- glucose**  
Six-carbon sugar that plays a major role in the metabolism of living cells. Stored in polymeric form as glycogen in animal cells and as starch in plant cells. (Panel 2–4, pp. 112–113)
- glycerol**  
Small organic molecule that is the parent compound of many small molecules in the cell, including phospholipids. (Panel 2–5, pp. 114–115)
- glycogen**  
Polysaccharide composed exclusively of glucose units. Used to store energy in animal cells. Large granules of glycogen are especially abundant in liver and muscle cells. (Figure 2–75 and Panel 2–4, pp. 112–113)
- glycolipid**  
Lipid molecule with a sugar residue or oligosaccharide attached. (Panel 2–5, pp. 114–115)
- glycolysis**  
Ubiquitous metabolic pathway in the cytosol in which sugars are incompletely degraded with production of ATP. Literally, “sugar splitting.” (Figure 2–70 and Panel 2–8, pp. 120–121)
- glycoprotein**  
Any protein with one or more oligosaccharide chains covalently linked to amino-acid side chains. Most secreted proteins and most proteins exposed on the outer surface of the plasma membrane are glycoproteins.
- glycosaminoglycan (GAG)**  
Long, linear, highly charged polysaccharide composed of a repeating pair of sugars, one of which is always an amino sugar. Mainly found covalently linked to a protein core in extracellular matrix proteoglycans. Examples include chondroitin sulfate, hyaluronan, and heparin. (Figure 19–55)
- glycosidic bond**  
Chemical bond formed by a condensation reaction between a hydroxyl group on the sugar carbon atom that carries the aldehyde or the ketone and another molecule, often another sugar. Glycosidic bonds are found in numerous structures including polysaccharides, nucleic acids, and glycoproteins. See *O*-linked and *N*-linked oligosaccharides. (Panel 2–4, pp. 112–113)
- glycosylase—see DNA glycosylase**
- glycosylation**  
Addition of one or more sugars to a protein or lipid molecule.
- glycosylphosphatidylinositol anchor—see GPI anchor**
- G<sub>2</sub>/M checkpoint**  
Point in the eucaryotic cell cycle at which the cell checks for completion of DNA replication before triggering the early mitotic events that lead to chromosome alignment on the spindle. (Figure 17–14)
- Golgi apparatus (Golgi complex)**  
Complex organelle in eucaryotic cells, centered on a stack of flattened membrane-bounded spaces, in which proteins and lipids transferred from the endoplasmic reticulum are modified and sorted. It is the site of synthesis of many cell wall polysaccharides in plants and extracellular matrix glycosaminoglycans in animal cells. (Figure 13–25)
- G<sub>0</sub> phase**  
State of withdrawal from the eucaryotic cell-division cycle by entry into a quiescent digression from the G<sub>1</sub> phase. A common, sometimes permanent, state for differentiated cells.
- G<sub>1</sub> phase**  
Gap 1 phase of the eucaryotic cell-division cycle, between the end of mitosis and the start of DNA synthesis. (Figure 17–4)
- G<sub>2</sub> phase**  
Gap 2 phase of the eucaryotic cell-division cycle, between the end of DNA synthesis and the beginning of mitosis. (Figure 17–4)
- GPI anchor (glycosylphosphatidylinositol anchor)**  
Lipid linkage by which some membrane proteins are bound to the membrane. The protein is joined, via an oligosaccharide linker, to a phosphatidylinositol anchor during its travel through the endoplasmic reticulum. (Figure 10–19(6))
- G protein (trimeric GTP-binding protein)**  
A trimeric GTP-binding protein with intrinsic GTPase activity that couples GPCRs to enzymes or ion channels in the plasma membrane. (Table 15–3, p. 919)
- G-protein-coupled receptor (GPCR)**  
A seven-pass cell-surface receptor that, when activated by its extracellular ligand, activates a G protein, which in turn, activates either an enzyme or ion channel in the plasma membrane. (Figures 15–16 and 15–30)
- grana (singular granum)**  
Stacked membrane discs (thylakoids) in chloroplasts that contain chlorophyll and are the site of the light-trapping reactions of photosynthesis. (Figures 14–35 and 14–36)
- granulocyte**  
Category of white blood cell distinguished by conspicuous cytoplasmic granules. Includes neutrophils, basophils, and eosinophils. Arises from a granulocyte/macrophage (GM) progenitor cell. (Figure 23–37)
- green fluorescent protein (GFP)**  
Fluorescent protein isolated from a jellyfish. Widely used as a marker in cell biology.
- growth cone**  
Migrating motile tip of a growing nerve cell axon or dendrite. (Figure 16–105)
- growth factor**  
Extracellular signal protein that can stimulate a cell to grow. They often have other functions as well, including stimulating cells to survive or proliferate. Examples include epidermal growth factor (EGF) and platelet-derived growth factor (PDGF).
- G<sub>1</sub>/S-Cdk**  
Cyclin-Cdk complex formed in vertebrate cells by a G<sub>1</sub>/S-cyclin and the corresponding cyclin-dependent kinase (Cdk). (Figure 17–16 and Table 17–1, p. 1063)
- G<sub>1</sub>/S-cyclin**  
Cyclin that activates Cdks in late G<sub>1</sub> of the eucaryotic cell cycle and thereby helps trigger progression through Start, resulting in a commitment to cell-cycle entry. Its level falls at the start of S phase. (Figure 17–16)
- GTP (guanosine 5′-triphosphate)**  
Nucleoside triphosphate produced by the phosphorylation of GDP (guanosine diphosphate). Like ATP, it releases a large amount of free energy on hydrolysis of its terminal phosphate group. Has a special role in microtubule assembly, protein synthesis, and cell signaling. (Figure 2–83)
- GTPase**  
An enzyme that converts GTP to GDE. GTPases fall into two large families. Large **trimeric G proteins** are composed of three different subunits and mainly couple GPCRs to enzymes or ion channels in the plasma membrane. Small

**monomeric GTP-binding proteins** (also called **monomeric GTPases**) consist of a single subunit and help relay signals from many types of cell-surface receptors and have roles in intracellular signaling pathways, regulating intracellular vesicle trafficking, and signaling to the cytoskeleton. Both trimeric G proteins and monomeric GTPases cycle between an active GTP-bound form and an inactive GDP-bound form and frequently act as molecular switches in intracellular signaling pathways. (Figure 15–19)

**GTPase-activating protein (GAP)**

Protein that binds to a GTPase and inhibits it by stimulating its GTPase activity, causing the enzyme to hydrolyze its bound GTP to GDP. (Figure 3–71)

**GTP-binding protein—see GTPase**

**guanine nucleotide exchange factor (GEF)**

Protein that binds to a GTPase and activates it by stimulating it to release its tightly bound GDP, thereby allowing it to bind GTP in its place. (Figure 3–73)

**guanosine triphosphate—see GTP**

**H<sup>+</sup>—see proton**

**H<sup>-</sup>—see hydride ion**

**hair cell—see auditory hair cell**

**haploid**

Having only a single copy of the genome (one set of chromosomes), as in a sperm cell, unfertilized egg, or bacterium. *Compare* diploid.

**haplotype**

Haploid genotype.

**haplotype block**

Combination of alleles and DNA markers that has been inherited in a large, linked block on one chromosome of a homologous pair—undisturbed by genetic recombination—across many generations.

**haplotype map (hapmap)**

Human genome map based on haplotype blocks. Intended to help identify and catalog human genetic variation.

**H chain—see heavy chain**

**heart muscle cell—see muscle cell**

**heat shock protein (Hsp, stress-response protein)**

One of a large family of highly conserved molecular chaperone proteins, so named because they are synthesized in increased amounts in response to an elevated temperature or other stressful treatment. Hsps have important roles in aiding correct protein folding or refolding. Prominent examples are Hsp60 and Hsp70.

**heavy chain (H chain)**

The larger of the two types of polypeptide chain in an immunoglobulin molecule.

**Hedgehog protein**

Secreted extracellular signal molecule that has many different roles controlling cell differentiation and gene expression in animal embryos and adult tissues. Excessive Hedgehog signaling can lead to cancer.

**HeLa cells**

'Immortal' line of human epithelial cells that grows vigorously in culture. Derived in 1951 from a human cervical carcinoma.

**helicase—see DNA helicase**

**α helix—see alpha helix**

**helix-loop-helix (HLH)**

DNA-binding structural motif present in many gene regulatory proteins, consisting of a short alpha helix connected by

a flexible loop to a second, longer alpha helix. Its structure enables two HLH-containing proteins to dimerize, forming a complex that binds to DNA. Distinct from the helix-turn-helix motif. (Figure 7–23)

**helix-turn-helix**

DNA-binding structural motif present in many gene regulatory proteins, consisting of two alpha helices held at a fixed angle and connected by a short chain of amino acids, constituting the turn. Proteins containing this motif frequently form symmetric dimers and bind to DNA sequences that are themselves similar and arranged symmetrically. Distinct from the helix-loop-helix motif. (Figures 7–10, 7–11, 7–12)

**helper T cell**

Type of T cell that helps stimulate B cells to make antibodies and macrophages to kill ingested microorganisms. Also helps activate dendritic cells and cytotoxic T cells.

**heme**

Cyclic organic molecule containing an iron atom that carries oxygen in hemoglobin and carries an electron in cytochromes. (Figure 14–22)

**hemidesmosome**

Specialized anchoring cell junction between an epithelial cell and the underlying basal lamina.

**hemopoiesis (hematopoiesis)**

Generation of blood cells, mainly in the bone marrow. (Figure 23–42)

**hemopoietic stem cell**

Self-renewing bone marrow cell that gives rise to all the various types of blood cells, as well as some other cell types.

**hepatocyte**

The major cell type in the liver.

**heterocaryon**

Cell with two or more genetically different nuclei; produced by the fusion of two or more different cells.

**heterochromatin**

Region of a chromosome that remains in the form of unusually condensed chromatin; generally transcriptionally inactive. *Compare* euchromatin.

**heterodimer**

Protein complex composed of two different polypeptide chains.

**heterophilic binding**

Binding between molecules of different kinds, especially those involved in cell–cell adhesion. (Figure 19–8)

**heterozygote**

Diploid cell or individual having two different alleles of one or more specified genes.

**high-energy bond**

Covalent bond whose hydrolysis releases an unusually large amount of free energy under the conditions existing in a cell. A group linked to a molecule by such a bond is readily transferred from one molecule to another. Examples include the phosphodiester bonds in ATP and the thioester linkage in acetyl CoA.

**high-performance liquid chromatography (HPLC)**

Type of chromatography that uses columns packed with tiny beads of matrix; the solution to be separated is pushed through under high pressure.

**histidine-kinase-associated receptor**

Transmembrane receptor found in the plasma membrane of bacteria, yeast, and plant cells, and involved, for example, in sensing stimuli that cause bacterial chemotaxis. Associated with a histidine protein kinase on its cytoplasmic side.

**histone**

One of a group of small abundant proteins, rich in arginine



and lysine. Histones form the nucleosome cores around which DNA is wrapped in eucaryotic chromosomes. (Figure 4–25)

**histone chaperone (chromatin assembly factor)**

Protein that binds free histones, releasing them once they have been incorporated into newly replicated chromatin. (Figure 4–30)

**histone code**

Combinations of chemical modifications to histones (e.g., acetylation, methylation) that are thought to determine how and when the DNA packaged in nucleosomes can be accessed (e.g., for replication or transcription). (Figure 4–44)

**histone H1**

'Linker' (as opposed to 'core') histone protein that binds to DNA where it exits from a nucleosome and helps package nucleosomes into the 30 nm chromatin fiber. (Figure 4–34)

**HIV**

Human immunodeficiency virus, the retrovirus that is the cause of AIDS (acquired immune deficiency syndrome). (Figures 13–19 and 24–16)

**HLH—see helix-loop-helix**

**hnRNP protein (heterogeneous nuclear ribonuclear protein)**

Any of a group of proteins that assemble on newly synthesized RNA, organizing it into a more compact form. (Figure 6–33)

**Holliday junction (cross-strand exchange)**

X-shaped structure observed in DNA undergoing recombination, in which the two DNA molecules are held together at the site of crossing-over, also called a cross-strand exchange. (Figure 5–61)

**homeobox**

Short (180 base pairs long) conserved DNA sequence that encodes a DNA-binding protein motif (homeodomain) famous for its presence in genes that are involved in orchestrating development in a wide range of organisms.

**homeodomain**

DNA-binding domain that defines a class of gene regulatory proteins important in animal development. (Figures 3–13 and 7–13)

**homeotic mutation**

Mutation that causes cells in one region of the body to behave as though they were located in another, causing a bizarre disturbance of the body plan. (Figures 22–42 and 22–127)

**homeotic selector gene**

In *Drosophila* development, a gene that defines and preserves the differences between body segments.

**homolog**

One of two or more genes that are similar in sequence as a result of derivation from the same ancestral gene. The term covers both orthologs and paralogs. (Figure 1–25) See homologous chromosomes.

**homologous**

Genes, proteins, or body structures that are similar as a result of a shared evolutionary origin.

**homologous chromosomes (homologs)**

The maternal and paternal copies of a particular chromosome in a diploid cell.

**homologous recombination (general recombination)**

Genetic exchange between a pair of identical or very similar DNA sequences, typically those located on two copies of the same chromosome. (Figures 5–51, 5–53, 5–59, and 5–64)

**homophilic binding**

Binding between molecules of the same kind, especially those involved in cell–cell adhesion. (Figure 19–8)

**homozygote**

Diploid cell or organism having two identical alleles of a specified gene or set of genes.

**hormone**

Signal molecule secreted by an endocrine cell into the bloodstream, which can then carry it to distant target cells.

**housekeeping gene**

Gene serving a function required in all the cell types of an organism, regardless of their specialized role.

**Hox gene complex**

Cluster of genes coding for gene regulatory factors, each gene containing a homeodomain, and specifying body-region differences. *Hox* mutations typically cause homeotic transformations.

**HPLC—see high-performance liquid chromatography**

**hyaluronan (hyaluronic acid)**

Type of nonsulfated glycosaminoglycan with a regular repeating sequence of up to 25,000 identical disaccharide units, not linked to a core protein. Found in the fluid lubricating joints and in many other tissues. (Figures 19–56 and 19–57)

**hybridization**

In molecular biology, the process whereby two complementary nucleic acid strands form a base-paired duplex DNA-DNA, DNA-RNA, or RNA-RNA molecule. Forms the basis of a powerful technique for detecting specific nucleotide sequences. (Figures 5–54 and 8–36)

**hybridoma**

Cell line used in the production of monoclonal antibodies. Obtained by fusing antibody-secreting B cells with cells of a B lymphocyte tumor. (Figure 8–8)

**hydride ion (H<sup>-</sup>)**

A proton (H<sup>+</sup>) plus two electrons (2e<sup>-</sup>). Equivalent to a hydrogen atom with one extra electron.

**hydrocarbon**

Compound that has only carbon and hydrogen atoms. (Panel 2–1, pp. 106–107)

**hydrogen bond**

Noncovalent bond in which an electropositive hydrogen atom is partially shared by two electronegative atoms. (Panel 2–3, pp. 110–111)

**hydrogen ion**

A proton (H<sup>+</sup>) in an aqueous solution. The basis of acidity. Since the proton readily combines with a water molecule to form H<sub>3</sub>O<sup>+</sup>, it is more accurate to call it a hydronium ion.

**hydrolase**

General term for enzyme that catalyses a hydrolytic cleavage reaction. Includes nucleases and proteases.

**hydrolysis (adjective hydrolytic)**

Cleavage of a covalent bond with accompanying addition of water. General formula: AB + H<sub>2</sub>O → AOH + BH.

**hydronium ion (H<sub>3</sub>O<sup>+</sup>)**

Water molecule associated with an additional proton. The form generally taken by protons in aqueous solution.

**hydrophilic**

Dissolving readily in water. Literally, "water loving."

**hydrophobic (lipophilic)**

Not dissolving readily in water. Literally, "water hating."

**hydrophobic force**

Force exerted by the hydrogen-bonded network of water molecules that brings two nonpolar surfaces together by excluding water between them. (Panel 2–3, pp. 110–111)

**hydroxyl (–OH)**

Chemical group consisting of a hydrogen atom linked to an oxygen, as in an alcohol. (Panel 2–1, pp. 106–107)

**hypertonic**

Having a sufficiently high concentration of solutes to cause water to move out of a cell by osmosis.

**hypervariable region**

Any of three small regions within the variable region of an immunoglobulin or T cell receptor chain that shows the highest variability from molecule to molecule. These regions determine the specificity of the antigen-binding site. (Figure 25–31)

**hypotonic**

Having a sufficiently low concentration of solutes to cause water to move into a cell by osmosis.

**IAP (inhibitor of apoptosis) family**

Intracellular protein inhibitors of apoptosis.

