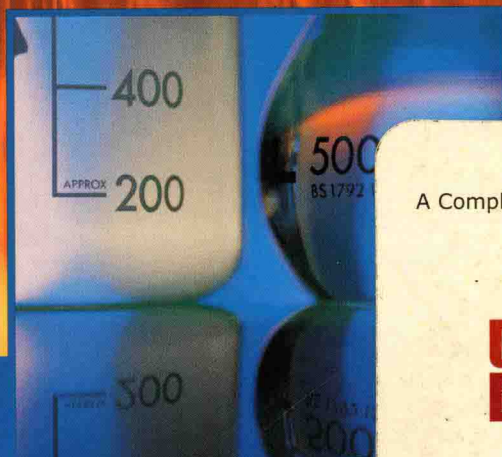



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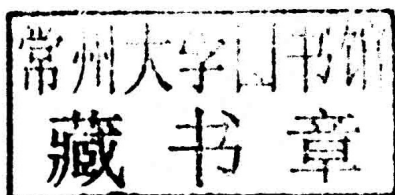
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**Principles of Biochemistry**  
**Laurence A. Moran Robert A. Horton**  
**Gray Scrimgeour Marc Perry**  
**Fifth Edition**

# Pearson New International Edition

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Laurence A. Moran Robert A. Horton  
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Fifth Edition



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# Glossary of Biochemical Terms

**A site.** Aminoacyl site. The site on a ribosome that is occupied during protein synthesis by an aminoacyl-tRNA molecule.

**acceptor stem.** The sequence at the 5' end and the sequence near the 3' end of a tRNA molecule that are base paired, forming a stem. The acceptor stem is the site of amino acid attachment. Also known as the amino acid stem.

**accessory pigments.** Pigments other than chlorophyll that are present in photosynthetic membranes. The accessory pigments include carotenoids and phycobilins.

**acid.** A substance that can donate protons. An acid is converted to its conjugate base by loss of a proton. (The Lewis theory defines an acid as an electron-pair acceptor [Lewis acid].)

**acid anhydride.** The product formed by condensation of two molecules of acid.

**acid dissociation constant ( $K_a$ ).** The equilibrium constant for the dissociation of a proton from an acid.

**acid-base catalysis.** Catalysis in which the transfer of a proton accelerates a reaction.

**ACP.** See acyl carrier protein.

**activation energy.** The free energy required to promote reactants from the ground state to the transition state in a chemical reaction.

**activator.** See transcriptional activator.

**active site.** The portion of an enzyme that contains the substrate-binding site and the amino-acid residues involved in catalyzing the conversion of substrate(s) to product(s). Active sites are usually located in clefts between domains or subunits of proteins or in indentations on the protein surface.

**active transport.** The process by which a solute specifically binds to a transport protein and is transported across a membrane against the solute concentration gradient. Energy is required to drive active transport. In primary active transport, the energy source may be light, ATP, or electron transport. Secondary active transport is driven by ion concentration gradients.

**acyl carrier protein (ACP).** A protein (in prokaryotes) or a domain of a protein (in eukaryotes) that binds activated intermediates of fatty acid synthesis via a thioester linkage.

**adipocyte.** A triacylglycerol-storage cell found in animals. An adipocyte consists of a fat droplet surrounded by a thin shell of cytosol in which the nucleus and other organelles are suspended.

**adipose tissue.** Animal tissue composed of specialized triacylglycerol-storage cells known as adipocytes.

**A-DNA.** The conformation of DNA commonly observed when purified DNA is dehydrated. A-DNA is a right-handed double helix containing approximately 11 base pairs per turn.

**aerobic.** Occurring in the presence of oxygen.

**affinity chromatography.** A chromatographic technique used to separate a mixture of proteins or other macromolecules in solution based on specific binding to a ligand that is covalently attached to the chromatographic matrix.

**affinity labeling.** A process by which an enzyme (or other macromolecule) is covalently inhibited by a reaction with a molecule that specifically interacts with the active site (or other binding site).

**aldoses.** A class of monosaccharides in which the most oxidized carbon atom, designated C-1, is aldehydic.

**allosteric effector.** See allosteric modulator.

**allosteric interaction.** The modulation of activity of a protein that occurs when a molecule binds to the regulatory site of the protein.

**allosteric modulator.** A biomolecule that binds to the regulatory site of an allosteric protein and thereby modulates its activity. An allosteric modulator may be an activator or an inhibitor. Also known as an allosteric effector.

**allosteric protein.** A protein whose activity is modulated by the binding of another molecule.

**allosteric site.** See regulatory site.

**allosteric transitions.** The changes in conformation of a protein between the active (R) state and the inactive (T) state.

**A helix.** A common secondary structure of proteins, in which the carbonyl oxygen of each amino acid residue (residue  $n$ ) forms a hydrogen bond with the amide hydrogen of the fourth residue further toward the C-terminus of the polypeptide chain (residue  $n + 4$ ). In an ideal right-handed  $\alpha$  helix, equivalent positions recur every 0.54 nm, each amino acid residue advances the helix by 0.15 nm along the long axis of the helix, and there are 3.6 amino acid residues per turn.

**amino acid.** An organic acid consisting of an  $\alpha$ -carbon atom to which an amino group, a carboxylate group, a hydrogen atom, and a specific side chain (R group) are attached. Amino acids are the building blocks of proteins.

**amino acid analysis.** A chromatographic procedure used for the separation and quantitation of amino acids in solutions such as protein hydrolysates.

**amino terminus.** See N-terminus.

**aminoacyl site.** See A site

**aminoacyl-tRNA synthetase.** An enzyme that catalyzes the activation and attachment of a specific amino acid to the 3' end of a corresponding tRNA molecule.

**amphibolic reaction.** A metabolic reaction that can be both catabolic and anabolic.

**amphipathic.** Describes a molecule that has both hydrophobic and hydrophilic regions.

**amyloplast.** Modified chloroplasts that specialize in starch synthesis.

**anabolic reaction.** A metabolic reaction that synthesizes a molecule needed for cell maintenance and growth.

**anaplerotic reaction.** A reaction that replenishes metabolites removed from a central metabolic pathway (cf. cataplerotic).

**angstrom ( $\text{\AA}$ ).** A unit of length equal to  $1 \times 10^{-10}$  m, or 0.1 nm.

**anion.** An ion with an overall negative charge.

**anode.** A positively charged electrode. In electrophoresis, anions move toward the anode.

**anomeric carbon.** The most oxidized carbon atom of a cyclized monosaccharide. The anomeric carbon has the chemical reactivity of a carbonyl group.

**anomers.** Isomers of a sugar molecule that have different configurations only at the anomeric carbon atom.

**antenna pigments.** Light-absorbing pigments associated with the reaction center of a photosystem. These pigments may form a separate antenna complex or may be bound directly to the reaction-center proteins.

**antibiotic.** A compound, produced by one organism, that is toxic to other organisms. Clinically useful antibiotics must be specific for pathogens and not affect the human host.

**antibody.** A glycoprotein synthesized by certain white blood cells as part of the immunological defense system. Antibodies specifically bind to foreign compounds, called antigens, forming antibody-antigen complexes that mark the antigen for destruction. Also known as an immunoglobulin.

**anticodon.** A sequence of three nucleotides in the anticodon loop of a tRNA molecule. The anticodon binds to the complementary codon in mRNA during translation.

**anticodon arm.** The stem-and-loop structure in a tRNA molecule that contains the anticodon.

**antigen.** A molecule or part of a molecule that is specifically bound by an antibody.

**antiport.** The cotransport of two different species of ions or molecules in opposite directions across a membrane by a transport protein.



**antisense strand.** In double-stranded DNA the antisense strand is the strand that does not contain codons. Also called the template strand. The opposite strand is called the sense strand or the coding strand.

**antisense RNA.** An RNA molecule that binds to a complementary mRNA molecule, forming a double-stranded region that inhibits translation of the mRNA.

**apoprotein.** A protein whose cofactor(s) is absent. Without the cofactor(s), the apoprotein lacks the biological activity characteristic of the corresponding holoprotein.

**apoptosis.** The programmed death of a cell.

**atomic mass unit.** The unit of atomic weight equal to 1/12th the mass of the  $^{12}\text{C}$  isotope of carbon. The mass of the  $^{12}\text{C}$  nuclide is exactly 12 by definition.

**attenuation.** A mechanism of regulation of gene expression that couples translation and transcription. Generally, the translation of a short reading frame at the beginning of a prokaryotic operon will determine whether transcription terminates before the rest of the operon is transcribed.

**autophosphorylation.** Phosphorylation of a protein kinase catalyzed by another molecule of the same kinase.

**autosome.** A chromosome other than a sex chromosome.

**autotroph.** An organism that can grow and reproduce using only inorganic substances (such as  $\text{CO}_2$ ) as its only source of essential elements.

**backbone.** 1. The repeating  $\text{N}-\text{C}_\alpha-\text{C}$  units connected by peptide bonds in a polypeptide chain. 2. The repeating sugar-phosphate units connected by phosphodiester linkages in a nucleic acid.

**bacteriophage.** A virus that infects a bacterial cell.

**base.** 1. A substance that can accept protons. A base is converted to its conjugate acid by addition of a proton. (The Lewis theory defines a base as an electron-pair donor [Lewis base].) 2. The substituted pyrimidine or purine of a nucleoside or nucleotide. The heterocyclic bases of nucleosides and nucleotides can participate in hydrogen bonding.

**base pairing.** The interaction between the bases of nucleotides in single-stranded nucleic acids to form double-stranded molecules, such as DNA, or regions of double-stranded secondary structure. The most common base pairs are formed by hydrogen bonding of adenine (A) with thymine (T) or uracil (U) and of guanine (G) with cytosine (C).

**B-DNA.** The most common conformation of DNA and the one proposed by Watson and Crick. B-DNA is a right-handed double helix with a diameter of 2.37 nm and approximately 10.4 base pairs per turn.

**$\beta$ -oxidation pathway.** The metabolic pathway that degrades fatty acids to acetyl CoA, producing NADH and  $\text{QH}_2$  and thereby generating large amounts of ATP. Each round of

$\beta$ -oxidation of fatty acids consists of four steps: oxidation, hydration, further oxidation, and thiolysis.

**$\beta$  pleated sheet.** See  $\beta$  sheet.

**$\beta$  sheet.** A common secondary structure of proteins that consists of extended polypeptide chains stabilized by hydrogen bonds between the carbonyl oxygen of one peptide bond and the amide hydrogen of another on the same or an adjacent polypeptide chain. The hydrogen bonds are nearly perpendicular to the extended polypeptide chains, which may be either parallel (running in the same N- to C-terminal direction) or antiparallel (running in opposite directions).

