

THIRD EDITION

# LIFE

THE SCIENCE OF BIOLOGY

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## THE COVER

American bison (*Bison bison*) meander among the geysers in Yellowstone National Park in Wyoming.

The American bison, or buffalo, is the largest mammal in North America. Before Europeans colonized the continent, as many as 60 million bison ranged from Alberta to Mexico and from western New York to the Rocky Mountains. By 1895, due to relentless overhunting for their meat and hides, fewer than 1,000 bison existed. At the turn of the century, however, conservationists in Canada and the United States began to work to forestall the extinction of the bison by creating wildlife preserves. Today virtually all of North America's 50,000 bison live in national parks and refuges. Chapter 49 discusses ways in which the discipline of conservation biology is attacking the pressures toward extinction that threaten thousands of species throughout the world today. Photograph © Erwin and Peggy Bauer.

## THE FRONTISPIECE

The Yellowstone River in Paradise Valley, Montana, at the northern end of the Greater Yellowstone Ecosystem. Photograph by Todd Wilkinson. From *Conservation Biology* 5, September 1991, page 334. Reprinted by permission of the Society for Conservation Biology and Blackwell Scientific Publications, Inc.

## LIFE: THE SCIENCE OF BIOLOGY, Third Edition

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# 3

## Large Molecules

**PREVIEW:** Living things are made up of many substances, especially lipids, carbohydrates, proteins, and nucleic acids. Some lipids are energy-storing “fuels,” some form membranes, and others serve as chemical messengers or as trappers of energy. Carbohydrates function as strengthening elements, as fuels, and in other ways. The diverse functions of proteins include accelerating chemical reactions, defending the animal

The **macromolecules**—giant molecules, or aggregates of molecules, with molecular weights in excess of 1,000 daltons—perform many essential functions in organisms. As we will see, these functions arise directly from the structures of the molecules. Some of the macromolecules fold into globular forms with surface features that enable them to recognize and interact with certain other molecules. Other macromolecules form long, fibrous systems that provide strength and rigidity to parts of an organism; still others contract and allow the organism to move itself. Some macromolecules aggregate to form structures that determine what materials enter or leave the compartments within an organism. The largest of the molecules are all **polymers**: molecules that are made by the combination of many smaller molecules. The small molecules that are a polymer’s subunits are called **monomers**. An **oligomer** contains only a few monomers.

There is a flow of *information* among the various classes of macromolecules. The source of the *information* is DNA (deoxyribonucleic acid), the genetic material. Within the structure of DNA molecules lies the necessary information to dictate the structures of the many different proteins in an organism. Transmitting the information in DNA to proteins is the task of various types of RNAs (ribonucleic acids). Some of these proteins (the enzymes) act to accelerate chemical reactions in the cell. In this chapter, we take a brief look at the major classes of macromolecules in order to see how their structures relate to their

body against microorganisms, and providing support and protection. Nucleic acids store, transmit, and interpret hereditary information.

This chapter deals with the structures and functions of lipids (triglycerides, phospholipids, steroids, and carotenoids), carbohydrates (monosaccharides, oligosaccharides, and polysaccharides), amino acids, proteins, nucleotides, DNA, and RNA.

functions; in later chapters we will return to the topics raised here and develop them in greater detail.

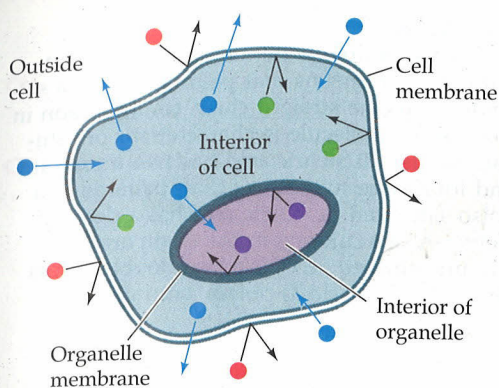
### FROM MONOMERS TO POLYMERS

The largest molecules in living things—polysaccharides, proteins, and nucleic acids—are polymers built from simpler monomers. These polymerization reactions belong to a class of reactions called **condensations** or **dehydrations**, which are of the general type



(A—H is a molecule consisting of a hydrogen atom attached to another part, A; B—OH is a molecule consisting of an —OH group attached to another part, B.) The product A—B is formed along with a molecule of water; the atoms of water are derived from the reactants, with one hydrogen atom coming from one reactant, and an oxygen atom and the other hydrogen atom from the other reactant. **Reactants** are the molecules undergoing a chemical reaction.