**IF—see initiation factor****Ig—see antibody****Ig superfamily**

Large and diverse family of proteins that contain immunoglobulin domains or immunoglobulin-like domains. Most are involved in cell–cell interactions or antigen recognition. (Figure 25–74)

**imaginal disc**

Group of cells that are set aside, apparently undifferentiated, in the *Drosophila* embryo and which will develop into an adult structure, e.g., eye, leg, wing. Overt differentiation occurs at metamorphosis. (Figure 22–51)

**immortalization**

Production of a cell line capable of an apparently unlimited number of cell divisions. Can be the result of mutations or viral transformation or of fusion of the original cells with cells of a tumor line.

**immune response**

Response made by the immune system when a foreign substance or microorganism enters the body; usually refers to an adaptive immune response. *See also* innate, adaptive, primary, and secondary immune responses.

**immune system**

System of lymphocytes and other cells in the body that provides defense against infection. There are two types of immune systems in vertebrates—innate and adaptive.

**immunoblotting—see blotting****immunoglobulin (Ig)**

An antibody molecule. Higher vertebrates have five classes of immunoglobulin—IgA, IgD, IgE, IgG, and IgM—each with a different role in adaptive immune responses.

**immunoglobulin domain (Ig domain)**

Characteristic protein domain of about 100 amino acids that is found in immunoglobulin light and heavy chains. Similar domains, known as immunoglobulin-like (Ig-like) domains, are present in many other proteins involved in cell–cell interactions and antigen recognition and define the Ig superfamily. (Figure 25–32)

**immunological memory**

Long-lived property of the adaptive immune system that follows a primary immune response to many antigens, in which subsequent encounter with the same antigen will provoke a more rapid and stronger secondary immune response. (Figure 25–10)

**immunoprecipitation (IP)**

Use of a specific antibody to draw the corresponding protein antigen out of solution. The technique can identify complexes of interacting proteins in cell extracts by using an antibody specific for one of the proteins to precipitate the complex. *See also* chromatin immunoprecipitation and co-immunoprecipitation.

**imprinting—see genomic imprinting****inducible promoter**

A regulatory DNA sequence that allows expression of an associated gene to be switched on by a particular molecular or physical stimulus (e.g., heat shock). (Figure 22–49)

**induction (inductive interaction)**

In developmental biology, a change in the developmental fate of one tissue caused by an interaction with another tissue. Such an effect is called an inductive interaction. (Figures 22–10 and 22–16)

**inflammatory response**

Local response of a tissue to injury or infection—characterized by tissue redness, swelling, heat, and pain. Caused by invasion of white blood cells, which release various local mediators such as histamine.

**inhibitor of apoptosis family—see IAP family****inhibitory G protein (G<sub>i</sub>)**

Trimeric G protein that can regulate ion channels and inhibit the enzyme adenylyl cyclase in the plasma membrane. *See also* G protein. (Table 15–3, p. 919)

**inhibitory neurotransmitter**

Neurotransmitter that opens transmitter-gated Cl<sup>-</sup> or K<sup>+</sup> channels in the post-synaptic membrane of a nerve or muscle cell and thus tends to inhibit the generation of an action potential.

**initiation factor (IF and eIF)**

Protein that promotes the proper association of ribosomes with mRNA and is required for the initiation of protein synthesis. Abbreviated eIF in eucaryotes, IF in procaryotes. eIFs help load Met-tRNA<sub>i</sub> on to the ribosome, thus initiating translation. (Figure 6–72)

**initiator tRNA**

Special tRNA that initiates translation. It always carries the amino acid methionine, forming the complex Met-tRNA<sub>i</sub>. (Figure 6–72)

**innate immune response**

Immune response (of both animals and plants) to a pathogen that involves the pre-existing defenses of the body (the innate immune system), which include antimicrobial molecules and phagocytic cells. Such a response is not specific for the pathogen, in contrast to an adaptive immune response.

**inner cell mass**

Cluster of undifferentiated cells in the early mammalian embryo from which the whole of the adult body is derived. (Figure 22–88)

**inositol**

Ring-shaped sugar molecule forming part of inositol phospholipids.

**inositol phospholipid (phosphoinositide)**

A lipid containing a phosphorylated inositol derivative. Minor component of the plasma membrane, but important in demarking different membranes and for intracellular signal transduction in eucaryotic cells. (Figure 15–37)

**inositol phospholipid signaling pathway**

Intracellular signaling pathway that starts with the activation of phospholipase C and the generation of IP<sub>3</sub> and diacylglycerol (DAG) from inositol phospholipids in the plasma membrane. The DAG helps to activate protein kinase C. (Figures 15–38 and 15–39)

**inositol 1,4,5-trisphosphate (IP<sub>3</sub>)**

Small intracellular signaling molecule produced during activation of the inositol phospholipid signaling pathway. Acts to release Ca<sup>2+</sup> from the endoplasmic reticulum. (Figures 15–38 and 15–39)

**in situ hybridization**

Technique in which a single-stranded RNA or DNA probe is used to locate a gene or mRNA molecule in a cell or tissue by hybridization.

**insulator element**

DNA sequence that prevents a gene regulatory protein bound to DNA in the control region of one gene from influencing the transcription of adjacent genes. (Figure 7–62)

**insulin**

Polypeptide hormone that is secreted by  $\beta$  cells in the pancreas to help regulate glucose metabolism in animals. (Figure 3–35)

**integral membrane protein**

Protein that is retained in a membrane by virtue of one or more domains that span or are embedded in the lipid bilayer. (Figure 10–19)

**integrin**

Transmembrane adhesion protein that is involved in the attachment of cells to the extracellular matrix and to each other. (Figure 19–4, and Table 19–2, p. 1135)

**intercalary regeneration**

Type of regeneration that fills in the missing tissues when the cells in two mismatched parts of a structure are grafted together. (Figure 22–56)

**interferon (IFN)**

Member of a class of cytokines secreted by virus-infected cells and certain types of activated T cells. Interferons induce antiviral responses, inhibiting viral replication and stimulating macrophages and natural killer cells to kill virus-infected cells. (Figure 25–60)

**interleukin (IL)**

Secreted cytokine that mainly mediates local interactions between white blood cells (leucocytes) during inflammation and immune responses. (Table 25–4, p. 1598)

**intermediate filament**

Fibrous protein filament (~10 nm diameter) that forms rope-like networks in animal cells. One of the three most prominent types of cytoskeletal filaments. (Panel 16–1, pp. 968–969)

**internal ribosome entry site (IRES)**

Specific site in a eucaryotic mRNA, other than at the 5' end, at which translation can be initiated. (Figure 7–108)

**interphase**

Long period of the cell cycle between one mitosis and the next. Includes  $G_1$  phase, S phase, and  $G_2$  phase. (Figure 17–4)

**interpolar microtubule**

In the mitotic or meiotic spindle, a microtubule interdigitating at the equator with the microtubules emanating from the other pole. (Figure 16–85)

**intracellular signaling protein**

Protein involved in a signaling pathway inside the cell. It usually activates the next protein in the pathway or generates a small intracellular mediator. (Figure 15–1)

**intron**

Noncoding region of a eucaryotic gene that is transcribed into an RNA molecule but is then excised by RNA splicing during production of the mRNA or other functional RNA. (Figure 4–15)

**inversion**

Type of mutation in which a segment of chromosome is inverted. (Panel 8–1, pp. 554–555)

***in vitro***

Taking place in an isolated cell-free extract, as opposed to in a living cell; also sometimes used to distinguish studies in cell cultures from studies in intact organisms. (Latin for “in glass.”)

***in vitro* fertilization (IVF)**

An infertility treatment in which eggs are fertilized with sperm outside the mother's body; successfully fertilized eggs are cultured for a few days, and the early embryos are then transferred into the mother's uterus.

***in vivo***

In an intact cell or organism. Latin for “in life.”

**ion**

An atom that has either gained or lost electrons to acquire a charge; for example  $\text{Na}^+$  and  $\text{Cl}^-$ .

**ion channel**

Transmembrane protein complex that forms a water-filled channel across the lipid bilayer through which specific inorganic ions can diffuse down their electrochemical gradients. (Figure 11–21)

**ion-channel-coupled receptor—see transmitter-gated ion channel****ionic bond (ionic interaction)**

Cohesion due to electrostatic attraction between two atoms, one with a positive charge, the other with a negative charge. One type of noncovalent bond. (Figure 2–5, and Panel 2–3, pp. 110–111)

**ionophore**

Small hydrophobic molecule that dissolves in lipid bilayers and increases their permeability to specific inorganic ions.

**IP<sub>3</sub>—see inositol 1,4,5-trisphosphate****IP<sub>3</sub> receptor (IP<sub>3</sub>-gated Ca<sup>2+</sup>-release channel)**

Gated Ca<sup>2+</sup> channel in the ER membrane that opens on binding cytosolic IP<sub>3</sub>, releasing stored Ca<sup>2+</sup> into the cytosol. (Figure 15–39)

**IRES—see internal ribosome entry site****iron-sulfur center**

Electron-transporting group consisting of either two or four iron atoms bound to an equal number of sulfur atoms, found in a class of electron-transport proteins. (Figure 14–23)

**isoelectric point (pI)**

The pH at which a molecule in solution has no net electric charge and therefore does not move in an electric field. (Figure 8–22)

**isoform**

One of a set of variant forms of a protein, derived either by alternative splicing of a common transcript or as products of different members of a set of closely homologous genes.

**isomer**

Molecule formed from the same atoms and linkages as another but having a different three-dimensional conformation. (Panel 2–4, pp. 112–113)

**isomerase**

Enzyme that catalyzes the rearrangement of bonds within a single molecule. *See also* topoisomerase.

**isoprenoid (polyisoprenoid)**

Lipid molecule with a carbon skeleton based on multiple five-carbon isoprene units. Examples include retinoic acid and dolichol. (Panel 2–5, pp. 114–115)

**isotope**

One of a number of forms of an atom that differ in atomic weight but have the same number of protons and electrons, and therefore the same chemistry. May be either stable or radioactive.

**JAK-STAT signaling pathway**

Signaling pathway activated by cytokines and some hormones, providing a rapid route from the plasma membrane to the nucleus to alter gene transcription. Involves cytoplasmic Janus kinases (JAKs), and signal transducers and activators of transcription (STATs).

**joule**

Standard unit of energy in the meter-kilogram-second system. One joule is the energy delivered in one second by a 1-watt power source. Approximately equal to 0.24 calories.



**K**—*see* equilibrium constant

**$K_a$** —*see* affinity constant

**$K_d$** —*see* dissociation constant

**$K_M$**   
The Michaelis-Menten constant. Equal to the concentration of substrate at which an enzyme works at half its maximum rate. Large values of  $K_M$  usually indicate that the enzyme binds to its substrate with relatively low affinity. (Panel 3–3)

**karyotype**

Display of the full set of chromosomes of a cell, arranged with respect to size, shape, and number.

**keratin**

Protein that forms keratin intermediate filaments, mainly in epithelial cells. Specialized keratins are found in hair, nails, and feathers.

**ketone**

Organic molecule containing a carbonyl group linked to two alkyl groups. (Panel 2–1, p 107)

**killer cell**

Any eucaryotic cell capable of directly killing another eucaryotic cell.

**kinase**

Enzyme that catalyzes the addition of phosphate groups to molecules. *See also* protein kinase.

**kinesin**

Member of one of the two main classes of motor proteins that use the energy of ATP hydrolysis to move along microtubules. (Figure 16–58)

**kinetochore**

Complex structure formed from proteins on a mitotic chromosome to which microtubules attach. Plays an active part in the movement of chromosomes to the poles. Forms on the chromosome centromere. (Figure 17–36)

**kinetochore microtubule**

In the mitotic or meiotic spindle, a microtubule that connects the spindle pole to the kinetochore of a chromosome.

**$K^+$  leak channel**

$K^+$ -transporting ion channel in the plasma membrane of animal cells that remains open even in a “resting” cell. (Panel 11–3, p. 679)

**knockout**

An engineered deletion or inactivating mutation of a gene.

**Krebs cycle**—*see* citric acid cycle

**lagging strand**

One of the two newly synthesized strands of DNA found at a replication fork. The lagging strand is made in discontinuous lengths that are later joined covalently. (Figure 5–7)

**lambda**—*see* bacteriophage lambda

**lamellipodium** (plural **lamellipodia**)

Flattened, sheetlike protrusion supported by a meshwork of actin filaments, which is extended at the leading edge of a crawling animal cell. (Figures 16–86 and 16–87)

**lamin**—*see* nuclear lamin

**laminin**

Extracellular matrix fibrous protein found in basal laminae, where it forms a sheetlike network. (Figures 19–42 and 19–43)

**lampbrush chromosome**

Huge paired chromosome in meiosis in immature amphibian eggs, in which the chromatin forms large stiff loops extending out from the linear axis of the chromosome. (Figure 4–54)

**L chain**—*see* light chain

**leading strand**

One of the two newly synthesized strands of DNA found at a replication fork. The leading strand is made by continuous synthesis in the 5′-to-3′ direction. (Figure 5–7)

**lecithin**—*see* phosphatidylcholine

**lectin**

Protein that binds tightly to a specific sugar. Abundant lectins from plant seeds are used as affinity reagents to purify glycoproteins or to detect them on the surface of cells.

**leptin**

Peptide hormone secreted by fat cells. Helps regulate the desire to eat by suppressing appetite.

**lethal mutation**

Mutation that causes the death of the cell or the organism that contains it. (Panel 8–1, pp. 554–555)

**leucine-rich repeat protein (LRR protein)**

Common type of receptor serine/threonine kinase in plants that contains a tandem array of leucine-rich repeat sequences in its extracellular portion.

**leucine zipper**

Structural motif seen in many DNA-binding proteins in which two alpha helices from separate proteins are joined together in a coiled-coil (rather like a zipper), forming a protein dimer. (Figure 7–19)

**leucocyte**—*see* white blood cell

**leukemia**

Cancer of white blood cells.

**ligand**

Any molecule that binds to a specific site on a protein or other molecule. From Latin *ligare*, to bind.

**ligase**

Enzyme that joins together (ligates) two molecules in an energy-dependent process. DNA ligase, for example, joins two DNA molecules together end-to-end through phosphodiester bonds.

**light chain (L chain)**

One of the smaller polypeptides of a multisubunit protein such as myosin (Figure 16–72) or immunoglobulin. (Figure 25–21)

**lignin**

Network of cross-linked phenolic compounds that forms a supporting network throughout the cell walls of xylem and woody tissue in plants.

**limit of resolution**

In microscopy, the smallest distance apart at which two point objects can be resolved as separate. Just under 0.2 mm for conventional light microscopy, a limit determined by the wavelength of light.

**lipase**

Enzyme that catalyzes the cleavage of fatty acids from the glycerol moiety of a triglyceride.

**lipid**

Organic molecule that is insoluble in water but tends to dissolve in nonpolar organic solvents. A special class, the phospholipids, forms the structural basis of biological membranes. (Panel 2–5, pp. 114–115)

**lipid bilayer (phospholipid bilayer)**

Thin double sheet of phospholipid molecules that forms the core structure of all cell membranes. The two layers of lipid molecules are packed with their hydrophobic tails pointing inward and their hydrophilic heads outward, exposed to water. (Figure 2–22 and Panel 2–5, pp.114–115)

**lipid raft**

Small region of the plasma membrane enriched in sphingolipids and cholesterol. (Figure 10–14)

**lipophilic**—*see* hydrophobic

**liposome**

Artificial phospholipid bilayer vesicle formed from an aqueous suspension of phospholipid molecules. (Figure 10–9)

**local mediator**

Secreted signal molecule that acts locally on nearby cells. (Figure 15–4)

**locus**

In genetics, the position on a chromosome. For example, in a diploid cell different alleles of the same gene occupy the same locus.

**long-term potentiation**

Long-lasting increase (days to weeks) in the sensitivity of certain synapses in the brain, induced by a short burst of repetitive firing in the presynaptic neurons. (Figure 11–42)

**loss-of-function mutation**

Mutation which reduces or abolishes the activity of a gene. Usually recessive. (Panel 8–1, pp. 554–555)

**low-density lipoprotein (LDL)**

Large complex composed of a single protein molecule and many esterified cholesterol molecules, together with other lipids. The form in which cholesterol is transported in the blood and taken up into cells. (Figure 13–50)

**LTP**—*see* long-term potentiation

**lymph**

Colorless fluid containing lymphocytes found in lymphatic vessels. (Figure 25–3)

**lymphocyte**

White blood cell responsible for the specificity of adaptive immune responses. Two main types: B cells, which produce antibody, and T cells, which interact directly with other effector cells of the immune system and with infected cells. T cells develop in the thymus and are responsible for cell-mediated immunity. B cells develop in the bone marrow in mammals and are responsible for the production of circulating antibodies. (Figure 25–7)

**lymphoid organ**

Organ involved in the production or function of lymphocytes. Lymphocytes are produced in primary lymphoid organs and respond to antigen in peripheral lymphoid organs. (Figure 25–3)

**lymphoma**

Cancer of lymphocytes, in which the cancer cells are mainly found in lymphoid organs (rather than in the blood, as in leukemias).