**$\beta$  strand.** An extended polypeptide chain within a  $\beta$  sheet secondary structure or having the same conformation as a strand within a  $\beta$  sheet.

**$\beta$  turn.** See turn.

**bile.** A suspension of bile salts, bile pigments, and cholesterol that originates in the liver and is stored in the gall bladder. Bile is secreted into the small intestine during digestion.

**binding-change mechanism.** A proposed mechanism for the phosphorylation of ADP and release of ATP from  $\text{F}_0\text{F}_1$  ATP synthase. The mechanism proposes three different binding-site conformations for ATP synthase: an open site from which ATP has been released, an ATP-bearing tight-binding site that is catalytically active, and an ADP and  $\text{P}_i$  loose-binding site that is catalytically inactive. Inward passage of protons through the ATP synthase complex into the mitochondrial matrix causes the open site to become a loose site; the loose site, already filled with ADP and  $\text{P}_i$ , to become a tight site; and the ATP-bearing site to become an open site.

**bioenergetics.** The study of energy changes in biological systems.

**biological membrane.** See membrane.

**biopolymer.** A biological macromolecule in which many identical or similar small molecules are covalently linked to one another to form a long chain. Proteins, polysaccharides, and nucleic acids are biopolymers.

**Bohr effect.** The phenomenon observed when exposure to carbon dioxide, which lowers the pH inside the cells, causes the oxygen affinity of hemoglobin in red blood cells to decrease.

**branch migration.** The movement of a crossover, or branch point, resulting in further exchange of DNA strands during recombination.

**branch site.** The point within an intron that becomes attached to the 5' end of the intron during splicing of mRNA precursors.

**buffer.** A solution of an acid and its conjugate base that resists changes in pH.

**buffer capacity.** The ability of a solution to resist changes in pH. For a given buffer, maximum buffer capacity is achieved at the pH at which the concentrations of the weak acid and its conjugate base are equal (i.e., when  $\text{pH} = \text{pK}_a$ ).

**$\text{C}_4$  pathway.** A pathway for carbon fixation in several plant species that minimizes photorespiration by concentrating  $\text{CO}_2$ . In this pathway,  $\text{CO}_2$  is incorporated into  $\text{C}_4$  acids in the mesophyll cells, and the  $\text{C}_4$  acids are decarboxylated in the bundle sheath cells, releasing  $\text{CO}_2$  for use by the reductive pentose phosphate cycle.

**calorie (cal).** The amount of energy required to raise the temperature of 1 gram of water by  $1^\circ\text{C}$  (from  $14.5^\circ\text{C}$  to  $15.5^\circ\text{C}$ ). One calorie is equal to 4.184 J.

**Calvin cycle.** A cycle of reactions that involve the fixation of carbon dioxide and the net production of glyceraldehyde-3-phosphate. Usually associated with photosynthesis. Also known as the Calvin-Benson cycle, the  $\text{C}_3$  pathway, and the reductive pentose phosphate (RPP) cycle.

**Calvin-Benson cycle.** See Calvin cycle.

**CAM.** See Crassulacean acid metabolism.

**cap.** A 7-methylguanosine residue attached by a pyrophosphate linkage to the 5' end of a eukaryotic mRNA molecule. The cap is added posttranscriptionally and is required for efficient translation. Further covalent modifications yield alternative cap structures.

**carbanion.** A carbon anion that results from the cleavage of a covalent bond between carbon and another atom in which both electrons from the bond remain with the carbon atom.

**carbocation.** A carbon cation that results from the cleavage of a covalent bond between carbon and another atom in which the carbon atom loses both electrons from the bond.

**carbohydrate.** Loosely defined as a compound that is a hydrate of carbon in which the ratio of C:H:O is 1:2:1. Carbohydrates include monomeric sugars (i.e., monosaccharides) and their polymers. Also known as a saccharide.

**carboxyl terminus.** See C-terminus.

**carnitine shuttle system.** A cyclic pathway that shuttles acetyl CoA from the cytosol to the mitochondria by formation and transport of acyl carnitine.

**cascade.** Sequential activation of several components, resulting in signal amplification.

**catabolic reaction.** A metabolic reaction that degrades a molecule to provide smaller molecular building blocks and energy to an organism.

**catabolite repression.** A regulatory mechanism that results in increased rates of transcription of many bacterial genes and operons when glucose is present. A complex between cAMP and cAMP regulatory protein (CRP) activates transcription.

**catalytic antibodies.** Antibody molecules that have been genetically manipulated so that they catalyze reactions involving the antigen.

**catalytic center.** The polar amino acids in the active site of an enzyme that participate in chemical changes during catalysis.

**catalytic constant ( $k_{\text{cat}}$ ).** A kinetic constant that is a measure of how rapidly an enzyme can catalyze a reaction when saturated with its



substrate(s). The catalytic constant is equal to the maximum velocity ( $V_{\max}$ ) divided by the total concentration of enzyme ( $[E]_{\text{total}}$ ), or the number of moles of substrate converted to product per mole of enzyme active sites per second, under saturating conditions. Also known as the turnover number.

**catalytic proficiency.** The ratio of the rate constants for a reaction in the presence of enzyme ( $k_{\text{cat}}/K_m$ ) to the rate constant for the chemical reaction in the absence of enzyme.

**cataplerotic reaction.** A reaction that removes intermediates in a pathway, especially the citric acid cycle (cf., anaplerotic).

**cathode.** A negatively charged electrode. In electrophoresis, cations move toward the cathode.

**cation.** An ion with an overall positive charge.

**cDNA.** See complementary DNA.

**Central Dogma.** The concept that the flow of information from nucleic acid to protein is irreversible. The term is often applied incorrectly to the actual pathway of information flow from DNA to RNA to protein.

**ceramide.** A molecule that consists of a fatty acid linked to the C-2 amino group of sphingosine by an amide bond. Ceramides are the metabolic precursors of all sphingolipids.

**cerebroside.** A glycosphingolipid that contains one monosaccharide residue attached via a  $\beta$ -glycosidic linkage to C-1 of a ceramide. Cerebrosides are abundant in nerve tissue and are found in myelin sheaths.

**channel.** An integral membrane protein with a central aqueous passage, which allows appropriately sized molecules and ions to traverse the membrane in either direction. Also known as a pore.

**channeling.** See metabolite channeling.

**chaotropic agent.** A substance that enhances the solubility of nonpolar compounds in water by disrupting regularities in hydrogen bonding among water molecules. Concentrated solutions of chaotropic agents, such as urea and guanidinium salts, decrease the hydrophobic effect and are thus effective protein denaturants.

**chaperone.** A protein that forms complexes with newly synthesized polypeptide chains and assists in their correct folding into biologically functional conformations. Chaperones may also prevent the formation of incorrectly folded intermediates, prevent incorrect aggregation of unassembled protein subunits, assist in translocation of polypeptide chains across membranes, and assist in the assembly and disassembly of large multiprotein structures.

**charge-charge interaction.** A noncovalent electrostatic interaction between two charged particles.

**chelate effect.** The phenomenon by which the constant for binding of a ligand having two or more binding sites to a molecule or atom is greater than the constant for binding of separate ligands to the same molecule or atom.

**chemiosmotic theory.** A theory proposing that a proton concentration gradient established during oxidation of substrates provides the energy to drive processes such as the formation of ATP from ADP and  $P_i$ .

**chemoautotroph.** An autotroph that derives chemical energy by oxidizing inorganic compounds (cf., photoautotroph).

**chemoheterotroph.** Non-photosynthetic organism that requires organic molecules as a carbon source and derives energy from oxidizing organic molecules.

**chemotaxis.** A mechanism that couples signal transduction to flagella movement in bacteria causing them to move toward a chemical (positive chemotaxis) or away from a chemical (negative chemotaxis).

**chiral atom.** An atom with asymmetric substitution that can exist in two different configurations.

**chloroplast.** A chlorophyll-containing organelle in algae and plant cells that is the site of photosynthesis.

**chromatin.** A DNA-protein complex in the nuclei of eukaryotic cells.

**chromatography.** A technique used to separate components of a mixture based on their partitioning between a mobile phase, which can be gas or liquid, and a stationary phase, which is a liquid or solid.

**chromosome.** A single DNA molecule containing many genes. An organism may have a genome consisting of a single chromosome or many.

**chylomicron.** A type of plasma lipoprotein that transports triacylglycerols, cholesterol, and cholesteryl esters from the small intestine to the tissues.

**citric acid cycle.** A metabolic cycle consisting of eight enzyme-catalyzed reactions that completely oxidizes acetyl units to  $\text{CO}_2$ . The energy released in the oxidation reactions is conserved as reducing power when the coenzymes  $\text{NAD}^+$  and ubiquinone (Q) are reduced. Oxidation of one molecule of acetyl CoA by the citric acid cycle generates three molecules of NADH, one molecule of  $\text{QH}_2$ , and one molecule of GTP or ATP. Also known as the Krebs cycle and the tricarboxylic acid cycle.

**clone.** One of the identical copies derived from the replication or reproduction of a single molecule, cell, or organism.

**cloning.** The generation of many identical copies of a molecule, cell, or organism. Cloning sometimes refers to the entire process of constructing and propagating a recombinant DNA molecule.

**cloning vector.** A DNA molecule that carries a segment of foreign DNA. A cloning vector introduces the foreign DNA into a cell where it can be replicated and sometimes expressed.

**coding strand.** The strand of DNA within a gene whose nucleotide sequence is identical to that of the RNA produced by transcription (with the replacement of T by U in RNA).

**codon.** A sequence of three nucleotide residues in mRNA (or DNA) that specifies a particular amino acid according to the genetic code.

**coenzyme.** An organic molecule required by an enzyme for full activity. Coenzymes can be further classified as cosubstrates or prosthetic groups.

**coenzyme A.** A large coenzyme used in transferring acyl groups.

**cofactor.** An inorganic ion or organic molecule required by an apoenzyme to convert it to a holoenzyme. There are two types of cofactors: essential ions and coenzymes.

**column chromatography.** A technique for purifying proteins. See affinity chromatography, gel-filtration chromatography, ion-exchange chromatography, HPLC, and affinity chromatography.

**competitive inhibition.** Reversible inhibition of an enzyme-catalyzed reaction by an inhibitor that prevents substrate binding.

**complementary DNA (cDNA).** DNA synthesized from an mRNA template by the action of reverse transcriptase.

**concerted theory of cooperativity and allosteric regulation.** A model of the cooperative binding of ligands to oligomeric proteins. According to the concerted theory, the change in conformation of a protein due to the binding of a substrate or an allosteric modulator shifts the equilibrium of the conformation of the protein between T (a low substrate-affinity conformation) and R (a high substrate-affinity conformation). This theory suggests that all subunits of the protein have the same conformation, either all T or all R. Also known as the symmetry-driven theory.