The actual polymerization reactions that produce the different kinds of macromolecules differ in detail. In all cases, energy must be added to the system for polymers to form. Other kinds of specific molecules participate; their function is to activate the reactants—to provide the necessary energy for the reactions to be carried out. Large molecules are assembled through the repeated condensations of activated monomers.



### 3.1 Lipid-Containing Membranes

Lipid-containing membranes separate the cell from its environment; they also separate the contents of some subcellular organelles from the rest of the cell. Materials that do not dissolve in lipids are generally unable to pass through the membranes from one region to another. Molecules that are lipid-soluble (bright blue symbols in this representation) move through membranes with relative ease.

## LIPIDS

The **lipids** are a diverse group of compounds that are insoluble in water but are readily soluble in organic (carbon-based) solvents such as ether. They release large amounts of energy when they break down. Each of these properties is significant in the biology of these compounds. Because lipids do not dissolve in water and water does not dissolve in lipids, a mixture of water and lipids forms two distinct layers. Also, many biological materials that are soluble in water are much less soluble in lipids.

Suppose that you must design compartments, separated from each other and from their environment by barriers that limit the passage of materials. Given the properties of lipids, an effective way to accomplish this would be to use lipid-containing membranes to separate the compartments (Figure 3.1). This is, in fact, the system that has evolved in nature. Molecular traffic within an organism or into and out of its compartments is strictly limited by the solubility properties of the lipid portion of the surrounding membrane. Compounds that dissolve readily in lipids can move rapidly through biological membranes; but compounds that are insoluble in lipids are prevented from passing, or must be transported across the membrane by specific proteins, as will be described in Chapter 5.

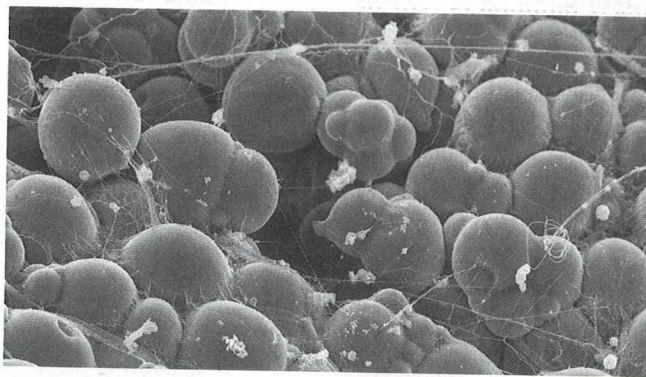
The role of lipids in energy storage relates to the topics of oxidation and reduction, which will be described in Chapter 6 when we discuss the processing of energy. For now, suffice it to say that the lipids are marvelous storehouses for energy. Many animal

species deposit fat (= lipid) droplets in their bodies as a means for storing energy—as you know, an excess of food results in fat deposition (Figure 3.2). Some plant species, such as olives, avocados, sesame seeds, and castor beans, have substantial amounts of lipids in their seeds or fruits that serve as energy reserves for the next generation.