**lysis**

Rupture of a cell's plasma membrane, leading to the release of cytoplasm and the death of the cell.

**lysosome**

Membrane-bounded organelle in eucaryotic cells containing digestive enzymes, which are typically most active at the acid pH found in the lumen of lysosomes. (Figures 12–2 and 13–37)

**lysozyme**

Enzyme that catalyzes the cutting of polysaccharide chains in the cell walls of bacteria.

**M**—*see* M phase

**macrophage**

Phagocytic cell derived from blood monocytes, resident in most tissues but able to roam. It has both scavenger and antigen-presenting functions in immune responses. (Figure 24–53)

**major histocompatibility complex**—*see* MHC complex

**malignant**

Of tumors and tumor cells: invasive and/or able to undergo metastasis. A malignant tumor is a cancer. (Figure 20–3)

**mannose 6-phosphate (M6P)**

Unique marker attached to the oligosaccharides on some glycoproteins destined for lysosomes. (Figure 13–43)

**MAP**—*see* microtubule-associated protein

**MAP kinase (mitogen-activated protein kinase)**

Protein kinase at the end of a three-component signaling module involved in relaying signals from the plasma membrane to the nucleus.

**MAP-kinase module (mitogen-activated protein kinase module)**

An intracellular signaling module composed of three protein kinases, acting in sequence, with MAP kinase as the third. Typically activated by a Ras protein in response to extracellular signals. (Figure 15–78)

**mass spectrometry (MS)**

Technique for identifying compounds on the basis of their precise mass-to-charge ratio. Powerful tool for identifying proteins and sequencing polypeptides. (Figure 8–21)

**maternal-effect gene**

Gene that acts in the mother to specify maternal mRNAs and proteins in the egg. Maternal-effect mutations affect the development of the embryo even if the embryo itself has not inherited the mutant gene.

**mating-type locus (Mat locus)**

In budding yeast, the locus that determines the mating type ( $\alpha$  or  $a$ ) of the haploid yeast cell. (Figure 7–65)

**matrix**

Space or supporting medium within which something is formed. (1) Large internal compartment of the mitochondrion. (2) The corresponding compartment in a chloroplast, more commonly known as the stroma. (3) Extracellular matrix. The extracellular composite of secreted proteins and polysaccharides in which cells are embedded. (Figure 14–37)

**matrix metalloprotease**

$\text{Ca}^{2+}$ - or  $\text{Zn}^{2+}$ -dependent proteolytic enzyme present in the extracellular matrix that degrades matrix proteins. Includes the collagenases.

**M-Cdk (M-phase Cdk)**

Cyclin-Cdk complex formed in vertebrate cells by an M-cyclin and the corresponding cyclin-dependent kinase (Cdk). (Figure 17–16 and Table 17–1, p. 1063)

**Mcm proteins**

Proteins in the eucaryotic cell needed for the initiation of DNA replication; thought to form the helicase present at moving DNA replication forks.

**M-cyclin**

A cyclin found in all eucaryotic cells that promotes the events of mitosis. (Figure 17–16)

**MDR protein**—*see* multidrug resistance protein

**megakaryocyte**

Large myeloid cell with a multilobed nucleus that remains in the bone marrow when mature. Buds off platelets from long cytoplasmic processes. (Figures 23–40 and 23–42)

**meiosis**

Special type of cell division that occurs in sexual reproduction. It involves two successive nuclear divisions with only one round of DNA replication, thereby producing haploid cells from a diploid cell. (Figure 21–5)

**melanocyte**

Cell that produces the dark pigment melanin. Responsible for the pigmentation of skin and hair. (Figure 23–1)

**membrane**

The lipid bilayer plus associated proteins that encloses all cells and, in eucaryotic cells, many organelles as well. (Figure 10–1)

**membrane-bound ribosome**

Ribosome attached to the cytosolic face of the endoplasmic reticulum. The site of synthesis of proteins that enter the endoplasmic reticulum. (Figure 12–41)

**membrane channel—see channel****membrane potential**

Voltage difference across a membrane due to a slight excess of positive ions on one side and of negative ions on the other. A typical membrane potential for an animal cell plasma membrane is  $-60$  mV (inside negative relative to the surrounding fluid). (Figure 11–22)

**membrane transport**

Movement of molecules across a membrane, mediated by a membrane transport protein. (Figures 11–3 and 11–4)

**membrane transport protein**

Membrane protein that mediates the passage of ions or molecules across a membrane. The two main classes are transporters (also called carriers or permeases) and channels. (Figures 11–3 and 11–4)

**meristem**

Organized group of dividing cells whose derivatives give rise to the tissues and organs of a flowering plant. Examples are the apical meristems at the tips of shoots and roots. (Panel 22–2, pp. 1404–1405, and Figure 22–118)

**mesenchyme**

Immature, unspecialized form of connective tissue in animals, consisting of cells embedded in a thin extracellular matrix.

**mesoderm**

Embryonic tissue that is the precursor to muscle, connective tissue, skeleton, and many of the internal organs. (Figures 22–3 and 22–70)

**messenger RNA (mRNA)**

RNA molecule that specifies the amino acid sequence of a protein. Produced in eucaryotes by processing of an RNA molecule made by RNA polymerase as a complementary copy of DNA. It is translated into protein in a process catalyzed by ribosomes. (Figures 6–21 and 6–22)

**metabolism**

The sum total of the chemical processes that take place in living cells. All of catabolism plus anabolism. (Figure 2–36)

**metaphase**

Stage of mitosis at which chromosomes are firmly attached to the mitotic spindle at its equator but have not yet segregated toward opposite poles. (Panel 17–1, pp. 1072–1073)

**metaphase plate**

Imaginary plane at right angles to the mitotic spindle and midway between the spindle poles; the plane in which chromosomes are positioned at metaphase. (Panel 17–1, pp. 1072–1073)

**metaphase-to-anaphase transition**

Checkpoint in the eucaryotic cell cycle preceding sister-chromatid separation at anaphase. If the cell is not ready to proceed to anaphase, the cell cycle is halted at this point. (Figure 17–14, and Panel 17–1, pp. 1072–1073)

**metastasis**

Spread of cancer cells from their site of origin to other sites in the body. (Figures 20–1 and 20–17)

**methyl group ( $-\text{CH}_3$ )**

Hydrophobic chemical group derived from methane ( $\text{CH}_4$ ).

**MHC complex (major histocompatibility complex)**

Complex of genes in vertebrates coding for a large family of cell-surface glycoproteins (MHC proteins). (Figure 25–51)

**MHC protein**

One of a large family of vertebrate cell-surface glycoproteins,

which are members of the Ig superfamily. MHC proteins bind peptide fragments of foreign antigens and present them to T cells to induce an adaptive immune response. *See also* class I MHC protein, class II MHC protein. (Figures 25–49 and 25–50)

**Michaelis-Menten constant—see  $K_M$** **microarray—see DNA microarray****microfilament—see actin filament****micron ( $\mu\text{m}$  or micrometer)**

Unit of measurement equal to  $10^{-6}$  meter or  $10^{-3}$  millimeter.

**micro RNA (miRNA)**

Short (21–26 nucleotide) eucaryotic RNAs, produced by the processing of specialized RNA transcripts coded in the genome, that regulate gene expression through complementary base-pairing with mRNA. Depending on the extent of base pairing, mRNAs can lead either to destruction of the mRNA or to a block in its translation. (Figures 7–112)

**microsome**

Small vesicle derived from endoplasmic reticulum that is produced by fragmentation when cells are homogenized. (Figure 12–37)

**microtubule**

Long hollow cylindrical structure composed of the protein tubulin. It is one of the three major classes of filaments of the cytoskeleton. (Panel 16–1, p. 968)

**microtubule-associated protein (MAP)**

Any protein that binds to microtubules and modifies their properties. Many different kinds have been found, including structural proteins, such as MAP2, and motor proteins, such as dynein. [Not to be confused with the 'MAP' (mitogen-activated protein kinase) of 'MAP kinase.']

**microtubule flux**

Movement of individual tubulin molecules in the microtubules of the spindle towards the poles by loss of tubulin at their minus ends. Helps to generate the poleward movement of sister chromatids after they separate in anaphase. (Figure 17–41)

**microtubule-organizing center (MTOC)**

Region in a cell, such as a centrosome or a basal body, from which microtubules grow.

**microvillus (plural microvilli)**

Thin cylindrical membrane-covered projection on the surface of an animal cell containing a core bundle of actin filaments. Present in especially large numbers on the absorptive surface of intestinal epithelial cells. (Figure 16–50)

**midbody**

Structure formed at the end of cleavage that can persist for some time as a tether between the two daughter cells in animals. (Figure 17–51)

**minus end**

End of a microtubule or actin filament at which the addition of monomers occurs least readily; the "slow-growing" end of the microtubule or actin filament. The minus end of an actin filament is also known as the pointed end. (Panel 16–2, pp. 978–979)

**miRNA—see micro RNA****mismatch repair**

DNA repair process that corrects mismatched nucleotides inserted during DNA replication. A short stretch of newly synthesized DNA including the mismatched nucleotide is removed and replaced with the correct sequence with reference to the template strand. (Figure 5–20)

**mitochondrion (plural mitochondria)**

Membrane-bounded organelle, about the size of a bacterium, that carries out oxidative phosphorylation and produces most of the ATP in eucaryotic cells. (Figure 1–33)



**mitogen**

Extracellular signal molecule that stimulates cells to proliferate.

**mitogen-activated protein kinase—see MAP kinase****mitosis**

Division of the nucleus of a eucaryotic cell, involving condensation of the DNA into visible chromosomes, and separation of the duplicated chromosomes to form two identical sets. From Greek *mitos*, a thread, referring to the threadlike appearance of the condensed chromosomes. (Panel 17-1, pp. 1072-1073)

**mitotic chromosome**

Highly condensed duplicated chromosome with the two new chromosomes still held together at the centromere as sister chromatids.

**mitotic spindle**

Array of microtubules and associated molecules that forms between the opposite poles of a eucaryotic cell during mitosis and serves to move the duplicated chromosomes apart. (Figure 17-28 and Panel 17-1, pp. 1072-1073)

**mobile genetic element**

Genetic element (DNA segment) that can move or copy itself to another position in the genome.

**model organism**

A species that has been studied intensively over a long period and thus serves as a "model" for deriving fundamental biological principles.

**molarity (M)**

Number of moles of a solute per liter of solution. A 'one molar' (1M) solution contains 1 mole of solute dissolved in 1 liter of solution.

**mole**

X grams of a substance, where X is its relative molecular mass (molecular weight). A mole consists of  $6.02 \times 10^{23}$  molecules of the substance.

**molecular chaperone—see chaperone****molecular weight (relative molecular mass)**

Mass of a molecule relative to the mass of a hydrogen atom (strictly, relative to 1/12 of the mass of an atom of  $^{12}\text{C}$ , i.e., one dalton).

**monoclonal antibody**

Antibody secreted by a hybridoma cell line. Because the hybridoma is generated by the fusion of a single B cell with a single tumor cell, each hybridoma produces antibodies that are all identical. (Figure 8-8)

**monocyte**

Type of white blood cell that leaves the bloodstream and matures into a macrophage in tissues. (Figure 23-37)

**monomer**

Small molecular building block that can serve as a subunit, being linked to others of the same type to form a larger molecule (a polymer).

**monomeric GTPase—see GTPase****monosaccharide**

Simple sugar with the general formula  $(\text{CH}_2\text{O})_n$ , where  $n = 3$  to 8. (Panel 2-4, pp. 112-113)

**morphogen**

Signal molecule that can impose a pattern on a field of cells by causing cells in different places to adopt different fates. (Figure 22-13)

**mosaic (genetic mosaic)**

In developmental biology, an individual organism made of a mixture of cells with different genotypes, but developed from a single zygote. Mosaics can arise naturally, as a result of a mutation in cells that give rise to new tissues, or can be made deliberately to aid genetic analysis. *Compare* chimera.

**motif**

Element of structure or pattern that recurs in many contexts. Specifically, a small structural domain that can be recognized in a variety of proteins.

**motor protein**

Protein that uses energy derived from nucleoside triphosphate hydrolysis to propel itself along a linear track (protein filament or other polymeric molecule).

**M6P—see mannose 6-phosphate****M phase**

Period of the eucaryotic cell cycle during which chromosomes are condensed and the nucleus and cytoplasm divide. (Figure 17-4, and Panel 17-1, pp. 1072-1073)

**M-phase Cdk—see M-Cdk****mRNA—see messenger RNA****MTOC—see microtubule-organizing center****mTOR (mammalian target of rapamycin)**

Mammalian serine/threonine protein kinase that is a downstream component of the PI 3-kinase/Akt signaling pathway. mTOR (the yeast homolog is called TOR) is part of two distinct protein complexes, one of which is sensitive to the drug rapamycin and stimulates cell growth, while the other helps activate the protein kinase Akt. (Figures 15-64 and 15-65)

**multidrug resistance protein (MDR protein)**

Type of ABC transporter protein that can pump hydrophobic drugs (such as some anti-cancer drugs) out of the cytoplasm of eucaryotic cells.

**multimeric**

Of proteins: containing more than one subunit.

**multi-pass transmembrane protein**

Membrane protein in which the polypeptide chain crosses the lipid bilayer more than once. (Figure 10-19)

**muscle cell**

Cell type specialized for contraction. The three main classes are skeletal, heart, and smooth muscle cells. (Figure 23-47)

**mutation**

Heritable change in the nucleotide sequence of a chromosome. (Panel 8-1, pp. 554-555)

**Myc**

Gene regulatory protein that is activated when a cell is stimulated to grow and divide by extracellular signals. It activates the transcription of many genes, including those that stimulate cell growth. (Figure 17-62)

**myelin sheath**

Insulating layer of specialized cell membrane wrapped around vertebrate axons. Produced by oligodendrocytes in the central nervous system and by Schwann cells in the peripheral nervous system. (Figure 11-32)

**myeloid cell**

Any white blood cell other than a lymphocyte. (Figure 23-42)

**myoblast**

Mononucleated, undifferentiated muscle precursor cell. A skeletal muscle cell is formed by the fusion of multiple myoblasts. (Figure 23-48)

**myoepithelial cell**

Type of unstriated muscle cell found in epithelia, e.g. in the iris of the eye and in glandular tissue. (Figure 23-47)

**myofibril**

Long, highly organized bundle of actin, myosin, and other proteins in the cytoplasm of muscle cells that contracts by a sliding filament mechanism.

**myosin**

Any of a large class of motor proteins that move along actin filaments. (Figure 16-57)

**NAD<sup>+</sup>/NADH (nicotinamide adenine dinucleotide/reduced nicotinamide adenine dinucleotide)**

Electron carrier system that participates in oxidation-reduction reactions, such as the oxidation of food molecules. NAD<sup>+</sup> accepts the equivalent of a hydride ion (H<sup>-</sup>, a proton plus two electrons) to become the activated carrier NADH. The NADH formed donates its high-energy electrons to the ATP-generating process of oxidative phosphorylation. (Figure 2–86)

**NADH dehydrogenase complex**

First of the three electron-driven proton pumps in the mitochondrial respiratory chain. It accepts electrons from NADH. (Figure 14–26)

**NADP<sup>+</sup>/NADPH (nicotinamide adenine dinucleotide phosphate/reduced nicotinamide adenine dinucleotide phosphate)**

Electron carrier system closely related to NAD<sup>+</sup>/NADH, but used almost exclusively in reductive biosynthetic, rather than catabolic, pathways. (Figure 2–60)

**Na<sup>+</sup>-K<sup>+</sup> pump (Na<sup>+</sup>-K<sup>+</sup> ATPase)**

Transmembrane carrier protein found in the plasma membrane of most animal cells that pumps Na<sup>+</sup> out of and K<sup>+</sup> into the cell, using energy derived from ATP hydrolysis. (Figure 11–14)

**nanometer (nm)**

Unit of length commonly used to measure molecules and cell organelles. 1 nm = 10<sup>-3</sup> micrometer (μm) = 10<sup>-9</sup> meter.

**natural killer cell (NK cell)**

Cytotoxic cell of the innate immune system that can kill virus-infected cells and some cancer cells. (Figure 24–57)

**negative feedback**

Control mechanism whereby the output of a reaction or pathway inhibits an earlier step in the same pathway.