**condensation.** A reaction involving the joining of two or more molecules accompanied by the elimination of water, alcohol, or other simple substance.

**configuration.** A spatial arrangement of atoms that cannot be altered without breaking and re-forming covalent bonds.

**conformation.** Any three-dimensional structure, or spatial arrangement, of a molecule that results from rotation of functional groups around single bonds. Because there is free rotation around single bonds, a molecule can potentially assume many conformations.

**conjugate acid.** The product resulting from the gain of a proton by a base.

**conjugate base.** The product resulting from the loss of a proton by an acid.

**consensus sequence.** The sequence of nucleotides most commonly found at each position within a region of DNA or RNA.

**cooperativity.** 1. The phenomenon whereby the binding of one ligand or substrate molecule to a protein influences the affinity of the protein for additional molecules of the same substance. Cooperativity may be positive or negative. 2. The phenomenon whereby formation



of structure in one part of a macromolecule promotes the formation of structure in the rest of the molecule.

**core particle.** See nucleosome core particle.

**corepressor.** A ligand that binds to a repressor of a gene causing it to bind DNA and prevent transcription.

**Cori cycle.** An interorgan metabolic loop that recycles carbon and transports energy from the liver to the peripheral tissues. Glucose is released from the liver and metabolized to produce ATP in other tissues. The resulting lactate is then returned to the liver for conversion back to glucose by gluconeogenesis.

**cosubstrate.** A coenzyme that is a substrate in an enzyme-catalyzed reaction. A cosubstrate is altered during the course of the reaction and dissociates from the active site of the enzyme. The original form of the cosubstrate can be regenerated in a subsequent enzyme-catalyzed reaction.

**cotransport.** The coupled transport of two different species of solutes across a membrane, in the same direction (symport) or the opposite direction (antiport), carried out by a transport protein.

**coupled reactions.** Two metabolic reactions that share a common intermediate.

**covalent catalysis.** Catalysis in which one substrate, or part of it, forms a covalent bond with the catalyst and then is transferred to a second substrate. Many enzymatic group-transfer reactions proceed by covalent catalysis.

**Crassulacean acid metabolism (CAM).** A modified sequence of carbon-assimilation reactions used primarily by plants in arid environments to reduce water loss during photosynthesis. In these reactions,  $\text{CO}_2$  is taken up at night, resulting in the formation of malate. During the day, malate is decarboxylated, releasing  $\text{CO}_2$  for use by the reductive pentose phosphate cycle.

**C-terminus.** The amino acid residue bearing a free carboxyl group at one end of a peptide chain. Also known as the carboxyl terminus.

**cyclic electron transport.** A modified sequence of electron transport steps in chloroplasts that operates to provide ATP without the simultaneous formation of NADPH.

**cytoplasm.** The part of a cell enclosed by the plasma membrane, excluding the nucleus.

**cytoskeleton.** A network of proteins that contributes to the structure and organization of a eukaryotic cell.

**cytosol.** The aqueous portion of the cytoplasm minus the subcellular structures.

**D arm.** The stem-and-loop structure in a tRNA molecule that contains dihydrouridylic (D) residues.

**dalton.** A unit of mass equal to one atomic mass unit.

**dark reactions.** The photosynthetic reactions in which NADPH and ATP are used to fix  $\text{CO}_2$  to carbohydrate. Also known as the light-independent reactions.

**degeneracy.** When referring to the genetic code, degeneracy refers to the fact that several different codons specify the same amino acid.

**dehydrogenase.** An enzyme that catalyzes the removal of hydrogen from a substrate or the oxidation of a substrate. Dehydrogenases are members of the IUBMB class of enzymes known as oxidoreductases.

**denaturation.** 1. A disruption in the native conformation of a biological macromolecule that results in loss of the biological activity of the macromolecule. 2. The complete unwinding and separation of complementary strands of DNA.

**detergent.** An amphipathic molecule consisting of a hydrophobic portion and a hydrophilic end that may be ionic or polar. Detergent molecules can aggregate in aqueous media to form micelles. Also known as a surfactant.

**dialysis.** A procedure in which low-molecular-weight solutes in a sample are removed by diffusion through a semipermeable barrier and replaced by solutes from the surrounding medium.

**diffusion controlled reaction.** A reaction that occurs with every collision between reactant molecules. In enzyme-catalyzed reactions, the  $k_{\text{cat}}/K_m$  ratio approaches a value of  $10^8 - 10^9 \text{ M}^{-1} \text{ s}^{-1}$ .

**diploid.** Having two sets of chromosomes or two copies of the genome.

**dipole.** Two equal but opposite charges, separated in space, resulting from the uneven distribution of charge within a molecule or a chemical bond.

**direct repair.** The removal of DNA damage by proteins that recognize damaged nucleotides and mismatched bases and repair them without cleaving the DNA or excising the base.

**distributive enzyme.** An enzyme that dissociates from its growing polymeric product after addition of each monomeric unit and must reassociate with the polymer for polymerization to proceed (cf., progressive enzyme).

**disulfide bond.** A covalent linkage formed by oxidation of the sulfhydryl groups of two cysteine residues. Disulfide bonds are important in stabilizing the three-dimensional structures of some proteins.

**domain.** A discrete, independent folding unit within the tertiary structure of a protein. Domains are usually combinations of several motifs forming a characteristic fold.

**double helix.** A nucleic acid conformation in which two antiparallel polynucleotide strands wrap around each other to form a two-stranded helical structure stabilized largely by stacking interactions between adjacent hydrogen-bonded base pairs.

**double-reciprocal plot.** A plot of the reciprocal of initial velocity versus the reciprocal of substrate concentration for an enzyme-catalyzed reaction. The  $x$  and  $y$  intercepts indicate the values of the reciprocals of the Michaelis constant and the maximum velocity,

respectively. A double-reciprocal plot is a linear transformation of the Michaelis-Menten equation. Also known as a Lineweaver-Burk plot.

**E.** See reduction potential.

**$E^\circ$ .** See standard reduction potential.

**E site.** Exit site: The site on a ribosome from which a deaminoacylated tRNA is released during protein synthesis.

**Edman degradation.** A procedure used to determine the sequence of amino acid residues from a free  $N$ -terminus of a polypeptide chain. The  $N$ -terminal residue is chemically modified, cleaved from the chain, and identified by chromatographic procedures, and the rest of the polypeptide is recovered. Multiple reaction cycles allow identification of the new  $N$ -terminal residue generated by each cleavage step.

**effector enzyme.** A membrane-associated protein that produces an intracellular second messenger in response to a signal from a transducer.

**eicosanoid.** An oxygenated derivative of a 20-carbon polyunsaturated fatty acid. Eicosanoids function as short-range messengers in the regulation of various physiological processes.

**electromotive force (emf).** A measure of the difference between the reduction potentials of the reactions on the two sides of an electrochemical cell (i.e., the voltage difference produced by the reactions).

**electrolyte.** A molecule such as NaCl that can dissociate to form ions.

**electron transport.** A set of reactions in which compounds such as NADH and reduced ubiquinone ( $\text{QH}_2$ ) are aerobically oxidized and ATP is generated from ADP and  $\text{P}_i$ . Membrane-associated electron transport consists of two tightly coupled phenomena: oxidation of substrates by the respiratory electron transport chain, accompanied by the translocation of protons across the inner mitochondrial membrane to generate a proton concentration gradient; and formation of ATP, driven by the flux of protons into the matrix through a channel in ATP synthase.

**electrophile.** A positively charged or electron-deficient species that is attracted to chemical species that are negatively charged or contain unshared electron pairs (nucleophiles).

**electrophoresis.** A technique used to separate molecules by their migration in an electric field, primarily on the basis of their net charge.

**electrospray mass spectrometry.** A technique in mass spectrometry where the target molecule is sprayed into the detector in tiny droplets.

**electrostatic interaction.** A general term for the electronic interaction between particles. Electrostatic interactions include charge-charge interactions, hydrogen bonds, and van der Waals forces.



**elongation factor.** A protein that is involved in extending the peptide chain during protein synthesis.

**enantiomers.** Stereoisomers that are non-superimposable mirror images.

**endocytosis.** The process by which matter is engulfed by a plasma membrane and brought into the cell within a lipid vesicle derived from the membrane.

**endonuclease.** An enzyme that catalyzes the hydrolysis of phosphodiester linkages at various sites within polynucleotide chains.

**endoplasmic reticulum.** A membranous network of tubules and sheets continuous with the outer nuclear membrane of eukaryotic cells. Regions of the endoplasmic reticulum coated with ribosomes are called the rough endoplasmic reticulum; regions having no attached ribosomes are known as the smooth endoplasmic reticulum. The endoplasmic reticulum is involved in the sorting and transport of certain proteins and in the synthesis of lipids.

**endosomes.** Smooth vesicles inside the cell that are receptacles for endocytosed material.

**energy-rich compound.** A compound whose hydrolysis occurs with a large negative free-energy change (equal to or greater than that for  $\text{ATP} \rightarrow \text{ADP} + \text{P}_i$ ).

**enthalpy ( $H$ ).** A thermodynamic state function that describes the heat content of a system.

**entropy ( $S$ ).** A thermodynamic state function that describes the randomness or disorder of a system.

**enzymatic reaction.** A reaction catalyzed by a biological catalyst, an enzyme. Enzymatic reactions are  $10^3$  to  $10^{17}$  times faster than the corresponding uncatalyzed reactions.

**enzyme.** A biological catalyst, almost always a protein. Some enzymes may require additional cofactors for activity. Virtually all biochemical reactions are catalyzed by specific enzymes.

**enzyme assay.** A method used to analyze the activity of a sample of an enzyme. Typically, enzymatic activity is measured under selected conditions such that the rate of conversion of substrate to product is proportional to enzyme concentration.

**enzyme inhibitor.** A compound that binds to an enzyme and interferes with its activity by preventing either the formation of the ES complex or its conversion to  $\text{E} + \text{P}$ .

**enzyme-substrate complex (ES).** A complex formed when substrate molecules bind non-covalently within the active site of an enzyme.

**epimers.** Isomers that differ in configuration at only one of several chiral centers.

**equilibrium.** The state of a system in which the rate of conversion of substrate to product is equal to the rate of conversion of product to substrate. The free-energy change for a reaction or system at equilibrium is zero.

**equilibrium constant ( $K_{eq}$ ).** The ratio of the concentrations of products to the concentrations of reactants at equilibrium. The equilibrium constant is related to the standard Gibbs free energy change of reaction.