### Triglycerides

One important group of lipids is the **triglycerides**, also known as *simple lipids*. Triglycerides that are solid at room temperature are called **fats**; those that are liquid at this temperature are called **oils**. The triglycerides are composed of two types of building blocks: **fatty acids** and **glycerol**. Fatty acids are carboxylic acids with long hydrocarbon tails. A typical fatty acid found in animal fats is palmitic acid,  $C_{15}H_{31}COOH$  (Figure 3.3). Another example is stearic acid,  $C_{17}H_{35}COOH$ , which has two more carbon atoms and four more hydrogen atoms. These are both **saturated** fatty acids because their hydrocarbon tails contain no double bonds. Another common fatty acid, oleic acid (Figure 3.3), is **unsaturated**. Notice the double bond near the middle of the hydrocarbon chain in oleic acid, causing a kink in the molecule. Other fatty acids, such as linoleic acid, have more than one carbon-carbon double bond and are thus **polyunsaturated**. These molecules have multiple kinks. Unsaturated and polyunsaturated fatty acids can accept hydrogen atoms—that is, they can become hydrogenated. The addition of two hydrogen atoms across the double bond of oleic acid, for example, would produce stearic acid.

Three fatty acid molecules combined with a molecule of glycerol give a molecule of a triglyceride (Figure 3.4). The three fatty acids in one triglyceride molecule are not always the same length, nor are they necessarily all either saturated or unsaturated. The kinks associated with double bonds are impor-

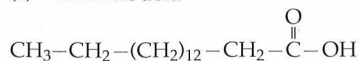


### 3.2 Fat Cells

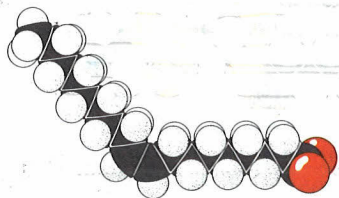
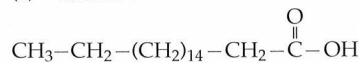
These cells served as stores of energy for a mouse.



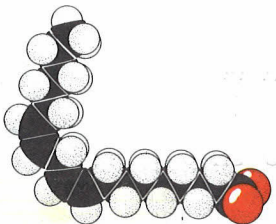
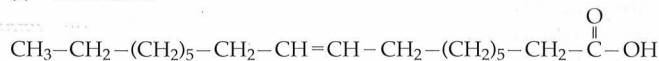
(a) Palmitic acid



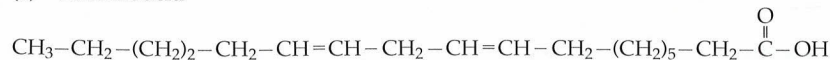
(b) Stearic acid



(c) Oleic acid



(d) Linoleic acid



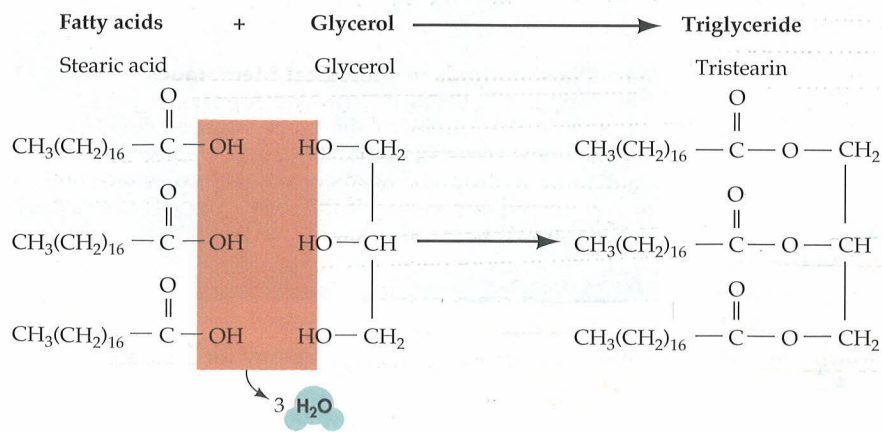
### 3.3 Fatty Acids

(a) The absence of double bonds between carbon atoms in the chain means that palmitic acid is a saturated fatty acid; the straight-chain configuration in the model of the molecule is characteristic of saturated fatty acids. (b) Stearic acid has two more carbons and four more hydrogens than palmitic acid and is also saturated. (c) Oleic acid has a double bond between two carbons in the chain and is therefore unsaturated. (d) With two double bonds in its chain, linoleic acid is polyunsaturated.