**Nernst equation**

Quantitative expression that relates the equilibrium ratio of concentrations of an ion on either side of a permeable membrane to the voltage difference across the membrane. (Panel 11–2, p. 670)

**nerve cell—see neuron****nerve impulse—see action potential****neural cell adhesion molecule (NCAM)**

Cell adhesion molecule of the immunoglobulin superfamily, expressed by many cell types including most nerve cells. A mediator of Ca<sup>2+</sup>-independent cell-cell attachment in vertebrates. (Figure 19–20)

**neural crest**

Collection of cells located along the line where the neural tube pinches off from the surrounding epidermis in the vertebrate embryo. Neural crest cells migrate to give rise to a variety of tissues, including neurons and glia of the peripheral nervous system, pigment cells of the skin, and the bones of the face and jaws. (Figures 19–11, 22–84, and 22–97)

**neural tube**

Tube of ectoderm that will form the brain and spinal cord in a vertebrate embryo. (Figure 22–78)

**neurite**

Long process growing from a nerve cell in culture. A generic term that does not specify whether the process is an axon or a dendrite. (Figure 16–105)

**neuroblast**

Embryonic nerve cell precursor. (Figure 22–66)

**neurofilament**

Type of intermediate filament found in nerve cells. (Figure 16–22)

**neuromuscular junction**

Specialized chemical synapse between an axon terminal of a

motor neuron and a skeletal muscle cell. (Figures 11–36 and 11–39)

**neuron (nerve cell)**

Impulse-conducting cell of the nervous system, with extensive processes specialized to receive, conduct, and transmit signals. (Figures 22–93 and 22–94)

**neuropeptide**

Peptide secreted by neurons as a signal molecule either at synapses or elsewhere.

**neurotransmitter**

Small signal molecule secreted by the presynaptic nerve cell at a chemical synapse to relay the signal to the postsynaptic cell. Examples include acetylcholine, glutamate, GABA, glycine, and many neuropeptides.

**neutron**

Uncharged heavy subatomic particle that forms part of an atomic nucleus. (Figure 2–1)

**neutrophil**

White blood cell that is specialized for the uptake of particulate material by phagocytosis. Enters tissues that become infected or inflamed. (Figures 24–55 and 25–24)

**NFκB protein**

Latent gene regulatory protein that is activated by various intracellular signaling pathways when cells are stimulated during immune, inflammatory, or stress responses. Also has important roles in animal development. (Figure 15–79)

**nicotinamide adenine dinucleotide—see NAD<sup>+</sup>/NADH****nicotinamide adenine dinucleotide phosphate—see NADP<sup>+</sup>/NADPH****nitric oxide (NO)**

Gaseous signal molecule that is widely used in cell-cell communication in both animals and plants. (Figure 15–12)

**nitrogen fixation**

Biochemical process carried out by certain bacteria that reduces atmospheric nitrogen (N<sub>2</sub>) to ammonia, leading eventually to various nitrogen-containing metabolites.

**NK cell—see natural killer cell****N-linked oligosaccharide**

Chain of sugars attached to a protein through the NH<sub>2</sub> group of the side chain of an asparagine residue. *Compare* O-linked oligosaccharide. (Figures 12–50 and 12–51)

**nm—see nanometer****NMR (nuclear magnetic resonance, NMR spectroscopy)**

NMR is the resonant absorption of electromagnetic radiation at a specific frequency by atomic nuclei in a magnetic field, due to flipping of the orientation of their magnetic dipole moments. The NMR spectrum provides information about the chemical environment of the nuclei. NMR is used widely to determine the three-dimensional structure of small proteins and other small molecules. The principles of NMR are also used for medical diagnostic purposes in magnetic resonance imaging (MRI). (Figure 8–29)

**NO—see nitric oxide****noncovalent bond (noncovalent attraction, noncovalent interaction)**

Chemical bond in which, in contrast to a covalent bond, no electrons are shared. Noncovalent bonds are relatively weak, but they can sum together to produce strong, highly specific interactions between molecules. (Panel 2–3, pp. 110–111)

**noncyclic photophosphorylation**

Photosynthetic process that produces both ATP and NADPH in plants and cyanobacteria. (Figure 14–49)

**nondisjunction**

Event occurring occasionally during meiosis in which a pair

of homologous chromosomes fails to separate so that the resulting germ cell has either too many or too few chromosomes.

**nonenveloped virus**

Virus consisting of a nucleic acid core and a protein capsid only. (Figure 24–24C and D)

**nonpolar (apolar)**

Lacking any asymmetric accumulation of positive and negative charge. Nonpolar molecules are generally insoluble in water. (Panels 2–2 and 2–3, pp. 108–111)

**nonretroviral retrotransposon—see retrotransposon**

**nonsense-mediated mRNA decay**

Mechanism for degrading aberrant mRNAs containing in-frame internal stop codons before they can be translated into protein. (Figure 6–80)

**Northern blotting**

Technique in which RNA fragments separated by electrophoresis are immobilized on a paper sheet, and a specific RNA is then detected by hybridization with a labeled nucleic acid probe.

**NO synthase (NOS)**

Enzyme that synthesizes nitric oxide (NO) by the deamination of arginine. (Figure 15–12B)

**Notch**

Transmembrane receptor protein (and latent gene regulatory protein) involved in many cell-fate choices in animal development, for example in the specification of nerve cells from ectodermal epithelium. Its ligands are cell-surface proteins such as Delta and Serrate. (Figure 15–76)

**notochord**

Stiff rod of cells defining the central axis of all chordate embryos. In vertebrates becomes incorporated into the vertebral column. (Figure 22–97)

**NPC—see nuclear pore complex**

**NSF (N-ethylmaleimide sensitive factor)**

Protein with ATPase activity that disassembles a complex of a v-SNARE and a t-SNARE. (Figures 13–18 and 13–22)

**N terminus (amino terminus)**

The end of a polypeptide chain that carries a free  $\alpha$ -amino group. (Figure 3–1)

**nuclear envelope (nuclear membrane)**

Double membrane (two bilayers) surrounding the nucleus. Consists of an outer and inner membrane and is perforated by nuclear pores. The outer membrane is continuous with the endoplasmic reticulum. (Figures 4–9 and 12–8)

**nuclear export signal**

Sorting signal contained in the structure of molecules and complexes, such as RNAs and new ribosomal subunits, that are transported from the nucleus to the cytosol through nuclear pore complexes. (Figure 12–15)

**nuclear lamin**

Protein subunit of the intermediate filaments that form the nuclear lamina.

**nuclear lamina**

Fibrous meshwork of proteins on the inner surface of the inner nuclear membrane. It is made up of a network of intermediate filaments formed from nuclear lamins.

**nuclear localization signal (NLS)**

Signal sequence or signal patch found in proteins destined for the nucleus that enables their selective transport into the nucleus from the cytosol through the nuclear pore complexes. (Figures 12–11 and 12–15)

**nuclear magnetic resonance—see NMR**

**nuclear pore complex (NPC)**

Large multiprotein structure forming an aqueous channel

(the nuclear pore) through the nuclear envelope that allows selected molecules to move between nucleus and cytoplasm. (Figure 12–9)

**nuclear receptor superfamily**

Intracellular receptors for hydrophobic signal molecules such as steroid and thyroid hormones and retinoic acid. The receptor-ligand complex acts as a transcription factor in the nucleus. (Figure 15–14)

**nuclear transplantation**

Transfer of a nucleus from one cell to another by microinjection. (Figure 8–6)

**nuclear transport receptor (karyopherin)**

Protein that escorts macromolecules either into or out of the nucleus: nuclear import receptor or nuclear export receptor. (Figure 12–15)

**nuclease**

Enzyme that splits nucleic acids by hydrolyzing bonds between nucleotides. *See also* endonuclease and exonuclease.

**nucleation**

Critical stage in the assembly of a polymeric structure, such as a microtubule, in which a small cluster of monomers aggregates in the correct arrangement to initiate rapid polymerization. (Panel 16–2, pp. 978–979) More generally, the rate-limiting step in an assembly process.

**nucleic acid**

RNA or DNA, a macromolecule consisting of a chain of nucleotides joined together by phosphodiester bonds.

**nucleic acid hybridization—see hybridization**

**nucleocapsid**

Viral nucleic acid plus its surrounding protein capsid. If a viral envelope is present, the envelope surrounds the nucleocapsid. (Figure 13–19)

**nucleolar organizer**

Region of a chromosome containing a cluster of rRNA genes that gives rise to part of a nucleolus. (Figure 6–47)

**nucleolus**

Structure in the nucleus where rRNA is transcribed and ribosomal subunits are assembled. (Figure 4–9)

**nucleoporin**

Any of a number of different proteins that make up nuclear pore complexes.

**nucleoside**

Purine or pyrimidine base covalently linked to a ribose or deoxyribose sugar. (Panel 2–6, pp. 116–117)

**nucleosome**

Beadlike structure in eucaryotic chromatin, composed of a short length of DNA wrapped around an octameric core of histone proteins. The fundamental structural unit of chromatin. (Figures 4–23 and 4–24)

**nucleotide**

Nucleoside with one or more phosphate groups joined in ester linkages to the sugar moiety. DNA and RNA are polymers of nucleotides. (Panel 2–6, pp. 116–117)

**nucleotide excision repair**

Type of DNA repair that corrects damage of the DNA double helix, such as those caused by chemical or UV damage, by cutting out the damaged region on one strand and resynthesizing it using the undamaged strand as template. *Compare* base excision repair. (Figure 5–48)

**nucleus**

Prominent membrane-bounded organelle in eucaryotic cells, containing DNA organized into chromosomes.

**null mutation**

Loss-of-function mutation that completely abolishes the activity of a gene. (Panel 8–1, pp. 554–555)



**nurse cell**

Cell in the invertebrate ovary that is connected by cytoplasmic bridges to a developing oocyte and thereby supplies the oocyte with ribosomes, mRNAs, and proteins needed for the development of the early embryo. (Figure 21–24)

**occluding junction**

Type of cell junction that seals cells together in an epithelium, forming a barrier through which even small molecules cannot pass—making the cell sheet an impermeable (or selectively permeable) barrier. (Figure 19–2, and Table 19–1, p. 1133)

**Okazaki fragments**

Short lengths of DNA produced on the lagging strand during DNA replication. Rapidly joined by DNA ligase to form a continuous DNA strand. (Figure 5–7)

**olfactory sensory neuron**

The sensory cell in the nasal olfactory epithelium responsible for detecting odors.

**oligodendrocyte**

Glial cell in the vertebrate central nervous system that forms a myelin sheath around axons. *Compare* Schwann cell.

**oligomer**

Short polymer.

**oligosaccharide**

Short linear or branched chain of covalently linked sugars. (Panel 2–4, pp. 112–113)

**O-linked oligosaccharide**

Chain of sugars attached to a protein through the OH group of serine or threonine residues. *Compare* N-linked oligosaccharide. (Figure 13–32)

**oncogene**

An altered gene whose product can act in a dominant fashion to help make a cell cancerous. Typically, an oncogene is a mutant form of a normal gene (proto-oncogene) involved in the control of cell growth or division. (Figure 20–27)

**oocyte**

Developing egg, before it has completed meiosis. (Figures 21–25 and 21–26)

**oogenesis**

Formation and maturation of oocytes in the ovary. (Figure 21–23)

**open reading frame (ORF)**

A continuous nucleotide sequence free from stop codons in at least one of the three reading frames (and thus with the potential to code for protein).

**operator**

Short region of DNA in a bacterial chromosome that controls the transcription of an adjacent gene. (Figure 7–34)

**operon**

In a bacterial chromosome, a group of contiguous genes that are transcribed into a single mRNA molecule. (Figure 7–34)

**ORC—see origin recognition complex****ORF—see open reading frame****organelle**

Subcellular compartment or large macromolecular complex, often membrane-enclosed, that has a distinct structure, composition, and function. Examples are nucleus, nucleolus, mitochondrion, Golgi apparatus, and centrosomes. (Figure 1–30)

**Organizer (Spemann's Organizer)**

Specialized tissue at the dorsal lip of the blastopore in an amphibian embryo; a source of signals that help to orchestrate formation of the embryonic body axis. (Named after H. Spemann and H. Mangold, co-discoverers) (Figure 22–74)

**origin of replication**

Site in a chromosome where DNA replication starts.

**origin recognition complex (ORC)**

Large protein complex that is bound to the DNA at origins of replication in eucaryotic chromosomes throughout the cell cycle. (Figure 5–36)

**orthologs**

Genes or proteins from different species that are similar in sequence because they are descendants of the same gene in the last common ancestor of those species. *Compare* paralogs. (Figure 1–25)

**osmosis**

Net movement of water molecules across a semipermeable membrane driven by a difference in concentration of solute on either side. The membrane must be permeable to water but not to the solute molecules. (Panel 11–1, p. 664)

**osteoblast**

Cell that secretes matrix of bone. (Figure 23–55)

**osteoclast**

Macrophage-like cell that erodes bone, enabling it to be remodeled during growth and in response to stresses throughout life. (Figure 23–59)

**osteocyte**

Nondividing cell in bone that develops from an osteoblast and is embedded in bone matrix. (Figure 23–55)

**ovulation**

Release of an egg from the ovary. (Figure 21–26)

**ovum**

Mature egg.

**oxidase**

Enzyme that catalyzes an oxidation reaction, especially one in which molecular oxygen is the electron acceptor.

**oxidation (verb oxidize)**

Loss of electrons from an atom, as occurs during the addition of oxygen to a molecule or when a hydrogen is removed. Opposite of reduction. (Figure 2–43)

**oxidative phosphorylation**

Process in bacteria and mitochondria in which ATP formation is driven by the transfer of electrons through the electron transport chain to molecular oxygen. Involves the intermediate generation of a proton gradient (pH gradient) across a membrane and a chemiosmotic coupling of that gradient to the ATP synthase. (Figures 14–10 and 14–14)

**p53**

Tumor suppressor gene found mutated in about half of human cancers. Encodes a gene regulatory protein that is activated by damage to DNA and is involved in blocking further progression through the cell cycle. (Figures 20–37 and 20–40)

**pairing (homolog pairing)**

In meiosis, the lining up of the two homologous chromosomes along their length. (Figure 21–6)

**pair-rule gene**

In *Drosophila* development, a gene expressed in a series of regular transverse stripes along the body of the embryo and which helps to determine its different segments. (Figure 22–37)

**palindromic sequence**

Nucleotide sequence that is identical to its complementary strand when each is read in the same chemical direction—e.g., GATC. (Figure 8–31)

**Par3, Par6**

Scaffold proteins involved in the specification of polarity in individual animal cells; Par3 and Par6 form a complex with atypical protein kinase C (aPKC). (Figure 19–31)

**paracrine signaling**

Short-range cell–cell communication via secreted signal molecules that act on neighboring cells. (Figure 15–4)

**paralogs**

Genes or proteins that are similar in sequence because they are the result of a gene duplication event occurring in an ancestral organism. *Compare* orthologs. (Figure 1–25)

**parthenogenesis**

Production of a new individual from an egg cell in the absence of fertilization by a sperm.

**passive transport (facilitated diffusion)**

Transport of a solute across a membrane down its concentration gradient or its electrochemical gradient, using only the energy stored in the gradient. (Figure 11–4)

**patch-clamp recording**

Electrophysiological technique in which a tiny electrode tip is sealed onto a patch of cell membrane, thereby making it possible to record the flow of current through individual ion channels in the patch. (Figure 11–33)

**pathogen (adjective pathogenic)**

An organism, cell, virus, or prion that causes disease.

**pattern recognition receptor**

Receptor present on or in cells of the innate immune system that recognizes and responds to pathogen-associated molecular patterns (PAMPs)—such as surface carbohydrates on bacteria and viruses and unmethylated GC sequences in bacterial DNA.

**PCR (polymerase chain reaction)**

Technique for amplifying specific regions of DNA by the use of sequence-specific primers and multiple cycles of DNA synthesis, each cycle being followed by a brief heat treatment to separate complementary strands. (Figure 8–45)

**PDZ domain**

Protein-binding domain present in many scaffold proteins, and often used as a docking site for intracellular tails of transmembrane proteins. (Figure 19–21)

**pectin**

Mixture of polysaccharides rich in galacturonic acid which forms a highly hydrated matrix in which cellulose is embedded in plant cell walls. (Figure 19–79)

**pentose**

Five-carbon sugar.

**peptide**

Short polymer of amino acids.

**peptide bond**

Chemical bond between the carbonyl group of one amino acid and the amino group of a second amino acid—a special form of amide linkage. Peptide bonds link amino acids together in proteins. (Panel 3–1, pp. 128–129)

**peripheral lymphoid organ (secondary lymphoid organ)**

Lymphoid organ in which T cells and B cells interact with foreign antigens. Examples are spleen, lymph nodes, and mucosal-associated lymphoid tissue. (Figure 25–3)

**peripheral membrane protein**

Protein that is attached to one face of a membrane only by noncovalent interactions with other membrane proteins, and which can be removed by relatively gentle treatments that leave the lipid bilayer intact. (Figure 10–19)

**permease—see transporter****permissive (nonrestrictive) conditions**

Circumstances (such as temperature or nutrient availability) in which the phenotypic effect of a conditional mutation will be absent: that is, the phenotype will be normal. (Figure 8–55 and Panel 8–1, pp. 554–555)

**peroxisome**

Small membrane-bounded organelle that uses molecular oxygen to oxidize organic molecules. Contains some enzymes that produce and others that degrade hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>). (Figure 12–30)

**pH**

Common measure of the acidity of a solution: “p” refers to power of 10, “H” to hydrogen. Defined as the negative logarithm of the hydrogen ion concentration in moles per liter (M).  $\text{pH} = -\log [\text{H}^+]$ . Thus a solution of pH 3 will contain 10<sup>-3</sup> M hydrogen ions. pH less than 7 is acidic and pH greater than 7 is alkaline.