**essential amino acid.** An amino acid that cannot be synthesized by an animal and must be obtained in the diet.

**essential fatty acid.** A fatty acid that cannot be synthesized by an animal and must be obtained in the diet.

**essential ion.** An ion required as a cofactor for the catalytic activity of certain enzymes. Some essential ions, called activator ions, are reversibly bound to enzymes and often participate in the binding of substrates, whereas tightly bound metal ions frequently participate directly in catalytic reactions.

**eukaryote.** An organism whose cells generally possess a nucleus and internal membranes (cf., prokaryote).

**excision repair.** The reversal of DNA damage by excision-repair endonucleases. Gross lesions that alter the structure of the DNA helix are repaired by cleavage on each side of the lesion and removal of the damaged DNA. The resulting single-stranded gap is filled by DNA polymerase and sealed by DNA ligase.

**exocytosis.** The process by which material destined for secretion from a cell is enclosed in lipid vesicles that are transported to and fuse with the plasma membrane, releasing the material into the extracellular space.

**exon.** A nucleotide sequence that is present in the primary RNA transcript and in the mature RNA molecule. The term exon also refers to the region of the gene that corresponds to a sequence present in the mature RNA (cf., intron).

**exonuclease.** An enzyme that catalyzes the sequential hydrolysis of phosphodiester linkages from one end of a polynucleotide chain.

**extrinsic membrane protein.** See peripheral membrane protein.

**facilitated diffusion.** See passive transport.

**facultative anaerobe.** An organism that can survive in the presence or absence of oxygen.

**fatty acid.** A long chain aliphatic hydrocarbon with a single carboxyl group at one end. Fatty acids are the simplest type of lipid and are components of many more complex lipids, including triacylglycerols, glycerophospholipids, sphingolipids, and waxes.

**feedback inhibition.** Inhibition of an enzyme that catalyzes an early step in a metabolic pathway by an end product of the same pathway.

**feed-forward activation.** Activation of an enzyme in a metabolic pathway by a metabolite produced earlier in the pathway.

**fermentation.** The anaerobic catabolism of metabolites for energy production. In alcoholic fermentation, pyruvate is converted to ethanol and carbon dioxide.

**fibrous proteins.** A major class of water-insoluble proteins that associate to form long fibers. Many fibrous proteins are physically tough and provide mechanical support to individual cells or entire organisms.

**first-order reaction.** A reaction whose rate is directly proportional to the concentration of only one reactant.

**Fischer projection.** A two-dimensional representation of the three-dimensional structures of sugars and related compounds. In a Fischer projection, the carbon skeleton is drawn vertically, with C-1 at the top. At a chiral center, horizontal bonds extend toward the viewer and vertical bonds extend away from the viewer.

**fluid mosaic model.** A model proposed for the structure of biological membranes. In this model, the membrane is depicted as a dynamic structure in which lipids and membrane proteins (both integral and peripheral) rotate and undergo lateral diffusion.

**fluorescence.** A form of luminescence in which visible radiation is emitted from a molecule as it passes from a higher to a lower electronic state.

**flux.** The flow of material through a metabolic pathway. Flux depends on the supply of substrates, the removal of products, and the catalytic capabilities of the enzymes involved in the pathway.

**fold.** A combination of secondary structures that form the core of a protein domain. Many different folds have been characterized.

**frameshift mutation.** An alteration in DNA caused by the insertion or deletion of a number of nucleotides not divisible by three. A frameshift mutation changes the reading frame of the corresponding mRNA molecule and affects translation of all codons downstream of the mutation.

**free energy change.** See Gibbs free energy change.

**free radical.** A molecule or atom with an unpaired electron.

**furanose.** A monosaccharide structure that forms a five-membered ring as a result of intramolecular hemiacetal formation.

**G protein.** A protein that binds guanine nucleotides.

$\Delta G$ . See Gibbs free energy change.

$\Delta G^\circ$ . See standard Gibbs free energy change.

**ganglioside.** A glycosphingolipid in which oligosaccharide chains containing *N*-acetylneuraminic acid are attached to a ceramide. Gangliosides are present on cell surfaces and provide cells with distinguishing surface markers that may serve in cellular recognition and cell-to-cell communication.

**gas chromatography.** A chromatographic technique used to separate components of a mixture based on their partitioning between the gas phase and a stationary phase, which can be a liquid or solid.



**gel-filtration chromatography.** A chromatographic technique used to separate a mixture of proteins or other macromolecules in solution based on molecular size, using a matrix of porous beads. Also known as molecular-exclusion chromatography.

**gene.** Loosely defined as a segment of DNA that is transcribed. In some cases, the term gene may also be used to refer to a segment of DNA that encodes a functional protein or corresponds to a mature RNA molecule.

**genetic code.** The correspondence between a particular three nucleotide codon and the amino acid it specifies. The standard genetic code of 64 codons is used by almost all organisms. The genetic code is used to translate the sequence of nucleotides in mRNA into protein.

**genetic recombination.** The exchange or transfer of DNA from one molecule of DNA to another (cf., homologous recombination).

**genome.** One complete set of the genetic information in an organism. It may be a single chromosome or a set of chromosomes (haploid). Mitochondria and chloroplasts have genomes separate from that in the nucleus of eukaryotic cells.

**Gibbs free energy change ( $\Delta G$ ).** A thermodynamic quantity that defines the equilibrium condition in terms of the changes in enthalpy ( $H$ ) and entropy ( $S$ ) of a system at constant pressure.  $\Delta G = \Delta H - T\Delta S$ , where  $T$  is absolute temperature. Free energy is a measure of the energy available within a system to do work.

**globular proteins.** A major class of proteins, many of which are water soluble. Globular proteins are compact and roughly spherical, containing tightly folded polypeptide chains. Typically, globular proteins include indentations, or clefts that specifically recognize and transiently bind other compounds.

**glucogenic compound.** A compound, such as an amino acid, that can be used for gluconeogenesis in animals.

**gluconeogenesis.** A pathway for synthesis of glucose from a noncarbohydrate precursor. Gluconeogenesis from pyruvate involves the seven near-equilibrium reactions of glycolysis traversed in the reverse direction. The three metabolically irreversible reactions of glycolysis are bypassed by four enzymatic reactions that do not occur in glycolysis.

**glucoside.** A glycoside where the anomeric carbon atom is from glucose.

**glycan.** A general term for an oligosaccharide or a polysaccharide. A homoglycan is a polymer of identical monosaccharide residues; a heteroglycan is a polymer of different monosaccharide residues.

**glycerophospholipid.** A lipid consisting of two fatty acyl groups bound to C-1 and C-2 of glycerol 3-phosphate and, in most cases, a polar substituent attached to the phosphate moiety. Glycerophospholipids are major components of biological membranes.

**glycoconjugate.** A carbohydrate derivative in which one or more carbohydrate chains are covalently linked to a peptide chain, protein, or lipid.

**glycoforms.** Glycoproteins containing identical amino acid sequences but different oligosaccharide-chain compositions.

**glycogen.** A branched homopolymer of glucose residues joined by  $\alpha$ -(1  $\rightarrow$  4) linkages with  $\alpha$ -(1  $\rightarrow$  6) linkages at branch points. Glycogen is a storage polysaccharide in animals and bacteria.

**glycolysis.** A catabolic pathway consisting of 10 enzyme-catalyzed reactions by which one molecule of glucose is converted to two molecules of pyruvate. In the process, two molecules of ATP are formed from ADP +  $P_i$ , and two molecules of  $NAD^+$  are reduced to NADH.

**glycoprotein.** A protein that contains covalently bound carbohydrate residues.

**glycosaminoglycan.** An unbranched polysaccharide of repeating disaccharide units. One component of the disaccharide is an amino sugar; the other component is usually a uronic acid.

**glycoside.** A molecule containing a carbohydrate in which the hydroxyl group of the anomeric carbon has been replaced through condensation with an alcohol, an amine, or a thiol.

**glycosidic bond.** Acetal linkage formed by condensation of the anomeric carbon atom of a saccharide with a hydroxyl, amino, or thiol group of another molecule. The most commonly encountered glycosidic bonds are formed between the anomeric carbon of one sugar and a hydroxyl group of another sugar. Nucleosidic bonds are *N*-linked glycosidic bonds.

**glycosphingolipid.** A lipid containing sphingosine and carbohydrate moieties.

**glycosylation.** See protein glycosylation.

**glyoxylate cycle.** A variation of the citric acid cycle in certain plants, bacteria, and yeast that allows net production of glucose from acetyl CoA via oxaloacetate. The glyoxylate cycle bypasses the two  $CO_2$  producing steps of the citric acid cycle.

**glyoxysome.** An organelle that contains specialized enzymes for the glyoxylate cycle.

**Golgi apparatus.** A complex of flattened, fluid-filled membranous sacs in eukaryotic cells, often found in proximity to the endoplasmic reticulum. The Golgi apparatus is involved in the modification, sorting, and targeting of proteins.

**granum.** A stack of flattened vesicles formed from the thylakoid membrane in chloroplasts.

**group transfer potential.** See phosphoryl group transfer potential.

**group transfer reaction.** A reaction in which a substituent or functional group is transferred from one substrate to another.

**H.** See enthalpy.

**hairpin. 1.** A secondary structure adopted by single-stranded polynucleotides that arises when short regions fold back on themselves and hydrogen bonds form between complementary bases. Also known as a stem-loop. **2.** A tight turn connecting two consecutive  $\beta$  strands of a polypeptide.

**haploid.** Having one set of chromosomes or one copy of the genome (cf., diploid).

**high energy molecule.** See energy-rich compound.

**Haworth projection.** A representation in which a cyclic sugar molecule is depicted as a flat ring that is projected perpendicular to the plane of the page. Heavy lines represent the part of the molecule that extends toward the viewer.

**HDL.** See high density lipoprotein.

**heat of vaporization.** The amount of heat required to evaporate 1 gram of a liquid.

**heat shock protein.** A protein whose synthesis is increased in response to stresses such as high temperature. Many heat shock proteins are chaperones that are also expressed in the absence of stress.

**helicase.** An enzyme that is involved in unwinding DNA.

**hemiacetal.** The product formed when an alcohol reacts with an aldehyde.

**hemiketal.** The product formed when an alcohol reacts with a ketone.

**Henderson-Hasselbalch equation.** An equation that describes the pH of a solution of a weak acid or a weak base in terms of the  $pK_a$  and the concentrations of the proton donor and proton acceptor forms.

**heterochromatin.** Regions of chromatin that are highly condensed.

**heterocyclic molecule.** A molecule that contains a ring structure made up of more than one type of atom.

**heteroglycan (heteropolysaccharide).** A carbohydrate polymer whose residues consist of two or more different types of monosaccharide.

**heterotroph.** An organism that requires at least one organic nutrient, such as glucose, as a carbon source.

**high density lipoprotein (HDL).** A type of plasma lipoprotein that is enriched in protein and transports cholesterol and cholesteryl esters from tissues to the liver.