tant in determining the fluidity and melting point of a lipid. Triglycerides with short or unsaturated chains are usually oily liquids, whereas those with long and saturated chains are waxy solids. Animal fats such as lard and tallow are usually solids with long-chain, saturated or singly unsaturated fatty acids. In these fats, hydrocarbon chain lengths range between 10 and 20 carbon atoms. The triglycerides of plants tend to be more unsaturated, oily liquids. Natural peanut butter, for example, contains a great deal of oil. Peanut butter manufacturers often hydrogenate their product in order to reduce the double bonds and give a saturated, solid product.

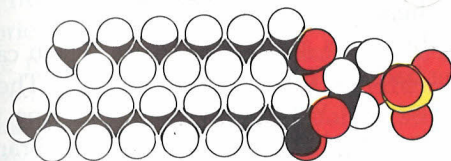
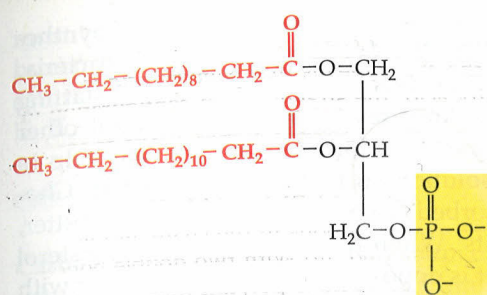
### Phospholipids

A triglyceride consists of glycerol with three fatty acids bound to it. Having certain phosphorus-containing compounds bound in the place of one of the fatty acids defines a class of substances known as phospholipids (Figure 3.5). Many phospholipids are important constituents of biological membranes. If you examine the structure of phospholipids closely, you will find it easy to understand how they are oriented in membranes. The phosphorus-containing portion of the phospholipid molecule carries one or more electric charges, so this portion is hydrophilic



### 3.4 A Triglyceride and Its Components

Tristearin is a triglyceride composed of glycerol and three molecules of the fatty acid stearic acid. The synthesis of a triglyceride from glycerol and three fatty acids is an example of a condensation. Condensations result in the release of water molecules. (In living things the reaction is more complex, but the end result is as shown here.)

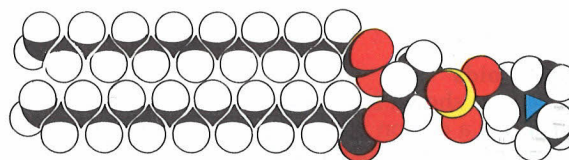
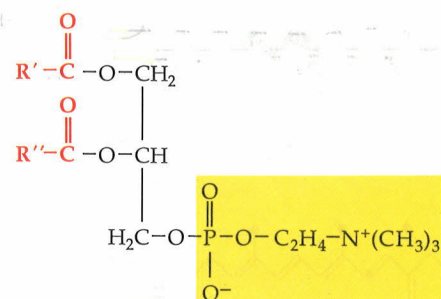


(a) Phosphatidate

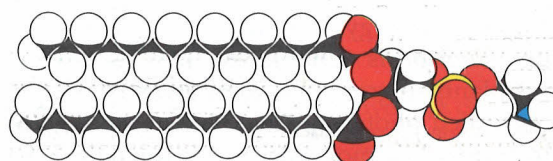
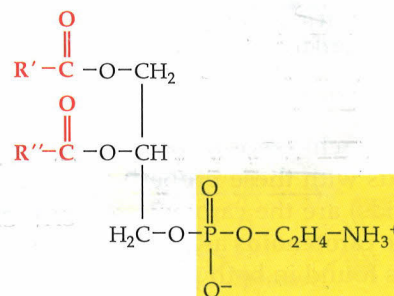
### 3.5 Some Phospholipids

A phospholipid consists of glycerol combined with two molecules of fatty acid and a molecule containing phosphorus. Examples of phosphorus-containing molecules are phosphoric acid, as in the yellow-shaded area of (a), and phosphocholine (yellow shaded area of b). Phospholipids that contain phosphocholine are called lecithins. (c) Cephalins are formed by the addition of both phosphoric acid and ethanolamine, as included in the yellow region. In these diagrams, R' and R'' stand for "residue" and represent any fatty-acid hydrocarbon chains. These chains, shown in red letters, are nonpolar, whereas the shaded phosphorus-containing portions are electrically charged. Other types of phospholipids exist.