**phage—see bacteriophage****phagocyte**

General term for a professional phagocytic cell—that is, a cell such as a macrophage or neutrophil that is specialized to take up particles and microorganisms by phagocytosis. (Figures 13–46 and 13–47)

**phagocytosis**

Process by which unwanted cells, debris, and other bulky particulate material is endocytosed (“eaten”) by a cell. Prominent in carnivorous cells, such as *Amoeba proteus*, and in vertebrate macrophages and neutrophils. From Greek *phagein*, to eat. (Figure 24–53)

**phagosome**

Large intracellular membrane-bounded vesicle that is formed as a result of phagocytosis. Contains ingested extracellular material. (Figure 24–30)

**phase-contrast microscope**

Type of light microscope that exploits the interference effects that occur when light passes through material of different refractive indexes. Used to view living cells. (Figures 9–7 and 22–101)

**PH domain—see pleckstrin homology domain****phenotype**

The observable character (including both physical appearance and behavior) of a cell or organism. (Panel 8–1, pp. 554–555)

**phosphatase**

Enzyme that catalyzes the hydrolytic removal of phosphate groups from a molecule.

**phosphatidylcholine (lecithin)**

Common phospholipid present in abundance in most biological membranes. (Figure 10–3)

**phosphatidylinositol**

An inositol phospholipid. (Figure 15–37)

**phosphatidylinositol 4,5-bisphosphate (PI(4,5)P<sub>2</sub>, PIP<sub>2</sub>)**

Membrane inositol phospholipid (a phosphoinositide) that is cleaved by phospholipase C into IP<sub>3</sub> and diacylglycerol at the beginning of the inositol phospholipid signaling pathway. It can also be phosphorylated by PI 3-kinase to produce PIP<sub>3</sub> docking sites for signaling proteins in the PI 3-kinase/Akt signaling pathway. (Figures 15–38 and 15–64)

**phosphoanhydride bond**

High-energy bond linking phosphate groups in, for instance, ATP and GTP. (Panel 2–6, pp. 116–117)

**phosphodiester bond**

A covalent chemical bond formed when two hydroxyl groups form ester linkages to the same phosphate group, such as between adjacent nucleotides in RNA or DNA. (Figure 2–28)

**phosphoglyceride**

Phospholipid derived from glycerol, abundant in biomembranes. (Figures 10–2 and 10–3)

**phosphoinositide—see inositol phospholipid**

**phosphoinositide 3-kinase (PI 3-kinase)**

Membrane-bound enzyme that is a component of the PI 3-kinase/Akt intracellular signaling pathway. It phosphorylates phosphatidylinositol 4,5-bisphosphate at the 3 position on the inositol ring to produce PIP<sub>3</sub> docking sites in the membrane for other intracellular signaling proteins. (Figure 15–64)

**phospholipase C (PLC)**

Membrane-bound enzyme that cleaves inositol phospholipids to produce IP<sub>3</sub> and diacylglycerol in the inositol phospholipid signaling pathway. PLC $\beta$  is activated by GPCRs via specific G proteins, while PLC $\gamma$  is activated by RTKs. (Figures 25–39 and 15–55)

**phospholipid**

The main category of lipids used to construct biomembranes. Generally composed of two fatty acids linked through glycerol (or sphingosine) phosphate to one of a variety of polar groups. (Figure 10–3, and Panel 2–5, pp. 114–115)

**phosphorylation**

Reaction in which a phosphate group is covalently coupled to another molecule.

**phosphorylation cascade**

Series of sequential protein phosphorylations mediated by a series of protein kinases, each of which phosphorylates and activates the next kinase in the chain. Such cascades are common in intracellular signaling pathways. (Figure 15–60)

**photoactivation**

Technique for studying intracellular processes in which an inactive form of a molecule of interest is introduced into the cell, and is then activated by a focused beam of light at a precise spot in the cell. (Figure 9–30)

**photochemical reaction center**

The part of a photosystem that converts light energy into chemical energy in photosynthesis. (Figure 14–43)

**photoreceptor**

Cell or molecule that is sensitive to light.

**photorespiration**

Wasteful metabolic process that occurs in plants in conditions of low CO<sub>2</sub> in which O<sub>2</sub> is used up and CO<sub>2</sub> liberated without the production of carbohydrate for storage.

**photosynthesis**

Process by which plants, algae and some bacteria use the energy of sunlight to drive the synthesis of organic molecules from carbon dioxide and water. (Figures 2–40 and 14–38)

**photosynthetic electron transfer**

Light-driven reactions in photosynthesis in which electrons move along an electron-transport chain in a membrane, generating ATP and NADPH. (Figure 14–38)

**photosystem**

Multiprotein complex involved in photosynthesis that captures the energy of sunlight and converts it to useful forms of energy. (Figure 14–43)

**phragmoplast**

Structure made of microtubules and actin filaments that forms in the prospective plane of division of a plant cell and guides formation of the cell plate. (Figure 17–57)

**phylogeny**

Evolutionary history of an organism or group of organisms, often presented in chart form as a phylogenetic tree. (Figures 4–75 and 14–72)

**pI—see isoelectric point****PI 3-kinase—see phosphoinositide 3-kinase****pinocytosis**

Literally, “cell drinking.” Type of endocytosis in which soluble materials are continually taken up from the environment in small vesicles and moved into endosomes along with the

membrane-bound molecules. *Compare* phagocytosis. (Figure 13–48)

**PKA—see cyclic-AMP-dependent protein kinase****PKB—see Akt****PKC—see protein kinase C****planar cell polarity**

Type of cellular asymmetry seen in some epithelia, such that each cell has a polarity vector oriented in the plane of the epithelium. (Figure 19–32)

**plant growth regulator (plant hormone)**

Signal molecule that helps coordinate growth and development. Examples are ethylene, auxins, gibberellins, cytokinins, abscisic acid, and the brassinosteroids.

**plasma membrane**

The membrane that surrounds a living cell. (Figure 10–1)

**plasmid**

Small circular extrachromosomal DNA molecule that replicates independently of the genome. Modified plasmids are used extensively as vectors for DNA cloning.

**plasmodesma (plural plasmodesmata)**

Plant equivalent of a gap junction. Communicating cell–cell junction in plants in which a channel of cytoplasm lined by plasma membrane connects two adjacent cells through a small pore in their cell walls.

**plastid**

Cytoplasmic organelle in plants, bounded by a double membrane, that carries its own DNA and is often pigmented. Chloroplasts are plastids.

**platelet**

Cell fragment, lacking a nucleus, that breaks off from a megakaryocyte in the bone marrow and is found in large numbers in the bloodstream. Helps initiate blood clotting when blood vessels are injured.

**PLC—see phospholipase C****pleckstrin homology domain (PH domain)**

Protein domain found in some intracellular signaling proteins. Some PH domains in intracellular signaling proteins bind to phosphatidylinositol 3,4,5-trisphosphate produced by PI 3-kinase, bringing the signaling protein to the plasma membrane when PI 3-kinase is activated.

**ploidy**

The number of complete homologous sets of chromosomes in a genome. Diploid organisms have two sets in their somatic cells; haploid organisms have a single set; polyploid organisms have more than two.

**plus end**

End of a microtubule or actin filament at which addition of monomers occurs most readily; the “fast-growing” end of a microtubule or actin filament. The plus end of an actin filament is also known as the barbed end. (Panel 16–2, pp. 978–979)

**point mutation**

Change of a single nucleotide pair, or a very small part of a single gene, in DNA. (Panel 8–1, pp. 554–555)

**polar**

In the electrical sense, describes a structure (for example, a chemical bond, chemical group, or molecule) with positive charge concentrated toward one end and negative charge toward the other as a result of an uneven distribution of electrons. Polar molecules are likely to be soluble in water. (Figure 2–10 and Panel 2–2, pp. 108–109)

**polar body**

Smaller of two daughter cells produced during meiosis by asymmetric division of a primary or secondary oocyte, the other (large) daughter being the oocyte or ovum itself. The polar bodies eventually degenerate. (Figure 21–23)



**polyadenylation**

Addition of a long sequence of A nucleotides (the poly-A tail) to the 3' end of a nascent mRNA molecule. (Figures 6–21 and 6–38)

**poly-A tail—see polyadenylation****polycistronic mRNA**

Individual mRNA that encodes several different proteins—commonly found in bacteria but not in eucaryotes. (Figure 6–73)

**polygenic trait**

Heritable characteristic that is influenced by multiple genes, each of which makes a small contribution to the phenotype.

**polymer**

Large molecule made by covalently linking multiple identical or similar units (monomers) together.

**polymerase**

Enzyme that catalyzes polymerization reactions such as the synthesis of DNA and RNA. *See also* DNA polymerase, RNA polymerase.

**polymerase chain reaction—see PCR****polymorphic**

Describes a gene with two or more alleles that coexist at high frequency in a population.

**polypeptide**

Linear polymer of amino acids. Proteins are large polypeptides, and the two terms can be used interchangeably. (Panel 3–1, pp. 128–129)

**polyploid**

Cell or organism that contains more than two sets of homologous chromosomes.

**polyribosome (polysome)**

Messenger RNA molecule to which are attached a number of ribosomes engaged in protein synthesis. (Figure 6–76)

**polysaccharide**

Linear or branched polymer of monosaccharides. Examples include glycogen, starch, hyaluronic acid, and cellulose. (Panel 2–4, p. 113)

**polytene chromosome**

Giant chromosome in which the DNA has undergone repeated replication and the many copies have stayed together. (Figures 4–58 and 4–59)

**porin**

Channel-forming proteins of the outer membranes of bacteria, mitochondria, and chloroplasts.

**position effect**

Difference in gene expression that depends on the position of the gene on the chromosome and probably reflects differences in the state of the chromatin along the chromosome. When an active gene is placed next to heterochromatin, the inactivating influence of the heterochromatin can spread to affect the gene to a variable degree, giving rise to *position effect variegation*. (Figure 4–36)

**positional information**

Information supplied to or possessed by cells according to their position in a multicellular organism. A cell's internal record of its positional information is called its positional value.

**positive feedback**

Control mechanism whereby the end product of a reaction or pathway stimulates its own production or activation.

**post-transcriptional control**

Any control on gene expression that is exerted at a stage after transcription has begun. (Figure 7–92)

**post-translational modification**

An enzyme-catalyzed change to a protein made after it is

synthesized. Examples are acetylation, cleavage, glycosylation, methylation, phosphorylation, and prenylation.

**pre-B cell**

Immediate precursor of a B cell. (Figure 25–22)

**preinitiation complex**

A multiprotein complex that is assembled on the origin of replication at the onset of the S phase of the eucaryotic cell cycle. Initiates DNA synthesis by unwinding the DNA helix and loading DNA polymerases and other replication enzymes onto the DNA strands. (Figure 17–23)

**pre-mRNA**

Precursor to messenger RNA. In eucaryotes, includes all intermediate stages of RNA processing.

**prenylation**

Covalent attachment of an isoprenoid lipid group to a protein. (Figure 10–20)

**preprophase band**

Circumferential band of microtubules and actin filaments that forms around a plant cell under the plasma membrane prior to mitosis and cell division. (Figure 17–57)

**prereplicative complex (pre-RC)**

Multiprotein complex that is assembled at origins of replication during late mitosis and early G<sub>1</sub> phases of the cell cycle; a prerequisite to license the assembly of a preinitiation complex, and the subsequent initiation of DNA replication. (Figures 17–22 and 17–23)

**primary cell wall**

The first cell wall produced by a developing plant cell; it is thin and flexible, allowing room for cell growth. (Figure 19–79)

**primary cilium**

Short, single, nonmotile, cilium lacking dynein that arises from a centriole and projects from the surface of many animal cell types. Some signaling proteins are concentrated in the primary cilium. (Figure 15–48)

**primary immune response**

Adaptive immune response to an antigen that is made on first encounter with that antigen. (Figure 25–10)

**primary structure**

Linear sequence of monomer units in a polymer, such as the amino acid sequence of a protein.

**primary transcript (primary RNA transcript)**

Freshly synthesized transcript, before it has undergone splicing or other modifications. (Figure 6–21)

**primary tumor**

Tumor at the original site at which a cancer first arose. Secondary tumors develop elsewhere by metastasis.

**primase—see DNA primase****primer**

Oligonucleotide that pairs with a template DNA or RNA strand and promotes the synthesis of a new complementary strand by a polymerase.

**primordial germ cell**

Cell in an embryo that is a precursor to cells that give rise to gametes. (Figures 21–17, 21–23, and 21–30)

**prion**

An infectious, abnormally folded form of a protein that is replicated in the host by inducing normal proteins of the same type to adopt the aberrant structure. (Figures 6–95 and 6–96)

**prion disease**

Transmissible spongiform encephalopathy—such as Kuru and Creutzfeldt-Jakob disease (CJD) in humans, scrapie in sheep, and bovine spongiform encephalopathy (BSE, or 'mad cow disease') in cows—that is caused and transmitted by an infectious, abnormally folded protein (prion). (Figure 24–18)

**probe**

Defined fragment of RNA or DNA, radioactively or chemically labeled, used to locate specific nucleic acid sequences by hybridization.

**procaryote (prokaryote)**

Single-celled microorganism whose cells lack a well-defined, membrane-enclosed nucleus. Either a bacterium or an archaeon. (Figure 1–21)

**procaspase**

Inactive precursor of a caspase, a proteolytic enzyme usually involved in apoptosis. (Figure 18–5)

**processive**

Of an enzyme: able to proceed along a polymer chain catalyzing the same reaction repeatedly without detaching from the chain.

**programmed cell death**

A form of cell death in which a cell kills itself by activating an intracellular death program.

**prometaphase**

Phase of mitosis preceding metaphase in which the nuclear envelope breaks down and chromosomes first attach to the spindle. (Panel 17–1, pp. 1072–1073)

**promoter**

Nucleotide sequence in DNA to which RNA polymerase binds to begin transcription. *See also* inducible promoter. (Figure 7–44)

**proneural gene**

Gene whose expression defines cells with the potential to develop as neural tissue.

**proofreading**

Process by which potential errors in DNA replication, transcription, and translation are detected and corrected.

**prophase**

First stage of mitosis, during which the chromosomes are condensed but not yet attached to a mitotic spindle. (Panel 17–1, pp. 1072–1073)

**protease (proteinase, proteolytic enzyme)**

Enzyme that degrades proteins by hydrolyzing some of the peptide bonds between amino acids.

**proteasome**

Large protein complex in the cytosol with proteolytic activity that is responsible for degrading proteins that have been marked for destruction by ubiquitylation or by some other means. (Figures 6–89 and 6–90)

**protein**

The major macromolecular constituent of cells. A linear polymer of amino acids linked together by peptide bonds in a specific sequence. (Figure 3–1)

**protein activity control**

The selective activation, inactivation, degradation, or compartmentalization of specific proteins after they have been made. One of the means by which a cell controls which proteins are active at a given time or location in the cell.

**protein domain—see domain****protein kinase**

Enzyme that transfers the terminal phosphate group of ATP to one or more specific amino acids (serine, threonine, or tyrosine) of a target protein.

**protein kinase A (PKA)—see cyclic-AMP-dependent protein kinase****protein kinase B—see Akt****protein kinase C (PKC)**

Ca<sup>2+</sup>-dependent protein kinase that, when activated by diacylglycerol and an increase in the concentration of cytosolic

Ca<sup>2+</sup>, phosphorylates target proteins on specific serine and threonine residues. (Figure 15–39)

**protein subunit**

An individual protein chain in a protein composed of more than one chain.

**protein translocator**

Membrane-bound protein that mediates the transport of another protein across a membrane. (Figure 12–23)

**protein tyrosine phosphatase**

Enzyme that removes phosphate groups from phosphorylated tyrosine residues on proteins. (Figure 25–71)

**proteoglycan**

Molecule consisting of one or more glycosaminoglycan chains attached to a core protein. (Figure 19–58)

**proteolysis**

Degradation of a protein by hydrolysis at one or more of its peptide bonds.

**proteolytic enzyme—see protease****proteomics**

Study of all the proteins, including all the covalently modified forms of each, produced by a cell, tissue, or organism. Proteomics often investigates changes in this larger set of proteins in 'the proteome'—caused by changes in the environment or by extracellular signals.

**protist**

Single-celled eucaryote. Includes protozoa, algae, yeasts. (Figure 1–41)

**proton**

Positively charged subatomic particle that forms part of an atomic nucleus. Hydrogen has a nucleus composed of a single proton (H<sup>+</sup>). (Figure 2–1)

**proton-motive force**

The force exerted by the electrochemical proton gradient that moves protons across a membrane. (Figure 14–13)

**proto-oncogene**

Normal gene, usually concerned with the regulation of cell proliferation, that can be converted into a cancer-promoting oncogene by mutation. (Figure 20–34)

**protozoa**

Free-living or parasitic, nonphotosynthetic, single-celled, motile eucaryotic organisms, such as *Paramecium* and *Amoeba*. Free-living protozoa feed on bacteria or other microorganisms. (Figure 1–41)

**pseudogene**

Nucleotide sequence of DNA that has accumulated multiple mutations that have rendered an ancestral gene inactive and nonfunctional.