**high-performance liquid chromatography (HPLC).** A chromatographic technique used to separate components of a mixture by dissolving the mixture in a liquid solvent and forcing it to flow through a chromatographic column under high pressure.

**histones.** A class of proteins that bind to DNA to form chromatin. The nuclei of eukaryotic cells contain five histones, known as H1, H2A, H2B, H3, and H4.

**Holliday junction.** The region of strand crossover resulting from recombination between two molecules of homologous double-stranded DNA.



**homoglycan (homopolysaccharide).** A carbohydrate polymer whose residues consist of a single type of monosaccharide.

**homologous.** Referring to genes or proteins that descend from a common ancestor.

**homologous recombination.** Recombination between molecules of DNA that have closely related sequences (i.e., they are homologous). This is the standard form of recombination that occurs between chromosomes in eukaryotic cells.

**homology.** The similarity of genes or proteins as a result of evolution from a common ancestor.

**hormone response element.** A DNA sequence that binds a transcriptional activator consisting of a steroid hormone receptor complex.

**housekeeping genes.** Genes that encode proteins or RNA molecules that are essential for the normal activities of all living cells.

**HPLC.** See high-performance liquid chromatography.

**hydration.** A state in which a molecule or ion is surrounded by water.

**hydrogen bond.** A weak electrostatic interaction formed when a hydrogen atom bonded covalently to a strongly electronegative atom is partially shared by interacting with electron pair of another electronegative atom.

**hydrolase.** An enzyme that catalyzes the hydrolytic cleavage of its substrate(s) (i.e., hydrolysis).

**hydropathy.** A measure of the hydrophobicity of amino acid side chains. The more positive the hydropathy value, the greater the hydrophobicity.

**hydrophilic.** "Water loving"—describing molecules that interact favorably with water.

**hydrophilicity.** The degree to which a compound or functional group interacts with water or is preferentially soluble in water.

**hydrophobic.** "Water fearing"—describing molecules that do not interact favorably with water and are much less soluble than hydrophilic molecules.

**hydrophobic effect.** The exclusion of hydrophobic groups or molecules by water. The hydrophobic effect appears to depend on the increase in entropy of solvent water molecules that are released from an ordered arrangement around the hydrophobic group.

**hydrophobic interaction.** A weak, noncovalent interaction between nonpolar molecules or substituents that results from the strong association of water molecules with one another. Such association leads to the shielding or exclusion of nonpolar molecules from an aqueous environment.

**hydrophobicity.** The degree to which a compound or functional group that is soluble in nonpolar solvents is insoluble or only sparingly soluble in water.

**IDL.** See intermediate density lipoprotein.

**induced fit.** Activation of an enzyme by a

substrate-initiated conformational change.

**inducer.** A ligand that binds to and inactivates a repressor thereby increasing the transcription of the gene controlled by the repressor.

**inhibition constant ( $K_i$ ).** The equilibrium constant for the dissociation of an inhibitor from an enzyme-inhibitor complex.

**inhibitor.** A compound that binds to an enzyme and inhibits its activity.

**initial velocity ( $v_0$ ).** The rate of conversion of substrate to product in the early stages of an enzymatic reaction, before appreciable product has been formed.

**initiation codon.** A codon that specifies the initiation site for protein synthesis. The methionine codon (AUG) is the most common initiation codon.

**initiation factor.** See translation initiation factor.

**initiator tRNA.** The tRNA molecule that is used exclusively at initiation codons. The initiator tRNA is usually a specific methionyl-tRNA.

**integral membrane protein.** A membrane protein that penetrates the hydrophobic core of the lipid bilayer and usually spans the bilayer completely. Also known as an intrinsic membrane protein.

**intercalating agent.** A compound containing a planar ring structure that can fit between the stacked base pairs of DNA. Intercalating agents distort the DNA structure, partially unwinding the double helix.

**intermediary metabolism.** The metabolic reactions by which the small molecules of cells are interconverted.

**intermediate density lipoprotein (IDL).** A type of plasma lipoprotein that is formed during the breakdown of VLDLs.

**intermediate filament.** A structure composed of different protein subunits, found in the cytoplasm of most eukaryotic cells. Intermediate filaments are components of the cytoskeletal network.

**intron.** An internal nucleotide sequence that is removed from the primary RNA transcript during processing. The term intron also refers to the region of the gene that corresponds to the corresponding RNA intron (cf., exon).

**inverted repeat.** A sequence of nucleotides that is repeated in the opposite orientation within the same polynucleotide strand. An inverted repeat in double-stranded DNA can give rise to a cruciform structure.

**ion pair.** An electrostatic interaction between ionic groups of opposite charge within the interior of a macromolecule such as a globular protein.

**ion product for water ( $K_w$ ).** The product of the concentrations of hydronium ions and hydroxide ions in an aqueous solution, equal to  $1.0 \times 10^{-14} \text{ M}^2$ .

**ion-exchange chromatography.** A chromatographic technique used to separate a mixture of

ionic species in solution, using a charged matrix. In anion-exchange chromatography, a positively charged matrix binds negatively charged solutes, and in cation-exchange chromatography, a negatively charged matrix binds positively charged solutes. The bound species can be serially eluted from the matrix by gradually changing the pH or increasing the salt concentration in the solvent.

**ionophore.** A compound that facilitates the diffusion of ions across bilayers and membranes by serving as a mobile ion carrier or by forming a channel for ion passage.

**irreversible enzyme inhibition.** A form of enzyme inhibition where the inhibitor binds covalently to the enzyme.

**isoacceptor tRNA molecules.** Different tRNA molecules that bind the same amino acid.

**isoelectric focusing.** A modified form of electrophoresis that uses buffers to create a pH gradient within a polyacrylamide gel. Each protein migrates to its isoelectric point (pI), that is, the pH in the gradient at which it no longer carries a net positive or negative charge.

**isoelectric point (pI).** The pH at which a zwitterionic molecule does not migrate in an electric field because its net charge is zero.

**isoenzymes.** See isozymes.

**isomerase.** An enzyme that catalyzes an isomerization reaction, a change in geometry or structure within one molecule.

**isoprene.** A branched, unsaturated five-carbon molecule that forms the basic structural unit of all isoprenoids, including the steroids and lipid vitamins.

**isoprenoid.** A lipid that is structurally related to isoprene.

**isozymes.** Different proteins from a single biological species that catalyze the same reaction. Also known as isoenzymes.

**junk DNA.** Regions of the genome with no known function.

**$K_a$ .** See acid dissociation constant.

**kb.** See kilobase pair.

**$k_{cat}$ .** See catalytic constant.

**$k_{cat}/K_m$ .** The second-order rate constant for conversion of enzyme and substrate to enzyme and product at low substrate concentrations. The ratio of  $k_{cat}$  to  $K_m$ , when used to compare several substrates, is called the specificity constant.

**$K_{eq}$ .** See equilibrium constant.

**ketogenesis.** The pathway that synthesizes ketone bodies from acetyl CoA in the mitochondrial matrix in mammals.

**ketogenic compound.** A compound, such as an amino acid, that can be degraded to form acetyl CoA and can thereby contribute to the synthesis of fatty acids or ketone bodies.

**ketone bodies.** Small molecules that are synthesized in the liver from acetyl CoA. During starvation, the ketone bodies  $\beta$ -hydroxybutyrate and acetoacetate become major metabolic fuels.



**ketoses.** A class of monosaccharides in which the most oxidized carbon atom, usually C-2, is ketonic.

**$K_j$ .** See inhibition constant.

**kilobase pair (kb).** A unit of length of double-stranded DNA, equivalent to 1000 base pairs.

**kinase.** An enzyme that catalyzes transfer of a phosphoryl group to an acceptor molecule. A protein kinase catalyzes the phosphorylation of protein substrates. Kinases are also known as phosphotransferases.

**kinetic mechanism.** A scheme used to describe the sequence of steps in a multisubstrate enzyme-catalyzed reaction.

**kinetic order.** The sum of the exponents in a rate equation, which reflects how many molecules are reacting in the slowest step of the reaction. Also known as reaction order.

**$K_m$ .** See Michaelis constant.

**Krebs cycle.** See citric acid cycle.

**$K_w$ .** See ion product of water.

**lagging strand.** The newly synthesized DNA strand formed by discontinuous 5'  $\rightarrow$  3' polymerization in the direction opposite replication fork movement.

**lateral diffusion.** The rapid motion of lipid or protein molecules within the plane of one leaflet of a lipid bilayer.

**LDL.** See low density lipoprotein.

**leader peptide.** The peptide encoded by a portion of the leader region of certain regulated operons. Synthesis of a leader peptide is the basis for regulating transcription of the entire operon by the mechanism of attenuation.

**leader region.** The sequence of nucleotides that lie between the transcription start site and the first coding region of an operon.

**leading strand.** The newly synthesized DNA strand formed by continuous 5'  $\rightarrow$  3' polymerization in the same direction as replication fork movement.

**leaflet.** One layer of a lipid bilayer.

**lectin.** A plant protein that binds specific saccharides in glycoproteins.

**leucine zipper.** A structural motif found in DNA-binding proteins and other proteins. The zipper is formed when the hydrophobic faces (frequently containing leucine residues) of two amphipathic  $\alpha$ -helices from the same or different polypeptide chains interact to form a coiled-coil structure.

**LHC.** See light-harvesting complex.

**ligand.** A molecule, group, or ion that binds noncovalently to another molecule or atom.

**ligand-gated ion channel.** A membrane ion channel that opens or closes in response to binding of a specific ligand.

**ligase.** An enzyme that catalyzes the joining, or ligation, of two substrates. Ligation reactions require the input of the chemical potential energy of a nucleoside triphosphate such as ATP. Ligases are commonly referred to as synthetases.

**light reactions.** The photosynthetic reactions in which protons derived from water are used in the chemiosmotic synthesis of ATP from ADP +  $P_i$  and a hydride ion from water reduces to NADPH. Also known as the light-dependent reactions.

**light-harvesting complex (LHC).** A large pigment complex in the thylakoid membrane that aids a photosystem in gathering light.

**limit dextrin.** A branched oligosaccharide derived from a glucose polysaccharide by the hydrolytic action of amylase or the phosphorytic action of glycogen phosphorylase or starch phosphorylase. Limit dextrins are resistant to further degradation catalyzed by amylase or phosphorylase. Limit dextrins can be further degraded only after hydrolysis of the  $\alpha$ -(1  $\rightarrow$  6) linkages.

**Lineweaver-Burk plot.** See double-reciprocal plot.

**linker DNA.** The stretch of DNA (approximately 54 base pairs) between two adjacent nucleosome core particles.

**lipase.** An enzyme that catalyzes the hydrolysis of triacylglycerols.

**lipid.** A water-insoluble (or sparingly soluble) organic compound found in biological systems, which can be extracted by using relatively nonpolar organic solvents.

**lipid bilayer.** A double layer of lipids in which the hydrophobic tails associate with one another in the interior of the bilayer and the polar head groups face outward into the aqueous environment. Lipid bilayers are the structural basis of biological membranes.

**lipid raft.** A patch of membrane rich in cholesterol and sphingolipid.

**lipid vitamin.** A polyprenyl compound composed primarily of a long hydrocarbon chain or fused ring. Unlike water-soluble vitamins, lipid vitamins can be stored by animals. Lipid vitamins include vitamins A, D, E, and K.

**lipid anchored membrane protein.** A membrane protein that is tethered to a membrane through covalent linkage to a lipid molecule.

**lipopolysaccharide.** A macromolecule composed of lipid A (a disaccharide of phosphorylated glucosamine residues with attached fatty acids) and a polysaccharide. Lipopolysaccharides are found in the outer membrane of gram-negative bacteria. These compounds are released from bacteria undergoing lysis and are toxic to humans and other animals. Also known as an endotoxin.

**lipoprotein.** A macromolecular assembly of lipid and protein molecules with a hydrophobic core and a hydrophilic surface. Lipids are transported via lipoproteins.

**liposome.** A synthetic vesicle composed of a phospholipid bilayer that encloses an aqueous compartment.

**loop.** A nonrepetitive polypeptide region that connects secondary structures within a protein molecule and provides directional

changes necessary for a globular protein to attain its compact shape. Loops contain from 2 to 16 residues. Short loops of up to 5 residues are often called turns.

**low density lipoprotein (LDL).** A type of plasma lipoprotein that is formed during the breakdown of IDLs and is enriched in cholesterol and cholesteryl esters.

**lumen.** The aqueous space enclosed by a biological membrane, such as the membrane of the endoplasmic reticulum or the thylakoid membrane.

**lyase.** An enzyme that catalyzes a nonhydrolytic or nonoxidative elimination reaction, or lysis, of a substrate, with the generation of a double bond. In the reverse direction, a lyase catalyzes addition of one substrate to a double bond of a second substrate.

**lysophosphoglyceride.** An amphipathic lipid that is produced when one of the two fatty acyl moieties of a glycerophospholipid is hydrolytically removed. Low concentrations of lysophosphoglycerides are metabolic intermediates, whereas high concentrations disrupt membranes, causing cells to lyse.

**lysosome.** A specialized digestive organelle in eukaryotic cells. Lysosomes contain a variety of enzymes that catalyze the breakdown of cellular biopolymers, such as proteins, nucleic acids, and polysaccharides, and the digestion of large particles, such as some bacteria ingested by the cell.

**major groove.** The wide groove on the surface of a DNA double helix created by the stacking of base pairs and the resulting twist in the sugar-phosphate backbones.

**MALDI.** See matrix-assisted laser desorption ionization.

**mass action ratio (Q).** The ratio of the concentrations of products to the concentrations of reactants of a reaction.

**mass spectrometry.** A technique that determines the mass of a molecule.

**matrix.** See mitochondrial matrix.

**matrix-assisted laser desorption ionization (MALDI).** A technique in mass spectrometry where the target molecule is released from a solid matrix by a laser beam.

**maximum velocity ( $V_{max}$ ).** The initial velocity of a reaction when the enzyme is saturated with substrate, that is, when all the enzyme is in the form of an enzyme-substrate complex.

**melting curve.** A plot of the change in absorbance versus temperature for a DNA molecule. The change in absorbance indicates unfolding of the double helix.

**melting point ( $T_m$ ).** The midpoint of the temperature range in which double-stranded DNA is converted to single-stranded DNA or a protein is converted from its native form to the denatured state.

**membrane.** A lipid bilayer containing associated proteins that serves to delineate and compartmentalize cells or organelles. Biological membranes are also the site of many important



biochemical processes related to energy transduction and intracellular signaling.

**membrane-associated electron transport.** See electron transport.

**membrane potential ( $\Delta\psi$ ).** The charge separation across a membrane that results from differences in ionic concentrations on the two sides of the membrane.

**messenger ribonucleic acid.** See mRNA.

**metabolic fuel.** A small compound that can be catabolized to release energy. In multicellular organisms, metabolic fuels may be transported between tissues.

**metabolically irreversible reaction.** A reaction in which the value of the mass action ratio is two or more orders of magnitude smaller than the value of the equilibrium constant. The Gibbs free energy change for such a reaction is a large negative number; thus, the reaction is essentially irreversible.

**metabolism.** The sum total of biochemical reactions carried out by an organism.

**metabolite.** An intermediate in the synthesis or degradation of biopolymers and their component units.

**metabolite channeling.** Transfer of the product of one reaction of a multifunctional enzyme or a multienzyme complex directly to the next active site or enzyme without entering the bulk solvent. Channeling increases the rate of a reaction pathway by decreasing the transit time for an intermediate to reach the next enzyme and by producing high local concentrations of the intermediate.

**metalloenzyme.** An enzyme that contains one or more firmly bound metal ions. In some cases, such metal ions constitute part of the active site of the enzyme and are active participants in catalysis.

**micelle.** An aggregation of amphipathic molecules in which the hydrophilic portions of the molecules project into the aqueous environment and the hydrophobic portions associated with one another in the interior of the structure to minimize contact with water molecules.

**Michaelis constant ( $K_m$ ).** The concentration of substrate that results in an initial velocity ( $v_0$ ) equal to one-half the maximum velocity ( $V_{max}$ ) for a given reaction.

**Michaelis-Menten equation.** A rate equation relating the initial velocity ( $v_0$ ) of an enzymatic reaction to the substrate concentration ( $[S]$ ), the maximum velocity ( $V_{max}$ ), and the Michaelis constant ( $K_m$ ).

**microfilament.** See actin filament.

**microtubule.** A protein filament composed of  $\alpha$  and  $\beta$  tubulin heterodimers. Microtubules are components of the cytoskeletal network and can form structures capable of directed movement.

**minor groove.** The narrow groove on the surface of a DNA double helix created by the stacking of base pairs and the resulting twist in the sugar-phosphate backbones.

**mismatch repair.** Restoration of the normal nucleotide sequence in a DNA molecule containing mismatched bases. In mismatch repair, the correct strand is recognized, a portion of the incorrect strand is excised, and correctly base-paired, double-stranded DNA is synthesized by the actions of DNA polymerase and DNA ligase.

**missense mutation.** An alteration in DNA that involves the substitution of one nucleotide for another, resulting in a change in the amino acid specified by that codon.

**mitochondrial matrix.** The gel-like phase enclosed by the inner membrane of the mitochondrion. The mitochondrial matrix contains many enzymes involved in aerobic energy metabolism.

**mitochondrion.** An organelle that is the main site of oxidative energy metabolism in most eukaryotic cells. Mitochondria contain an outer and an inner membrane, the latter characteristically folded into cristae.

**mixed inhibition.** A form of enzyme inhibition where both  $K_m$  and  $V_{max}$  are affected.

**molar mass.** The weight in grams of one mole of a compound.

**molecular chaperone.** See chaperone.

**molecular crowding.** The decrease in diffusion rate that occurs when molecules collide with each other.

**molecular weight.** See relative molecular mass.

**monocistronic mRNA.** An mRNA molecule that encodes only a single polypeptide. Most eukaryotic mRNA molecules are monocistronic.

**monomer. 1.** A small compound that becomes a residue when polymerized with other monomers. **2.** A single subunit of a multisubunit protein.

**monosaccharide.** A simple sugar of three or more carbon atoms with the empirical formula  $(CH_2O)_n$ .

**monounsaturated fatty acid.** An unsaturated fatty acid with a single carbon-carbon double bond.

**motif.** A combination of secondary structure that appears in a number of different proteins. Also known as supersecondary structure.

**$M_r$ .** See relative molecular mass.

**mRNA.** A class of RNA molecules that serve as templates for protein synthesis.

**mRNA precursor.** A class of RNA molecules synthesized by eukaryotic RNA polymerase II. mRNA precursors are processed posttranscriptionally to produce mature messenger RNA.

**mucin.** A high-molecular-weight O-linked glycoprotein containing as much as 80% carbohydrate by mass. Mucins are extended, negatively charged molecules that contribute to the viscosity of mucus, the fluid found on the surfaces of the gastrointestinal, genitourinary, and respiratory tracts.

**multienzyme complex.** An oligomeric protein that catalyzes several metabolic reactions.

**mutagen.** An agent that can cause DNA damage.

**mutation.** A heritable change in the sequence of nucleotides in DNA that causes a permanent alteration of genetic information.

**near-equilibrium reaction.** A reaction in which the value of the mass action ratio is close to the value of the equilibrium constant. The Gibbs free energy change for such a reaction is small; thus, the reaction is reversible.

**Nernst equation.** An equation that relates the observed change in reduction potential ( $\Delta E$ ) to the change in standard reduction potential ( $\Delta E^\circ$ ) of a reaction.

**neutral phospholipids.** Glycerophospholipids, such as phosphatidyl choline, having no net charge.

**neutral solution.** An aqueous solution that has a pH value of 7.0.

**nick translation.** The process in which DNA polymerase binds to a gap between the 3' end of a nascent DNA chain and the 5' end of the next RNA primer, catalyzes hydrolytic removal of ribonucleotides using 5'  $\rightarrow$  3' exonuclease activity, and replaces them with deoxyribonucleotides using 5'  $\rightarrow$  3' polymerase activity.

**nitrogen cycle.** The flow of nitrogen from  $N_2$  to nitrogen oxides ( $NO_2^\ominus$  and  $NO_3^\ominus$ ) ammonia, nitrogenous biomolecules, and back to  $N_2$ .

**nitrogen fixation.** The reduction of atmospheric nitrogen to ammonia. Biological nitrogen fixation occurs in only a few species of bacteria and algae.

**N-linked oligosaccharide.** An oligosaccharide chain attached to a protein through covalent bonds to the amide nitrogen atom of side chain of asparagine residues. The oligosaccharide chains of N-linked glycoproteins contain a core pentasaccharide of two N-acetylglucosamine residues and three mannose residues.

**NMR spectroscopy.** See nuclear magnetic resonance spectroscopy.

**noncompetitive inhibition.** Inhibition of an enzyme-catalyzed reaction by a reversible inhibitor that binds to either the enzyme or the enzyme-substrate complex.

**nonessential amino acid.** An amino acid that an animal can produce in sufficient quantity to meet metabolic needs.

**nonhomologous recombination.** Recombination between unrelated sequences that do not share significant sequence similarity.