**pseudopodium (plural pseudopodia)**

Large, thick cell-surface protrusion formed by amoeboid cells as they crawl. More generally, any similarly shaped dynamic actin-rich extension of the surface of an animal cell. *Compare* filopodium, lamellipodium. (Figure 16–94)

**pump**

Transmembrane protein that drives the active transport of ions or small molecules across the lipid bilayer.

**purifying selection**

Natural selection operating to retard divergence in gene sequences within a population in the course of evolution by eliminating individuals carrying deleterious mutations.

**purine**

Nitrogen-containing ring compound found in DNA and RNA: adenine or guanine. (Panel 2–6, pp. 116–117)

**pyrimidine**

Nitrogen-containing ring compound found in DNA and

RNA: cytosine, thymine, or uracil. (Panel 2–6, pp. 116–117)

**pyruvate (CH<sub>3</sub>COCOO<sup>-</sup>)**

End-product of the glycolytic pathway. Enters mitochondria and feeds into the citric acid cycle and other biosynthetic pathways.

**quaternary structure**

Three-dimensional relationship of the different polypeptide chains in a multisubunit protein or protein complex.

**quinone (Q)**

Small, lipid-soluble mobile electron carrier molecule found in the respiratory and photosynthetic electron-transport chains. (Figure 14–24)

**Rab (Rab protein)**

Monomeric GTPase in the Ras superfamily present in the plasma membrane and organelle membranes. Involved in conferring specificity on vesicle docking. (Table 15–5, p. 926)

**Ran (Ran protein)**

Monomeric GTPase in the Ras superfamily present in both cytosol and nucleus. Required for the active transport of macromolecules into and out of the nucleus through nuclear pore complexes. (Table 15–5, p. 926)

**Ras (Ras protein)**

Monomeric GTPase of the Ras superfamily that helps to relay signals from cell-surface RTK receptors to the nucleus, frequently in response to signals that stimulate cell division. Named for the *ras* gene, first identified in viruses that cause rat sarcomas. (Figure 3–72)

**Ras superfamily**

Large superfamily of monomeric GTPases (also called small GTP-binding proteins) of which Ras is the prototypical member. (Table 15–5, p. 926)

**Rb—see retinoblastoma protein**

**reading frame**

Phase in which nucleotides are read in sets of three to encode a protein. A mRNA molecule can be read in any one of three reading frames, only one of which will give the required protein. (Figure 6–51)

**RecA (RecA protein)**

Prototype for a class of DNA-binding proteins that catalyze synthesis of DNA strands during genetic recombination. (Figure 5–56)

**receptor**

Any protein that binds a specific signal molecule (ligand) and initiates a response in the cell. Some are on the cell surface, while others are inside the cell. (Figure 15–3)

**receptor-mediated endocytosis**

Internalization of receptor-ligand complexes from the plasma membrane by endocytosis. (Figure 13–53)

**receptor serine/threonine kinase**

Cell-surface receptor with an extracellular ligand-binding domain and an intracellular kinase domain that phosphorylates signaling proteins on serine or threonine residues in response to ligand binding. The TGFβ receptor is an example. (Figure 15–69)

**receptor tyrosine kinase (RTK)**

Cell-surface receptor with an extracellular ligand-binding domain and an intracellular kinase domain that phosphorylates signaling proteins on tyrosine residues in response to ligand binding. (Figure 15–52 and Table 15–4, p. 923)

**recessive**

In genetics, the member of a pair of alleles that fails to be expressed in the phenotype of the organism when the dominant allele is present. Also refers to the phenotype of an individual that has only the recessive allele. (Panel 8–1, pp. 554–555)

**recombinant DNA**

Any DNA molecule formed by joining DNA segments from different sources.

**recombinant DNA technology—see genetic engineering**

**recombination (genetic recombination)**

Process in which DNA molecules are broken and the fragments are rejoined in new combinations. Can occur naturally in the living cell—for example, through crossing-over during meiosis—or *in vitro* using purified DNA and enzymes that break and ligate DNA strands. Three broad classes are homologous (general), conservative site-specific, and transpositional recombination.

**recombination complex**

In meiosis, a protein complex that assembles at a DNA double-strand break and helps mediate homologous recombination.

**recycling endosome**

Large intracellular membrane-bounded vesicle formed from a fragment of an endosome; an intermediate stage on the passage of recycled receptors back to the cell membrane. (Figure 13–60)

**red blood cell—see erythrocyte**

**redox pair**

Pair of molecules in which one acts as an electron donor and one as an electron acceptor in an oxidation–reduction reaction: for example, NADH (electron donor) and NAD<sup>+</sup> (electron acceptor). (Panel 14–1, p. 830)

**redox potential**

The affinity of a redox pair for electrons, generally measured as the voltage difference between an equimolar mixture of the pair and a standard reference. NADH/NAD<sup>+</sup> has a low redox potential and O<sub>2</sub>/H<sub>2</sub> has a high redox potential (high affinity for electrons). (Panel 14–1, p. 830)

**redox reaction**

Reaction in which one component becomes oxidized and the other reduced; an oxidation–reduction reaction. (Panel 14–1, p. 830)

**reduction (verb reduce)**

Addition of electrons to an atom, as occurs during the addition of hydrogen to a biological molecule or the removal of oxygen from it. Opposite of oxidation. (Figure 2–43)

**regulative**

Of embryos or parts of embryos: self-adjusting, so that a normal structure emerges even if the starting conditions are perturbed.

**regulator of G protein signaling (RGS)**

A GAP protein that binds to a trimeric G protein and enhances its GTPase activity, thus helping to limit G-protein-mediated signaling. (Figure 15–19)

**regulatory sequence**

DNA sequence to which a gene regulatory protein binds to control the rate of assembly of the transcriptional complex at the promoter. (Figure 7–44)

**release factor**

Protein that enables release of a newly synthesized protein from the ribosome by binding to the ribosome in the place of tRNA (whose structure it mimics). (Figure 16–74)

**replication—see DNA replication**

**replication fork**

Y-shaped region of a replicating DNA molecule at which the two strands of the DNA are being separated and the daughter strands are being formed. (Figures 5–7 and 5–19)

**replication origin**

Location on a DNA molecule at which duplication of the DNA begins. (Figures 4–21 and 5–25)



**replicative cell senescence—see also senescence**

Phenomenon observed in primary cell cultures in which cell proliferation slows down and finally irreversibly halts.

**reporter gene**

Genetic construct, usually artificial, in which a copy of the regulatory DNA of a gene of interest is linked to a sequence coding for an easily-detectable product. The presence or absence of this product (the 'reporter protein') in a cell containing the construct indicates whether the gene of interest is active or inactive. (Figure 8–70)

**repressor (gene repressor protein, transcriptional repressor)**

Protein that binds to a specific region of DNA to prevent transcription of an adjacent gene.

**respiration**

General term for an energy-generating process in cells that involves the oxidative breakdown of sugars or other organic molecules and requires the uptake of O<sub>2</sub> while producing CO<sub>2</sub> and H<sub>2</sub>O as waste products. (Figure 2–41)

**respiratory chain—see electron transport chain****respiratory enzyme complex**

Any of the major protein complexes of the mitochondrial respiratory chain that act as electron-driven proton pumps to generate the proton gradient across the inner membrane. (Figures 14–14 and 14–26)

**resting membrane potential**

Membrane potential in equilibrium conditions in which there is no net flow of ions across the plasma membrane. *See also* membrane potential.

**restriction fragment**

Fragment of DNA generated by the action of restriction enzyme(s).

**restriction map**

Diagrammatic representation of a DNA molecule indicating the sites of cleavage by various restriction enzymes.

**restriction nuclease (restriction enzyme)**

One of a large number of nucleases that can cleave a DNA molecule at any site where a specific short sequence of nucleotides occurs. Extensively used in recombinant DNA technology. (Figures 8–31 and 8–32)

**restriction point—see Start****restrictive (nonpermissive) conditions**

Circumstances (such as temperature or nutrient availability) in which the phenotypic effect of a conditional mutation will be evident. (Figure 8–55, and Panel 8–1, pp. 554–555)

**retinoblastoma protein (Rb)**

Tumor suppressor protein involved in the regulation of cell division. Mutated in the cancer retinoblastoma, as well as in many other tumors. Its normal activity is to regulate the eucaryotic cell cycle by binding to and inhibiting the E2F proteins, thus blocking progression to DNA replication and cell division. (Figure 17–62)

**retrotransposon**

Type of transposable element that moves by being first transcribed into an RNA copy that is then reconverted to DNA by reverse transcriptase and inserted ('retro-transposed') elsewhere in the genome. There are two types: retroviral-like retrotransposons and nonretroviral retrotransposons. (Table 5–3, p. 318)

**retrovirus**

RNA-containing virus that replicates in a cell by first making an RNA-DNA intermediate and then a double-stranded DNA molecule that becomes integrated into the cell's DNA. (Figure 5–71)

**reverse genetics**

Approach to discovering gene function that starts from the DNA (gene) and its protein product and then creates mutants to analyze the gene's function.

**reverse transcriptase**

Enzyme first discovered in retroviruses that makes a double-stranded DNA copy from a single-stranded RNA template molecule.

**reverse transcription**

Transcription from RNA to DNA. This is in the opposite direction to that prescribed by central dogma, which holds that DNA is transcribed into RNA and RNA is translated into protein.

**RGD sequence**

Tripeptide sequence of arginine-glycine-aspartic acid that forms a binding site for integrins; present in fibronectin and some other extracellular proteins. (Figure 19–72C)

**RGS—see regulator of G protein signaling****Rho (Rho protein family)**

Family of monomeric GTPases within the Ras superfamily involved in signaling the rearrangement of the cytoskeleton. Includes Rho, Rac, and Cdc42. (Table 15–5, p. 926)

**rhodopsin**

Seven-span membrane protein of the GPCR family that acts as a light sensor in rod photoreceptor cells in the vertebrate retina. Contains the light-sensitive prosthetic group retinol. (Figure 15–49)

**ribonuclease**

Enzyme that cuts an RNA molecule by hydrolyzing one or more of its phosphodiester bonds.

**ribonucleic acid—see RNA****ribose**

The five-carbon monosaccharide component of RNA. C<sub>5</sub>H<sub>10</sub>O<sub>5</sub>. *Compare* deoxyribose.

**ribosomal RNA (rRNA)**

Any one of a number of specific RNA molecules that form part of the structure of a ribosome and participate in the synthesis of proteins. Often distinguished by their sedimentation coefficient (e.g., 28S rRNA, 5S rRNA).

**ribosome**

Particle composed of rRNAs and ribosomal proteins that catalyzes the synthesis of protein using information provided by mRNA. (Figure 1–10)

**ribozyme**

RNA with catalytic activity.

**RNA (ribonucleic acid)**

Polymer formed from covalently linked ribonucleotide monomers. *See also* messenger RNA, ribosomal RNA, transfer RNA. (Table 6–1, p. 336, and Panel 2–6, pp. 116–117)

**RNA editing**

Type of RNA processing that alters the nucleotide sequence of a pre-mRNA transcript after it is synthesized by inserting, deleting, or altering individual nucleotides.

**RNA interference (RNAi)**

As originally described, mechanism by which an experimentally introduced double-stranded RNA induces sequence-specific destruction of complementary mRNAs. The mechanism, which is highly conserved in eucaryotes, proceeds through short double-stranded small interfering RNAs (siRNAs) produced by endonucleolytic cleavage. The term RNAi is often used broadly to also include the inhibition of gene expression by microRNAs (miRNAs), which are encoded in the cell's own genome. RNA interference is widely used experimentally to study the effects of inactivating specific genes. (Figure 7–115)

**RNA polymerase**

Enzyme that catalyzes the synthesis of an RNA molecule on a DNA template from ribonucleoside triphosphate precursors. (Figure 6–8)

**RNA primer**

Short stretch of RNA synthesized on a DNA template. It is

required by DNA polymerases to start their DNA synthesis.

#### RNA processing

Broad term for the various modifications an RNA transcript undergoes as it reaches its mature form. May include 5' capping, 3' polyadenylation, 3' cleavage, splicing, and editing.

#### RNA splicing

Process in which intron sequences are excised from RNA transcripts in the nucleus during formation of messenger and other RNAs.

#### rod photoreceptor (rod)

Photoreceptor cell in the vertebrate retina that is responsible for noncolor vision in dim light. (Figure 23–17)

#### rough endoplasmic reticulum (rough ER)

Endoplasmic reticulum with ribosomes on its cytosolic surface. Involved in the synthesis of secreted and membrane-bound proteins.

#### rRNA—see ribosomal RNA

#### rRNA gene

Gene that specifies a ribosomal RNA (rRNA).

#### RTK—see receptor tyrosine kinase

#### RT-PCR (reverse transcription–polymerase chain reaction)

Technique in which a population of mRNAs is converted into cDNAs via reverse transcription, and the cDNAs are then amplified by PCR.

#### S—see S phase

#### saccharide

Sugar.

#### Saccharomyces

Genus of yeasts that reproduce asexually by budding or sexually by conjugation. Economically important in brewing and baking. *Saccharomyces cerevisiae* is widely used as a simple model organism in the study of eucaryotic cell biology. See also *Schizosaccharomyces*.

#### sarcoma

Cancer of connective tissue.

#### sarcomere

Repeating unit of a myofibril in a muscle cell, composed of an array of overlapping thick (myosin) and thin (actin) filaments between two adjacent Z discs. (Figure 16–74)

#### sarcoplasmic reticulum

Specialized type of endoplasmic reticulum in the cytoplasm of muscle cells that contains high concentrations of sequestered  $\text{Ca}^{2+}$  that is released into the cytosol during muscle excitation. (Figure 16–77)

#### satellite DNA

Region of highly repetitive DNA from a eucaryotic chromosome, identifiable by its unusual nucleotide composition. Typically present at centromeres (as well as other sites) in higher eucaryotes, and thought to play a part in centromere function. (Figure 4–49)

#### scaffold protein

Protein that binds groups of intracellular signaling proteins into a signaling complex, often anchoring the complex at a specific location in the cell. (Figure 15–17)

#### scanning electron microscope

Type of electron microscope that produces an image of the surface of an object.

#### S-Cdk

Cyclin-Cdk complex formed in vertebrate cells by an S-cyclin and the corresponding cyclin-dependent kinase (Cdk). (Figure 17–16 and Table 17–1, p. 1063)

#### *S. cerevisiae*—see *Saccharomyces*

#### *Schizosaccharomyces*

Genus of rod-shaped yeasts that reproduce by binary fission. *S. pombe*, along with the budding yeast *Saccharomyces cerevisiae*, is a model organism used in many different studies.

#### SCF (SCF protein)

Family of ubiquitin ligases formed as a complex of several different proteins. One is involved in regulating the eucaryotic cell cycle, directing the destruction of inhibitors of S-Cdks in late  $G_1$  and thus promoting the activation of S-Cdks and DNA replication. (Figures 3–79 and 17–20)

#### Schwann cell

Glial cell responsible for forming myelin sheaths in the peripheral nervous system. Compare oligodendrocyte. (Figure 11–32)

#### S-cyclin

Member of a class of cyclins that accumulate during late  $G_1$  phase and bind Cdks soon after progression through Start; they help stimulate DNA replication and chromosome duplication. Levels remain high until late mitosis, after which these cyclins are destroyed. (Figure 17–16)

#### SDS-PAGE (sodium dodecyl sulfate–polyacrylamide gel electrophoresis)

Type of electrophoresis used to separate proteins by size. The protein mixture to be separated is first treated with a powerful negatively charged detergent (SDS) and with a reducing agent ( $\beta$  mercaptoethanol), before being run through a polyacrylamide gel. The detergent and reducing agent unfold the proteins, free them from association with other molecules, and separate the polypeptide subunits. See also electrophoresis.

#### secondary cell wall

Permanent rigid cell wall that is laid down underneath the thin primary cell wall in certain plant cells that have completed their growth. (Figure 19–77C)

#### secondary immune response

Adaptive immune response to an antigen that is made on a second or subsequent encounter with a given antigen. More rapid in onset and stronger than the primary immune response. (Figure 25–10)

#### secondary structure

Regular local folding pattern of a polymeric molecule; in proteins,  $\alpha$ -helices and  $\beta$ -sheets.

#### second messenger (small intracellular mediator)

Small intracellular signaling molecule that is formed or released for action in response to an extracellular signal and helps to relay the signal within the cell. Examples include cyclic AMP, cyclic GMP,  $\text{IP}_3$ ,  $\text{Ca}^{2+}$ , and diacylglycerol. (Figure 15–17)

#### secretory vesicle

Membrane-bounded organelle in which molecules destined for secretion are stored prior to release. Sometimes called secretory granule because darkly staining contents make the organelle visible as a small solid object. (Figures 13–63 and 13–66)

#### securin

Protein that binds to the protease separase and thereby prevents its cleavage of the protein linkages that hold sister chromatids together in early mitosis. Securin is destroyed at the metaphase-to-anaphase transition. (Figure 17–44)

#### seed

In plants, the structure containing the dormant embryo, along with a food store, enclosed in a hard protective coat. (Panel 22–1, p. 1401)

#### segment-polarity gene

In *Drosophila* development, a gene involved in specifying the anteroposterior organization of each body segment. (Figures 22–37 and 22–41)

**selectable marker gene**

Gene included in a DNA construct to signal presence of that construct in a cell, and making it possible to select cells according to whether they contain the construct.

**selectin**

Member of a family of cell-surface carbohydrate-binding proteins that mediate transient,  $\text{Ca}^{2+}$ -dependent cell-cell adhesion in the bloodstream—for example between white blood cells and the endothelium of the blood vessel wall. (Figure 19–19)

**selectivity filter**

The part of an ion channel structure that determines which ions it can transport. (Figures 11–23 and 11–24)

**senescence**

(1) aging of an organism. (2) replicative cell senescence: phenomenon observed in primary cell cultures in which cell proliferation slows down and finally halts irreversibly.

**sensory hair cell—see auditory hair cell****separase**

Protease that cleaves the cohesin protein linkages that hold sister chromatids together. Acts at anaphase, enabling chromatid separation and segregation. (Figure 17–44)

**septate junction**

Main type of occluding cell junction in invertebrates; its structure is distinct from that of vertebrate tight junctions. (Figure 19–28)

**sequencing**

Determination of the order of nucleotides or amino acids in a nucleic acid or protein molecule. (Figure 8–50)

**serine protease**

Type of protease that has a reactive serine in the active site. (Figures 3–12 and 3–38)

**serine/threonine kinase**

Enzyme that phosphorylates specific proteins on serine or threonines. (Figure 15–70)

**sex chromosome**

Chromosome that may be present or absent, or present in a variable number of copies, determining the sex of the individual; in mammals, the X and Y chromosomes.

**SH2 domain**

Src homology region 2, a protein domain present in many signaling proteins. Binds a short amino acid sequence containing a phosphotyrosine. (Panel 3–2, pp. 132–133)

 **$\beta$ -sheet—see beta sheet****side chain**

The part of an amino acid that differs between amino acid types. The side chains give each type of amino acid its unique physical and chemical properties. (Panel 3–1, pp. 128–129)

**signaling cascade**

Sequence of linked intracellular reactions, typically involving multiple amplification steps in a relay chain, triggered by an activated cell-surface receptor.

**signal molecule**

Extracellular chemical produced by a cell that signals to other cells in the organism to alter the cells' behavior. (Figure 15–1)

**signal patch**

Protein-sorting signal that consists of a specific three-dimensional arrangement of atoms on the folded protein's surface. (Figure 13–45)

**signal peptidase**

Enzyme that removes a terminal signal sequence from a protein once the sorting process is complete. (Figure 12–25)

**signal-recognition particle (SRP)**

Ribonucleoprotein particle that binds an ER signal sequence on a partially synthesized polypeptide chain and directs the polypeptide and its attached ribosome to the endoplasmic reticulum. (Figure 12–39)

**signal-relaying junction**

Complex type of cell-cell junction that allows signals to be relayed from one cell to another across their plasma membranes at sites of cell-to-cell contact. Typically includes anchorage proteins as well as proteins mediating signal transduction. (Figure 19–2, and Table 19–1, p. 1133)

**signal sequence**

Short continuous sequence of amino acids that determines the eventual location of a protein in the cell. An example is the N-terminal sequence of 20 or so amino acids that directs nascent secretory and transmembrane proteins to the endoplasmic reticulum. (Table 12–3, p. 702)

**signal transduction**

Conversion of a signal from one physical or chemical form to another (e.g., conversion of light to a chemical signal or of extracellular signals to intracellular ones).

**single-nucleotide polymorphism (SNP)**

Variation between individuals in a population at a specific nucleotide in their DNA sequence.

**single-pass transmembrane protein**

Membrane protein in which the polypeptide chain crosses the lipid bilayer only once. (Figure 10–19)

**single-strand DNA-binding protein**

Protein that binds to the single strands of the opened-up DNA double helix, preventing helical structures from reforming while the DNA is being replicated. (Figure 5–16)

**siRNA—see small interfering RNA****sister chromatids**

Tightly linked pair of chromosomes that arise from chromosome duplication during S phase. They separate during M phase and segregate into different daughter cells. (Figure 17–26)

**site-directed mutagenesis**

Technique by which a mutation can be made at a particular site in DNA. (Figure 8–63)

**site-specific recombination**

Type of recombination that occurs at specific DNA sequences and is carried out by specific proteins that recognize these sequences. Can occur between two different DNA molecules or within a single DNA molecule.

**skeletal muscle cell—see muscle cell****sliding clamp**

Protein complex that holds the DNA polymerase on DNA during DNA replication. (Figure 5–18)

**Smad protein**

Latent gene regulatory protein that is phosphorylated and activated by receptor serine/threonine kinases and carries the signal from the cell surface to the nucleus. (Figure 15–69)

**small interfering RNA (siRNA)**

Short (21–26 nucleotides) double-stranded RNAs that inhibit gene expression by directing destruction of complementary mRNAs. Production of siRNAs is triggered by exogenously introduced double-stranded RNA. (Figure 7–115)

**small intracellular mediator—see second messenger****small nuclear ribonucleoprotein (snRNP)**

Complex of an snRNA with proteins that forms part of a spliceosome. (Figure 6–29)

**small nuclear RNA (snRNA)**

Small RNA molecules that are complexed with proteins to



form the ribonucleoprotein particles (snRNPs) involved in RNA splicing. (Figures 6–29 and 6–30)

**small nucleolar RNA (snoRNA)**

Small RNAs found in the nucleolus, with various functions, including guiding the modifications of precursor rRNA. (Table 6–1, p. 336, and Figure 6–43)

**smooth endoplasmic reticulum (smooth ER)**

Region of the endoplasmic reticulum not associated with ribosomes. Involved in lipid synthesis. (Figure 12–36)

**smooth muscle cell—see muscle cell**

**SNARE**

Member of a large family of transmembrane proteins present in organelle membranes and the vesicles derived from them. SNAREs catalyze the many membrane fusion events in cells. They exist in pairs—a v-SNARE in the vesicle membrane that binds specifically to a complementary t-SNARE in the target membrane.

**SNP—see single-nucleotide polymorphism**

**snRNA—see small nuclear RNA**

**solute**

Any molecule that is dissolved in a liquid. The liquid is called a solvent.

**somatic cell**

Any cell of a plant or animal other than cells of the germ line. From Greek *soma*, body.

**somatic hypermutation**

Accumulation of point mutations in the assembled variable-region-coding sequences of immunoglobulin genes that occurs when B cells are activated to form memory cells. Results in the production of antibodies with altered antigen-binding sites.

**somite**

One of a series of paired blocks of mesoderm that form during early development and lie on either side of the notochord in a vertebrate embryo. They give rise to the segments of the body axis, including the vertebrae, muscles, and associated connective tissue. (Figure 22–81)

**sorting signal**

Amino acid sequence that directs the delivery of a protein to a specific location, such as a particular intracellular compartment.

**Southern blotting**

Technique in which DNA fragments separated by electrophoresis are immobilized on a paper sheet. Specific fragments are then detected with a labeled nucleic acid probe. (Named after E.M. Southern, inventor of the technique.)

**spectrin**

Abundant protein associated with the cytosolic side of the plasma membrane in red blood cells, forming a network that supports the membrane. Also present in other cells. (Figure 10–41)

**Spemann's Organizer—see Organizer**

**sperm (spermatozoon, plural spermatozoa)**

Mature male gamete in animals. Motile and usually small compared with the egg. (Figure 21–27)

**spermatogenesis**

Development of sperm in the testes. (Figure 21–30)

**S phase**

Period of a eucaryotic cell cycle in which DNA is synthesized. (Figure 17–4)

**sphingolipid**

Phospholipid derived from sphingosine. (Figure 10–3)

**spindle assembly checkpoint (metaphase-to-anaphase transition checkpoint)**

Checkpoint that operates during mitosis to ensure that all chromosomes are properly attached to the spindle before sister-chromatid separation starts. (Figure 17–14, and Panel 17–1, pp. 1072–1073)

**spliceosome**

Large assembly of RNA and protein molecules that performs pre-mRNA splicing in eucaryotic cells. (Figures 6–29 and 6–30)

**splicing**

Removal of introns from a pre-mRNA transcript by splicing together the exons that lie on either side of each intron. *See also* alternative RNA splicing, *and* trans-splicing.

***S. pombe*—see Schizosaccharomyces**

**Src (Src protein family)**

Family of cytoplasmic tyrosine kinases (pronounced “sark”) that associate with the cytoplasmic domains of some enzyme-linked cell-surface receptors (for example, the T cell antigen receptor) that lack intrinsic tyrosine kinase activity. They transmit a signal onwards by phosphorylating the receptor itself and specific intracellular signaling proteins on tyrosines. (Figures 3–10 and 15–70)

**SRP—see signal-recognition particle**

**standard free-energy change ( $\Delta G^\circ$ )**

Free-energy change of two reacting molecules at standard temperature and pressure when all components are present at a concentration of 1 mole per liter. (Table 2–4, p. 77, and Figure 14–18)

**starch**

Polysaccharide composed exclusively of glucose units, used as an energy storage material in plant cells. (Figure 2–75)

**Start (Start checkpoint, restriction point)**

Important checkpoint at the end of G<sub>1</sub> in the eucaryotic cell cycle. Passage through Start commits the cell to enter S phase. The term was originally used for this checkpoint in the yeast cell cycle only; the equivalent point in the mammalian cell cycle was called the restriction point. In this book we use Start for both. (Figure 17–14)

**start-transfer signal**

Short amino acid sequence that enables a polypeptide chain to start being translocated across the endoplasmic reticulum membrane through a protein translocator. Multipass membrane proteins have both N-terminal (signal sequence) and internal start-transfer signals. (Figures 12–45–12–48)

**STAT (signal transducer and activator of transcription)**

Latent gene regulatory protein that is activated by phosphorylation by JAK kinases and enters the nucleus in response to signaling from receptors of the cytokine receptor family. (Figure 15–68)

**stem cell**

Undifferentiated cell that can continue dividing indefinitely, throwing off daughter cells that can either commit to differentiation or remain a stem cell (in the process of self-renewal). (Figure 23–5)

**stem-cell niche**

The specialized microenvironment in a tissue in which self-renewing stem cells can be maintained. (Figure 23–27)

**stereocilium**

A large, rigid microvillus found in “organ pipe” arrays on the apical surface of hair cells in the ear. A stereocilium contains a bundle of actin filaments, rather than microtubules, and is thus not a true cilium. (Figures 23–13 and 23–15)

**steroid**

Hydrophobic lipid molecule with a characteristic four-ringed structure; derived from cholesterol. Many important

- hormones, including cortisol, estrogen, and testosterone, are steroids that activate intracellular nuclear receptors. (Panel 2–5, pp. 114–115)
- stimulatory G protein ( $G_s$ )**  
G protein that, when activated, activates the enzyme adenylyl cyclase and thus stimulates the production of cyclic AMP. (See also G protein, and Table 15–3, p. 919.)
- stochastic**  
Random. Involving chance, probability, or random variables.
- stop-transfer signal**  
Hydrophobic amino acid sequence that halts translocation of a polypeptide chain through the endoplasmic reticulum membrane, thus anchoring the protein chain in the membrane. (Figure 12–48 and 12–49)
- striated muscle**  
Muscle composed of transversely striped (striated) myofibrils. Skeletal and heart muscle of vertebrates are examples. (Figure 16–74)
- stroma**  
(1) 'Bedding': the connective tissue in which a glandular or other epithelium is embedded. Stromal cells provide the environment necessary for the development of other cells within the tissue. (Figure 20–19) (2) The large interior space of a chloroplast, containing enzymes that incorporate  $CO_2$  into sugars. (Figure 12–21)
- structural gene**  
Region of DNA that codes for a protein or for an RNA molecule that forms part of a structure or has an enzymatic function. Distinguished from regions of DNA that regulate gene expression.
- substrate**  
Molecule on which an enzyme acts.
- substratum**  
Solid surface to which a cell adheres.
- sucrose**  
Disaccharide composed of one glucose unit and one fructose unit. The major form in which glucose is transported between plant cells. (Panel 2–4, pp.112–113)
- sugar**  
Small carbohydrate with a monomer unit of general formula  $(CH_2O)_n$ . Examples are the monosaccharides glucose, fructose and mannose, and the disaccharide sucrose (glucose and fructose linked). (Panel 2–4, pp.112–113)
- sulfhydryl (thiol, –SH)**  
Chemical group containing sulfur and hydrogen; found in the amino acid cysteine and other molecules. Two sulfhydryls can join to produce a disulfide bond. (Panel 2–1, pp. 106–107, and Figure 3–28)
- suppressor mutation**  
Mutation that suppresses the phenotypic effect of another mutation, so that the double mutant individual seems normal. (Panel 8–1, pp. 554–555)
- surface plasmon resonance (SPR)**  
Technique used to characterize molecular interactions, such as antibody-antigen binding, ligand-receptor coupling, and the binding of proteins to DNA. Binding interactions are detected by monitoring the reflection of a beam of light off the interface between an aqueous solution of potential binding molecules and a biosensor surface carrying the immobilized bait protein.
- survival factor**  
Extracellular signal that promotes cell survival by inhibiting apoptosis. (Figure 18–14)
- symbiosis**  
Intimate association between two organisms of different species from which both derive a long-term selective advantage. (Figure 1–16)
- symporter**  
Carrier protein that transports two types of solute across the membrane in the same direction. (Figure 11–8)
- synapse**  
Communicating cell–cell junction that allows signals to pass from a nerve cell to another cell. In a chemical synapse, the signal is carried by a diffusible neurotransmitter. (Figure 19–22) In an electrical synapse, a direct connection is made between the cytoplasm of the two cells via gap junctions. (Figure 19–34)
- synapsis**  
(1) In genetic recombination, the initial formation of base pairs between complementary DNA strands in different DNA molecules that occurs at sites of crossing-over between chromosomes. (Figure 5–56) (2) In meiosis, the formation of a synaptonemal complex between two tightly aligned homologous chromosomes. (Figure 21–9)
- synaptic vesicle**  
Small neurotransmitter-filled secretory vesicle found at the axon terminals of nerve cells. Its contents are released into the synaptic cleft by exocytosis when an action potential reaches the axon terminal.
- synaptonemal complex**  
Structure that holds paired homologous chromosomes tightly together in pachytene of prophase I in meiosis and promotes the final steps of crossing over. (Figures 21–8 and 21–9)
- syncytium**  
Mass of cytoplasm containing many nuclei enclosed by a single plasma membrane. Typically the result either of cell fusion or of a series of incomplete division cycles in which the nuclei divide but the cell does not.
- synteny**  
The presence, in different species, of regions of chromosomes with the same genes in the same order.
- synthetic lethality**  
An interaction between two mutant genes in which the two mutant genes together result in cell death, whereas either single mutation alone does not.
- tap-tagging (tandem affinity purification tagging)**  
Highly efficient method for protein purification, based on construction of a fusion protein in which the protein of interest is linked to two protein domains in tandem that act as tags for affinity chromatography purification. Two rounds of affinity purification, first using one tag and then the other, result in a very pure preparation.
- TATA box**  
Sequence in the promoter region of many eucaryotic genes that binds a general transcription factor and hence specifies the position at which transcription is initiated. (Figures 6–16 and 6–17)
- TCA (tricarboxylic acid) cycle—see citric acid cycle**
- T cell (T lymphocyte)**  
Type of lymphocyte responsible for T-cell-mediated adaptive immune responses; the class includes cytotoxic T cells, helper T cells, and regulatory T cells.
- T-cell-mediated immune response**  
Any adaptive immune response mediated by antigen-specific T cells.
- telomerase**  
Enzyme that elongates telomere sequences in DNA, which occur at the ends of eucaryotic chromosomes.
- telomere**  
End of a chromosome, associated with a characteristic DNA sequence that is replicated in a special way. Counteracts the tendency of the chromosome otherwise to shorten with each round of replication. From Greek *telos*, end.

**telophase**

Final stage of mitosis in which the two sets of separated chromosomes decondense and become enclosed by nuclear envelopes. (Panel 17–1, pp. 1072–1073)

**temperature-sensitive (ts) mutant**

Organism or cell carrying a mutation that shows its phenotypic effect in one temperature range (usually high temperature) but not at other (usually low) temperatures. (Panel 8–1, pp. 554–555, and Figure 8–55)

**template**

Single strand of DNA or RNA whose nucleotide sequence acts as a guide for the synthesis of a complementary strand. (Figure 1–3)

**terminator**

Signal in bacterial DNA that halts transcription.