**nonrepetitive structure.** An element of protein structure in which consecutive residues do not have a single repeating conformation.

**nonsense mutation.** An alteration in DNA that involves the substitution of one nucleotide for another, changing a codon that specifies an amino acid to a termination



codon. A nonsense mutation results in premature termination of a protein's synthesis.

**N-terminus.** The amino acid residue bearing a free  $\alpha$ -amino group at one end of a peptide chain. In some proteins, the N-terminus is blocked by acylation. The N-terminal residue is usually assigned the residue number 1. Also known as the amino terminus.

**nuclear envelope.** The double membrane that surrounds the nucleus and contains protein-lined nuclear pore complexes that regulate the import and export of material to and from the nucleus. The outer membrane of the nuclear envelope is continuous with the endoplasmic reticulum; the inner membrane is lined with filamentous proteins, constituting the nuclear lamina.

**nuclear magnetic resonance spectroscopy (NMR spectroscopy).** A technique used to study the structures of molecules in solution. In nuclear magnetic resonance spectroscopy, the absorption of electromagnetic radiation by molecules in magnetic fields of varying frequencies is used to determine the spin states of certain atomic nuclei.

**nuclease.** An enzyme that catalyzes hydrolysis of the phosphodiester linkages of a polynucleotide chain. Nucleases can be classified as endonucleases and exonucleases.

**nucleic acid.** A polymer composed of nucleotide residues linked in a linear sequence by 3'-5' phosphodiester linkages. DNA and RNA are nucleic acids composed of deoxyribonucleotide residues and ribonucleotide residues, respectively.

**nucleoid region.** The region within a prokaryotic cell that contains the chromosome.

**nucleolus.** The region of the eukaryotic nucleus where rRNA transcripts are processed and ribosomes are assembled.

**nucleophile.** An electron-rich species that is negatively charged or contains unshared electron pairs and is attracted to chemical species that are positively charged or electron-deficient (electrophiles).

**nucleophilic substitution.** A reaction in which one nucleophile (e.g.,  $Y^-$ ) displaces another (e.g.,  $X^-$ ).

**nucleoside.** A purine or pyrimidine N-glycoside of ribose or deoxyribose.

**nucleosome.** A DNA-protein complex that forms the fundamental unit of chromatin. A nucleosome consists of a nucleosome core particle (approximately 146 base pairs of DNA plus a histone octamer), linker DNA (approximately 54 base pairs), and histone H1 (which binds the core particle and linker DNA).

**nucleosome core particle.** A DNA-protein complex composed of approximately 146 base pairs of DNA wrapped around an octamer of histones (two each of H2A, H2B, H3, and H4).

**nucleotide.** The phosphate ester of a nucleoside, consisting of a nitrogenous base linked

to a pentose phosphate. Nucleotides are the monomeric units of nucleic acids.

**nucleus.** An organelle that contains the principal genetic material of eukaryotic cells and functions as the major site of RNA synthesis and processing.

**obligate aerobe.** An organism that requires the presence of oxygen for survival.

**obligate anaerobe.** An organism that requires an oxygen-free environment for survival.

**Okazaki fragments.** Relatively short strands of DNA that are produced during discontinuous synthesis of the lagging strand of DNA.

**oligomer.** A multisubunit molecule whose arrangement of subunits always has a defined stoichiometry and almost always displays symmetry.

**oligonucleotide.** A polymer of several (up to about 20) nucleotide residues linked by phosphodiester bonds.

**oligopeptide.** A polymer of several (up to about 20) amino acid residues linked by peptide bonds.

**oligosaccharide.** A polymer of 2 to about 20 monosaccharide residues linked by glycosidic bonds.

**oligosaccharide processing.** The enzyme-catalyzed addition and removal of saccharide residues during the maturation of a glycoprotein.

**O-linked oligosaccharide.** An oligosaccharide attached to a protein through a covalent bond to the hydroxyl oxygen atom of a serine or threonine residue.

**open reading frame.** A stretch of nucleotide triplets that contains no termination codons. Protein-encoding regions are examples of open reading frames.

**operator.** A DNA sequence to which a specific repressor protein binds, thereby blocking transcription of a gene or operon.

**operon.** A bacterial transcriptional unit consisting of several different coding regions cotranscribed from one promoter.

**ordered sequential reaction.** A reaction in which both the binding of substrates to an enzyme and the release of products from the enzyme follow an obligatory order.

**organelle.** Any specialized membrane-bounded structure within a eukaryotic cell. Organelles are uniquely organized to perform specific functions.

**origin of replication.** A DNA sequence at which replication is initiated.

**osmosis.** The movement of solvent molecules from a less concentrated solution to an adjacent, more concentrated solution.

**osmotic pressure.** The pressure required to prevent the flow of solvent from a less concentrated solution to a more concentrated solution.

**oxidase.** An enzyme that catalyzes an oxidation-reduction reaction in which  $O_2$  is the electron acceptor. Oxidases are members of

the IUBMB class of enzymes known as oxidoreductases.

**oxidation.** The loss of electrons from a substance through transfer to another substance (the oxidizing agent). Oxidations can take several forms, including the addition of oxygen to a compound, the removal of hydrogen from a compound to create a double bond, or an increase in the valence of a metal ion.

**oxidative phosphorylation.** See electron transport.

**oxidizing agent.** A substance that accepts electrons in an oxidation-reduction reaction and thereby becomes reduced.

**oxidoreductase.** An enzyme that catalyzes an oxidation-reduction reaction. Some oxidoreductases are known as dehydrogenases, oxidases, peroxidases, oxygenases, or reductases.

**oxygenation.** The reversible binding of oxygen to a macromolecule.

$\Delta p$ . See protonmotive force.

**PAGE.** See polyacrylamide gel electrophoresis.

**passive transport.** The process by which a solute specifically binds to a transport protein and is transported across a membrane, moving with the solute concentration gradient. Passive transport occurs without the expenditure of energy. Also known as facilitated diffusion.

**Pasteur effect.** The slowing of glycolysis in the presence of oxygen.

**pathway.** A sequence of metabolic reactions.

**pause site.** A region of a gene where transcription slows. Pausing is exaggerated at palindromic sequences, where newly synthesized RNA can form a hairpin structure.

**PCR.** See polymerase chain reaction.

**pentose phosphate pathway.** A pathway by which glucose 6-phosphate is metabolized to generate NADPH and ribose 5-phosphate. In the oxidative stage of the pathway, glucose 6-phosphate is converted to ribulose 5-phosphate and  $CO_2$  rating two molecules of NADPH. In the nonoxidative stage, ribulose 5-phosphate can be isomerized to ribose 5-phosphate or converted to intermediates of glycolysis. Also known as the hexose monophosphate shunt.

**peptide.** Two or more amino acids covalently joined in a linear sequence by peptide bonds.

**peptide bond.** The covalent secondary amide linkage that joins the carbonyl group of one amino acid residue to the amino nitrogen of another in peptides and proteins.

**peptide group.** The nitrogen and carbon atoms involved in a peptide bond and their four substituents: the carbonyl oxygen atom, the amide hydrogen atom, and the two adjacent  $\alpha$ -carbon atoms.

**peptidoglycan.** A macromolecule containing a heteroglycan chain of alternating N-acetylglucosamine and N-acetylmuramic acid cross-linked to peptides of varied composition. Peptidoglycans are the major components of the cell walls of many bacteria.

**peptidyl site.** See P site.



**peptidyl transferase.** The enzymatic activity responsible for the formation of a peptide bond during protein synthesis.

**peptidyl-tRNA.** The tRNA molecule to which the growing peptide chain is attached during protein synthesis.

**peripheral membrane protein.** A membrane protein that is weakly bound to the interior or exterior surface of a membrane through ionic interactions and hydrogen bonding with the polar heads of the membrane lipids or with an integral membrane protein. Also known as an extrinsic membrane protein.

**periplasmic space.** The region between the plasma membrane and the cell wall in bacteria.

**permeability coefficient.** A measure of the ability of an ion or small molecule to diffuse across a lipid bilayer.

**peroxisome.** An organelle in all animal and many plant cells that carries out oxidation reactions, some of which produce the toxic compound hydrogen peroxide ( $H_2O_2$ ). Peroxisomes contain the enzyme catalase, which catalyzes the breakdown of toxic  $H_2O_2$  to water and  $O_2$ .

**pH.** A logarithmic quantity that indicates the acidity of a solution, that is, the concentration of hydronium ions in solution. pH is defined as the negative logarithm of the hydronium ion concentration.

**pH optimum.** In an enzyme-catalyzed reaction, the pH at the point of maximum catalytic activity.

**phage.** See bacteriophage.

**phase-transition temperature ( $T_m$ ).** The midpoint of the temperature range in which lipids or other macromolecular aggregates are converted from a highly ordered phase or state (such as a gel) to a less-ordered state (such as a liquid crystal).

**$\phi$  (phi).** The angle of rotation around the bond between the  $\alpha$ -carbon and the nitrogen of a peptide group.

**phosphagen.** A "high energy" phosphate storage molecule found in animal muscle cells. Phosphagens are phosphoamides and have a higher phosphoryl-group-transfer potential than ATP.

**phosphatase.** An enzyme that catalyzes the hydrolytic removal of a phosphoryl group.

**phosphatidate.** A glycerophospholipid that consists of two fatty acyl groups esterified to C-1 and C-2 of glycerol 3-phosphate. Phosphatidates are metabolic intermediates in the biosynthesis or breakdown of more complex glycerophospholipids.

**phosphoanhydride.** A compound formed by condensation of two phosphate groups.

**phosphodiester linkage.** A linkage in nucleic acids and other molecules in which two alcoholic hydroxyl groups are joined through a phosphate group.

**phosphoester linkage.** The bond by which a phosphoryl group is attached to an alcoholic or phenolic oxygen.

**phospholipid.** A lipid containing a phosphate moiety.

**phosphorolysis.** Cleavage of a bond within a molecule by group transfer to an oxygen atom of phosphate.

**phosphorylase.** An enzyme that catalyzes the cleavage of its substrate(s) via nucleophilic attack by inorganic phosphate ( $P_i$ ) (i.e., via phosphorolysis).

**phosphorylation.** A reaction involving the addition of a phosphoryl group to a molecule.

**phosphoryl group transfer potential.** A measure of the ability of a compound to transfer a phosphoryl group to another compound. Under standard conditions, group transfer potentials have the same values as the standard free energies of hydrolysis but are opposite in sign.

**photoautotroph.** A photosynthetic organism that can utilize  $CO_2$  as its main carbon source.

**photon.** A quantum of light energy.

**photophosphorylation.** The light-dependent formation of ATP from ADP and  $P_i$  catalyzed by chloroplast ATP synthase.