**tertiary structure**

Complex three-dimensional form of a folded polymer chain, especially a protein or RNA molecule.

**TGF $\beta$  superfamily (transforming growth factor- $\beta$  superfamily)**

Large family of structurally related secreted proteins that act as hormones and local mediators to control a wide range of functions in animals, including during development. It includes the TGF $\beta$ /activin and bone morphogenetic protein (BMP) subfamilies. (Figure 15–69)

**TGN—see trans Golgi network****thioester bond**

High-energy bond formed by a condensation reaction between an acid (acyl) group and a thiol group (–SH). Seen, for example, in acetyl CoA and in many enzyme-substrate complexes. (Figure 2–62)

**thiol—see sulfhydryl****thylakoid**

Flattened sac of membrane in a chloroplast that contains chlorophyll and other pigments and carries out the light-trapping reactions of photosynthesis. Stacks of thylakoids form the grana of chloroplasts. (Figures 14–35 and 14–36)

**tight junction**

Cell–cell junction that seals adjacent epithelial cells together, preventing the passage of most dissolved molecules from one side of the epithelial sheet to the other. (Figures 19–3 and 19–26)

**TIM complexes**

Protein translocators in the mitochondrial inner membrane. The TIM23 complex mediates the transport of proteins into the matrix and the insertion of some proteins into the inner membrane; the TIM22 complex mediates the insertion of a subgroup of proteins into the inner membrane. (Figure 12–23)

**T lymphocyte—see T cell****Toll-like receptor family (TLR)**

Important family of mammalian pattern recognition receptors abundant on or in cells of the innate immune system. They recognize pathogen-associated immunostimulants such as lipopolysaccharide and peptidoglycan. (Figure 24–51)

**TOM complex**

Multisubunit protein complex that transports proteins across the mitochondrial outer membrane. (Figure 12–23)

**topoisomerase (DNA topoisomerase)**

Enzyme that binds to DNA and reversibly breaks a phosphodiester bond in one or both strands. Topoisomerase I creates transient single-strand breaks, allowing the double helix to swivel and relieving superhelical tension. Topoisomerase II creates transient double-strand breaks, allowing one double helix to pass through another and thus resolving tangles. (Figures 5–22 and 5–23)

**totipotent**

Describes a cell that is able to give rise to all the different cell types in an organism.

**trans**

On the other (far) side.

**transcellular transport**

Transport of solutes, such as nutrients, across an epithelium, by means of membrane transport proteins in the apical and basal faces of the epithelial cells. (Figure 11–11)

**transcript**

RNA product of DNA transcription. (Figure 6–21)

**transcription (DNA transcription)**

Copying of one strand of DNA into a complementary RNA sequence by the enzyme RNA polymerase. (Figure 6–21)

**transcriptional activator—see activator****transcriptional repressor—see repressor****transcription attenuation**

Inhibition of gene expression by the premature termination of transcription.

**transcription factor**

Term loosely applied to any protein required to initiate or regulate transcription in eucaryotes. Includes gene regulatory proteins, the general transcription factors, coactivators, co-repressors, histone-modifying enzymes, and chromatin remodeling complexes. (Figures 6–19 and 7–44)

**transcytosis**

Uptake of material at one face of a cell by endocytosis, its transfer across a cell in vesicles, and discharge from another face by exocytosis. (Figure 13–60)

**transfection**

Introduction of a foreign DNA molecule into a cell. Usually followed by expression of one or more genes in the newly introduced DNA.

**transfer RNA (tRNA)**

Set of small RNA molecules used in protein synthesis as an interface (adaptor) between mRNA and amino acids. Each type of tRNA molecule is covalently linked to a particular amino acid. (Figures 1–9 and 6–52)

**transformation**

(1) Insertion of new DNA (e.g., a plasmid) into a cell or organism, such as into competent *E. coli*. (2) Conversion of a normal cell into one that behaves in many ways like a cancer cell (i.e., unregulated proliferation, anchorage-independent growth in culture).

**transforming growth factor- $\beta$  superfamily—see TGF $\beta$  superfamily****transgenic organism**

Plant or animal that has stably incorporated one or more genes from another cell or organism (through insertion, deletion, and/or replacement) and can pass them on to successive generations. The gene that has been added is called a transgene. (Figures 8–64 and 8–65)

**transit amplifying cell**

Cell derived from a stem cell that divides a limited number of cycles before terminally differentiating. (Figure 23–7)

**transition state**

Structure that forms transiently in the course of a chemical reaction and has the highest free energy of any reaction intermediate. Its formation is a rate-limiting step in the reaction. (Figure 3–46)

**translation (RNA translation)**

Process by which the sequence of nucleotides in a mRNA molecule directs the incorporation of amino acids into protein. Occurs on a ribosome. (Figures 6–66 and 6–67)



**translocation**

- (1) Type of mutation in which a portion of one chromosome is broken off and attached to another. (Panel 8–1 and Figure 20–5)
- (2) The process of transferring a protein across a membrane.

**transmembrane protein**

Membrane protein that extends through the lipid bilayer, with part of its mass on either side of the membrane. (Figure 10–19)

**transmitter-gated ion channel (ion-channel-coupled receptor, ionotropic receptor)**

Ion channel found at chemical synapses in the postsynaptic plasma membranes of nerve and muscle cells. Opens only in response to the binding of a specific extracellular neurotransmitter. The resulting inflow of ions leads to the generation of a local electrical signal in the postsynaptic cell. (Figures 15–16 and 11–35)

**transporter (carrier protein, permease)**

Membrane transport protein that binds to a solute and transports it across the membrane by undergoing a series of conformational changes. Transporters can transport ions or molecules passively down an electrochemical gradient or can link the conformational changes to a source of metabolic energy such as ATP hydrolysis to drive active transport. *Compare* channel protein. *See also* membrane transport protein. (Figure 11–3)

**transposable element (transposon)**

Segment of DNA that can move from one genome position to another by transposition. (Table 5–3, p. 318)

**transposase**

Enzyme that cuts a transposon sequence in a chromosome and causes the DNA sequence to be inserted into a new target site. The transposase is usually encoded by the transposon that it acts upon. (Figure 5–69)

**transposition (transpositional recombination)**

Movement of a DNA sequence from one genome site to another. (Table 5–3, p. 318)

**transposon—see transposable element****trans-splicing**

Type of RNA splicing present in a few eucaryotic organisms in which exons from two separate RNA transcripts are joined together to form an mRNA. (Figure 6–34)

**treadmilling**

Process by which a polymeric protein filament is maintained at constant length by addition of protein subunits at one end and loss of subunits at the other. (Panel 16–2, pp. 978–979)

**triacylglycerol (triglyceride)**

Molecule composed of three fatty acids esterified to glycerol. The main constituent of fat droplets in animal tissues (where the fatty acids are saturated) and of vegetable oils (where the fatty acids are mainly unsaturated). (Panel 2–5, pp. 114–115)

**tricarboxylic acid (TCA) cycle—see citric acid cycle****trimeric G protein (trimeric GTP-binding protein)—see G protein****triglyceride—see triacylglycerol****tRNA—see transfer RNA****ts mutant—see temperature-sensitive mutant****t-SNARE—see SNARE****tubulin**

The protein subunit of microtubules. (Panel 16–1, p. 968, and Figure 16–11)

 **$\gamma$ -tubulin ring complex ( $\gamma$ TuRC)—see gamma tubulin ring complex****tumor**

Abnormal mass of cells resulting from a defect in cell-prolif-

eration control. A tumor can be noninvasive (benign) or invasive (cancerous, malignant). (Figure 20–3)

**tumor necrosis factor (TNF $\alpha$ )**

Cytokine that is especially important in inducing inflammatory responses. (Figure 15–79)

**tumor progression**

Process by which an initial mildly disordered cell behavior gradually evolves into a full-blown cancer. (Figures 20–9 and 20–11)

**tumor suppressor gene**

Gene that appears to help prevent formation of a cancer. Loss-of-function mutations in such genes favor the development of cancer. (Figure 20–27)

**tumor virus**

Virus that can make the cell it infects cancerous.

**turgor pressure**

Large hydrostatic pressure developed inside a plant cell as the result of the intake of water by osmosis; it is the force driving cell expansion in plant growth and it maintains the rigidity of plant stems and leaves. (Panel 11–1, p. 664)

**two-hybrid system—see yeast two-hybrid system****type III secretion system**

Bacterial system for delivering toxic proteins into the cells of their host. (Figure 24–8)

**tyrosine kinase**

Enzyme that phosphorylates specific proteins on tyrosines. *See also* cytoplasmic tyrosine kinase. (Figure 15–70)

**ubiquitin**

Small, highly conserved protein present in all eucaryotic cells that becomes covalently attached to lysines of other proteins. Attachment of a short chain of ubiquitins to such a lysine can tag a protein for intracellular proteolytic destruction by a proteasome. (Figure 6–92)

**ubiquitin ligase**

Any one of a large number of enzymes that attach ubiquitin to a protein, often marking it for destruction in a proteasome. The process catalyzed by a ubiquitin ligase is called ubiquitylation. (Figure 3–79)

**unfolded protein response**

Cellular response triggered by an accumulation of misfolded proteins in the endoplasmic reticulum. Involves increased transcription of ER chaperones and degradative enzymes. (Figure 12–55)

**uniporter**

Carrier protein that transports a single solute from one side of the membrane to the other. (Figure 11–8)

**UTR (untranslated region)**

Noncoding region of an mRNA molecule. The 3' UTR extends from the stop codon that terminates protein synthesis to the start of the poly-A tail. (Figure 7–105) The 5' UTR extends from the 5' cap to the start codon that initiates protein synthesis.

 **$V_{\text{MAX}}$** 

Maximum rate of an enzymatic reaction. (Figure 3–45 and Panel 3–3, pp. 162–163)

**vacuole**

Very large fluid-filled vesicle found in most plant and fungal cells, typically occupying more than a third of the cell volume. (Figure 13–39)

**valence**

Number of electrons that an atom must gain or lose (either by sharing or by transfer) to fill its outer shell. The valence of an atom is equal to the number of single bonds that the atom can form.

**van der Waals attraction**

Type of (individually weak) noncovalent bond that is formed

- at close range between nonpolar atoms. (Table 2–1, p. 53 and Panel 2–3, pp. 110–111)
- variable region**  
Region of an immunoglobulin light or heavy chain that differs from a molecule to molecule and forms the antigen-binding site. (Figures 25–30 and 25–31)
- vascular endothelial growth factor (VEGF)**  
Secreted protein that stimulates the growth of blood vessels. (Table 15–4, p. 923, and Figure 23–35)
- V(D)J recombination**  
Somatic recombination process by which gene segments are brought together to form a functional gene for a polypeptide chain of an immunoglobulin or T cell receptor. (Figures 25–36, 25–37, and 25–38)
- vector**  
In cell biology, the DNA of an agent (virus or plasmid) used to transmit genetic material to a cell or organism. *See also* cloning vector, expression vector. (Figure 8–39)
- vegetal pole**  
The end at which most of the yolk is located in an animal egg. The end opposite the animal pole. (Figure 22–68)
- VEGF—see vascular endothelial growth factor**
- vesicle**  
Small, membrane-bounded, organelle in the cytoplasm of a eucaryotic cell; often spherical. (Figure 11–35)
- vesicular transport**  
Transport of proteins from one cell compartment to another by means of membrane-bounded intermediaries such as vesicles or organelle fragments.
- V gene segment**  
Gene segment encoding most of the variable region of an immunoglobulin or T cell receptor polypeptide chain.
- viral envelope**  
Phospholipid bilayer, derived from host-cell plasma membrane, covering an enveloped virus. Encloses the nucleocapsid. (Figure 24–15)
- virion**  
A single virus particle. (Figure 24–13)
- virulence gene**  
Gene that contributes to an organism's ability to cause disease.
- virus**  
Particle consisting of nucleic acid (RNA or DNA) enclosed in a protein coat and capable of replicating within a host cell and spreading from cell to cell. (Figure 24–13)
- voltage-gated cation channel**  
Type of ion channel found in the membranes of electrically excitable cells (such as nerve, endocrine, egg, and muscle cells). Opens in response to a shift in membrane potential past a threshold value.
- v-SNARE—see SNARE**
- Wee1**  
Protein kinase that inhibits Cdk activity by phosphorylating amino acids in the Cdk active site. Important in regulating entry into M phase of the cell cycle.
- Western blotting (immunoblotting)**  
Technique by which proteins are separated by electrophoresis and immobilized on a paper sheet and then analyzed, usually by means of a labeled antibody.
- white blood cell (leucocyte)**  
General name for all the nucleated blood cells lacking hemoglobin. Includes lymphocytes, granulocytes, and monocytes.
- wild-type**  
Normal, nonmutant form of an organism; the form found in nature (in the wild).
- Wnt (Wnt protein)**  
Member of a family of secreted signal proteins that have many different roles in controlling cell differentiation, proliferation, and gene expression in animal embryos and adult tissues.
- Wnt signaling pathway**  
Signaling pathway activated by binding of a Wnt protein to its cell-surface receptors. The pathway has several branches. In the major (canonical) branch, activation causes increased amounts of  $\beta$ -catenin to enter the nucleus, where it regulates the transcription of genes controlling cell differentiation and proliferation. Overactivation of the Wnt/ $\beta$ -catenin pathway can lead to cancer. (Figure 15–77)
- X chromosome**  
One of the two sex chromosomes of mammals. The cells of women contain two X chromosomes, while those of men contain only one.
- Xenopus laevis (South African clawed toad)**  
Species of frog (not toad) frequently used in studies of early vertebrate development.
- XIC—see X-inactivation center**
- X-inactivation**  
Inactivation of one copy of the X chromosome in the somatic cells of female mammals.
- X-inactivation center (XIC)**  
Site in an X chromosome at which inactivation is initiated and spreads outwards.
- X-ray crystallography (X-ray diffraction)**  
Technique for determining the three-dimensional arrangement of atoms in a molecule based on the diffraction pattern of X-rays passing through a crystal of the molecule. (Figure 8–28)
- Y chromosome**  
One of the two sex chromosomes of mammals. The cells of men contain one Y and one X chromosome.
- yeast**  
Common name for several families of unicellular fungi. Includes species used for brewing and bread-making, as well as pathogenic species. Among the simplest of eucaryotes.
- yeast two-hybrid system**  
Molecular genetic technique for identifying protein-protein and protein-DNA interactions. (Figure 8–24)
- yolk**  
Nutritional reserves rich in lipids, proteins and polysaccharides, present in the eggs of many animals.
- Z disc (Z line)**  
Platelike region of a muscle sarcomere to which the plus ends of actin filaments are attached. Seen as a dark transverse line in micrographs.
- zinc finger**  
DNA-binding structural motif present in many gene regulatory proteins. All zinc finger motifs incorporate one or more zinc atoms that help hold the protein conformation together.
- zona pellucida**  
Glycoprotein layer on the surface of the unfertilized egg. It is often a barrier to fertilization across species. (Figure 21–22)
- zonula adherens—see adhesion belt**
- zygote**  
Diploid cell produced by fusion of a male and female gamete. A fertilized egg.

# Index

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The Genetic Code					
1st position (5' end)	2nd Position				3rd Position (3' end)
↓	U	C	A	G	↓
U	Phe Phe Leu Leu	Ser Ser Ser Ser	Tyr Tyr <b>STOP</b> <b>STOP</b>	Cys Cys <b>STOP</b> Trp	U C A G
C	Leu Leu Leu Leu	Pro Pro Pro Pro	His His Gln Gln	Arg Arg Arg Arg	U C A G
A	Ile Ile Ile Met	Thr Thr Thr Thr	Asn Asn Lys Lys	Ser Ser Arg Arg	U C A G
G	Val Val Val Val	Ala Ala Ala Ala	Asp Asp Glu Glu	Gly Gly Gly Gly	U C A G

AMINO ACIDS AND THEIR SYMBOLS			CODONS
A	Ala	Alanine	GCA GCC GCG GCU
C	Cys	Cysteine	UGC UGU
D	Asp	Aspartic acid	GAC GAU
E	Glu	Glutamic acid	GAA GAG
F	Phe	Phenylalanine	UUC UUU
G	Gly	Glycine	GGA GGC GGG GGU
H	His	Histidine	CAC CAU
I	Ile	Isoleucine	AUA AUC AUU
K	Lys	Lysine	AAA AAG
L	Leu	Leucine	UUA UUG CUA CUC CUG CUU
M	Met	Methionine	AUG
N	Asn	Asparagine	AAC AAU
P	Pro	Proline	CCA CCC CCG CCU
Q	Gln	Glutamine	CAA CAG
R	Arg	Arginine	AGA AGG CGA CGC CGG CGU
S	Ser	Serine	AGC AGU UCA UCC UCG UCU
T	Thr	Threonine	ACA ACC ACG ACU
V	Val	Valine	GUA GUC GUG GUU
W	Trp	Tryptophan	UGG
Y	Tyr	Tyrosine	UAC UAU