**photoheterotroph.** Photosynthetic organism that requires organic molecules as a carbon source.

**photoreactivation.** The direct repair of damaged DNA by an enzyme that is activated by visible light.

**photorespiration.** The light-dependent uptake of  $O_2$  and the subsequent metabolism of phosphoglycolate that occurs primarily in  $C_3$  photosynthetic plants. Photorespiration can occur because  $O_2$  competes with  $CO_2$  for the active site of ribulose 1,5-bisphosphate carboxylase-oxygenase, the enzyme that catalyzes the first step of the reductive pentose phosphate cycle.

**photosynthesis.** The conversion of light energy (photons) to chemical energy in the form of ATP and/or NADPH.

**photosystem.** A functional unit of the light-dependent electron-transfer reactions of photosynthesis. Each membrane-embedded photosystem contains a reaction center, which forms the core of the photosystem, and a pool of light-absorbing antenna pigments.

**phototroph.** An organism that can convert light energy into chemical potential energy (i.e., an organism capable of photosynthesis).

**physiological pH.** The normal pH of human blood, which is 7.4.

**pI.** See isoelectric point.

**ping-pong reaction.** A reaction in which an enzyme binds one substrate and releases a product, leaving a substituted enzyme that then binds a second substrate and releases a second product, thereby restoring the enzyme to its original form.

**pitch.** The axial distance for one complete turn of a helical structure.

**$pK_a$ .** A logarithmic value that indicates the strength of an acid.  $pK_a$  is defined as the

negative logarithm of the acid dissociation constant,  $K_a$ .

**plasma membrane.** The membrane that surrounds the cytoplasm of a cell and thus defines the perimeter of the cell.

**plasmalogen.** A glycerophospholipid that has a hydrocarbon chain linked to C-1 of glycerol 3-phosphate through a vinyl ether linkage. Plasmalogens are found in the central nervous system and in peripheral nerve and muscle tissue.

**plasmid.** A relatively small, extrachromosomal DNA molecule that is capable of autonomous replication. Plasmids are usually closed, circular, double-stranded DNA molecules.

**P:O ratio.** The ratio of molecules of ADP phosphorylated to atoms of oxygen reduced during oxidative phosphorylation.

**polar.** Having uneven distribution of charge. A molecule or functional group is polar if its center of negative charge does not coincide with its center of positive charge.

**poly A tail.** A stretch of polyadenylate, up to 250 nucleotide residues long, that is added to the 3' end of a eukaryotic mRNA molecule following transcription.

**polyacrylamide gel electrophoresis (PAGE).** A technique used to separate molecules of different net charge and/or size based on their migration through a highly cross-linked gel matrix in an electric field.

**polycistronic mRNA.** An mRNA molecule that contains multiple coding regions. Many prokaryotic mRNA molecules are polycistronic.

**polymerase chain reaction (PCR).** A method for amplifying the amount of DNA in a sample and for enriching a particular DNA sequence in a population of DNA molecules. In the polymerase chain reaction, oligonucleotides complementary to the ends of the desired DNA sequence are used as primers for multiple rounds of DNA synthesis.

**polynucleotide.** A polymer of many (usually more than 20) nucleotide residues linked by phosphodiester bonds.

**polypeptide.** A polymer of many (usually more than 20) amino acid residues linked by peptide bonds.

**polyribosome.** See polysome.

**polysaccharide.** A polymer of many (usually more than 20) monosaccharide residues linked by glycosidic bonds. Polysaccharide chains can be linear or branched.

**polysome.** The structure formed by the binding of many translation complexes to a large mRNA molecule. Also known as a polyribosome.

**polyunsaturated fatty acid.** An unsaturated fatty acid with two or more carbon-carbon double bonds.

**pore.** See channel.

**posttranscriptional processing.** RNA processing that occurs after transcription is complete.



**posttranslational modification.** Covalent modification of a protein that occurs after synthesis of the polypeptide is complete.

**prenylated protein.** A lipid-anchored protein that is covalently linked to an isoprenoid moiety via the sulfur atom of a cysteine residue at the C-terminus of the protein.

**primary structure.** The sequence in which residues are covalently linked to form a polymeric chain.

**primary transcript.** A newly synthesized RNA molecule before processing.

**primase.** An enzyme in the primosome that catalyzes the synthesis of short pieces of RNA about 10 residues long. These oligonucleotides are the primers for synthesis of Okazaki fragments.

**primosome.** A multiprotein complex, including primase and helicase in *E. coli*, that catalyzes the synthesis of the short RNA primers needed for discontinuous DNA synthesis of the lagging strand.

**processive enzyme.** An enzyme that remains bound to its growing polymeric product through many polymerization steps (cf., distributive enzyme).

**prochiral atom.** An atom with multiple substituents, two of which are identical. A prochiral atom can become chiral when one of the identical substituents is replaced.

**prokaryote.** An organism, usually a single cell, which contains no nucleus or internal membranes (cf., eukaryote).

**promoter.** The region of DNA where RNA polymerase binds during transcription initiation.

**prostaglandin.** An eicosanoid that has a cyclopentane ring. Prostaglandins are metabolic regulators that act in the immediate neighborhood of the cells in which they are produced.

**prosthetic group.** A coenzyme that is tightly bound to an enzyme. A prosthetic group, unlike a cosubstrate, remains bound to a specific site of the enzyme throughout the catalytic cycle of the enzyme.

**protease.** An enzyme that catalyzes hydrolysis of peptide bonds. The physiological substrates of proteases are proteins.

**protein.** A biopolymer consisting of one or more polypeptide chains. The biological function of each protein molecule depends not only on the sequence of covalently linked amino acid residues, but also on its three-dimensional structure (conformation).

**protein coenzyme.** A protein that does not itself catalyze reactions but is required for the action of certain enzymes.

**protein glycosylation.** The covalent addition of carbohydrate to proteins. In *N*-glycosylation, the carbohydrate is attached to the amide group of the side chain of an asparagine residue. In *O*-glycosylation, the carbohydrate is attached to the hydroxyl group of the side chain of a serine or threonine residue.

**protein kinase.** See kinase.

**protein phosphatase.** See phosphatase.

**proteoglycan.** A complex of protein with glycosaminoglycan chains covalently bound through their anomeric carbon atoms. Up to 95% of the mass of a proteoglycan may be glycosaminoglycan.

**proteomics.** The study of all proteins produced in a certain cell type, tissue, organ, or organism.

**protonmotive force ( $\Delta p$ ).** The energy stored in a proton concentration gradient across a membrane.

**proximity effect.** The increase in the rate of a nonenzymatic or enzymatic reaction attributable to high effective concentrations of reactants, which result in more frequent formation of transition states.

**pseudo first-order reaction.** A multi-reactant reaction carried out under conditions where the rate depends on the concentration of only one reactant.

**pseudogene.** A nonexpressed sequence of DNA that evolved from a protein-encoding gene. Pseudogenes often contain mutations in their coding regions and cannot produce functional proteins.

$\psi$  (**psi**). The angle of rotation around the bond between the  $\alpha$ -carbon and the carbonyl carbon of a peptide group.

$\Delta\psi$ . See membrane potential.

**P site.** Peptidyl site. The site on a ribosome that is occupied during protein synthesis by a tRNA molecule attached to the growing polypeptide chain (peptidyl tRNA).

**purine.** A nitrogenous base having a two-ring structure in which a pyrimidine is fused to imidazole. Adenine and guanine are substituted purines found in both DNA and RNA.

**pyranose.** A monosaccharide structure that forms a six-membered ring as a result of intramolecular hemiacetal formation.

**pyrimidine.** A nitrogenous base having a heterocyclic ring that consists of four carbon atoms and two nitrogen atoms. Cytosine, thymine, and uracil are substituted pyrimidines found in nucleic acids (cytosine in DNA and RNA, uracil in RNA, and thymine principally in DNA).

**Q.** See mass action ratio.

**Q cycle.** A cyclic pathway proposed to explain the sequence of electron transfers and proton movements within Complex III of mitochondria or the cytochrome *b<sub>f</sub>* complex in chloroplasts. The net result of the two steps of the Q cycle is oxidation of two molecules of QH<sub>2</sub> or plastoquinol (PQH<sub>2</sub>); formation of one molecule of QH<sub>2</sub> or PQH<sub>2</sub>; transfer of two electrons; and net translocation of four protons across the inner mitochondrial membrane to the intermembrane space or across the thylakoid membrane to the lumen.

**quaternary structure.** The organization of two or more polypeptide chains within a multisubunit protein.

**R state.** The more active conformation of an allosteric protein; opposite of T state.

**Ramachandran plot.** A plot of  $\phi$  versus  $\psi$  values for amino acid residues in a polypeptide chain. Certain  $\phi$  and  $\psi$  values are characteristic of different conformations.

**random sequential reaction.** A reaction in which neither the binding of substrates to an enzyme nor the release of products from the enzyme follows an obligatory order.

**rate acceleration.** The ratio of the rate constant for a reaction in the presence of enzyme ( $k_{\text{cat}}$ ) divided by the rate constant for that reaction in the absence of enzyme ( $k_n$ ). The rate acceleration value is a measure of the efficiency of an enzyme.

**rate equation.** An expression of the observed relationship between the velocity of a reaction and the concentration of each reactant.

**rate determining step.** The slowest step in a chemical reaction. The rate determining step has the highest activation energy among the steps leading to formation of a product from the substrate.

**reaction center.** A complex of proteins, electron transport cofactors, and a special pair of chlorophyll molecules that forms the core of a photosystem. The reaction center is the site of conversion of photochemical energy to electrochemical energy during photosynthesis.

**reaction mechanism.** The step-by-step atomic or molecular events that occur during chemical reactions.

**reaction order.** See kinetic order.

**reaction specificity.** The lack of formation of wasteful by-products by an enzyme. Reaction specificity results in essentially 100% product yields.

**reactive center.** The part of a coenzyme to which mobile metabolic groups are attached.

**reading frame.** The sequence of nonoverlapping codons of an mRNA molecule that specifies the amino acid sequence. The reading frame of an mRNA molecule is determined by the position where translation begins; usually an AUG codon.

**receptor.** A protein that binds a specific ligand, such as a hormone, leading to some cellular response.

**recombinant DNA.** A DNA molecule that includes DNA from different sources.

**recombination.** See genetic recombination.

**reducing agent.** A substance that loses electrons in an oxidation-reduction reaction and thereby becomes oxidized.

**reducing end.** The residue containing a free anomeric carbon in a polysaccharide. A polysaccharide usually contains no more than one reducing end.

**reduction.** The gain of electrons by a substance through transfer from another substance (the reducing agent). Reductions can take several forms, including the loss of oxygen from a compound, the addition of