(water-loving; remember that water is a polar molecule). The two fatty acid regions, however, are **hydrophobic** (water-fearing). Thus in a biological membrane, phospholipids line up in such a way that the nonpolar, hydrophobic "tails" pack tightly together to form the interior of the membrane, and the phosphorus-containing "heads" face outward (some to one side of the membrane and some to the other), where they interact with water, which is excluded from the interior of the membrane (Figure 3.6). The phospholipids form a bilayer, that is, a sheet two molecules thick. Biological membranes and their many important functions will be the subject of Chapter 5. For now, we emphasize that the dark lines of Figure 3.1 represent membranes that are composed of phospholipid bilayers as depicted in Figure 3.6.



(b) Phosphatidyl choline (a lecithin)



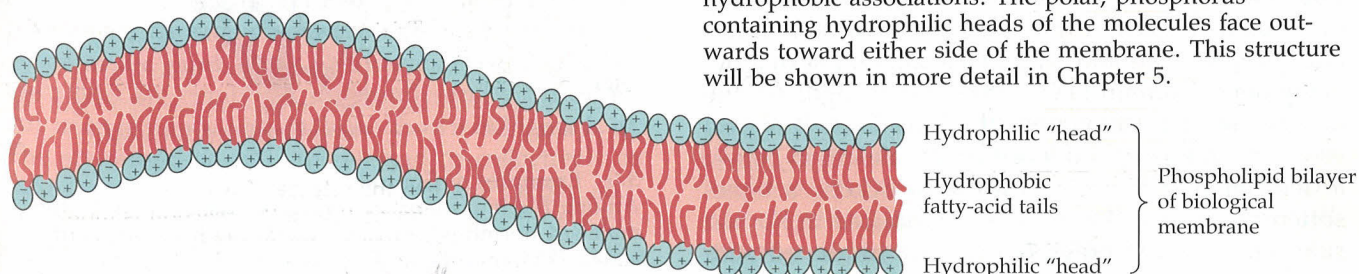
(c) Phosphatidyl ethanolamine (a cephalin)

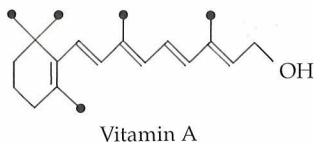
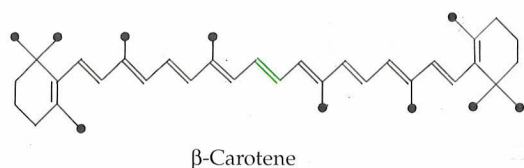
### Other lipids

The lipids we have considered thus far (phospholipids and triglycerides) are chemically similar. The term *lipid*, however, defines compounds not on the basis of structural similarity, but in terms of their solubility. Remember that lipids are insoluble in water but readily soluble in organic solvents such

### 3.6 Phospholipids in Biological Membranes

The nonpolar hydrocarbon (fatty-acid) chains gather together in the interior of the phospholipid bilayer by hydrophobic associations. The polar, phosphorus-containing hydrophilic heads of the molecules face outward toward either side of the membrane. This structure will be shown in more detail in Chapter 5.





### 3.7 Carotenoids

Carotenoids are shown here in a shorthand chemical notation in which a carbon atom is present at each junction in the rings and at each bend of the chains. Each black dot corresponds to a methyl ( $-\text{CH}_3$ ) group.  $\beta$ -Carotene is symmetrical around the central (green) double bond; the ends of the molecule on either side of the double bond are the same, although the ends are rotated 180 degrees with respect to one another. Two vitamin A molecules are produced by splitting  $\beta$ -carotene in the middle.

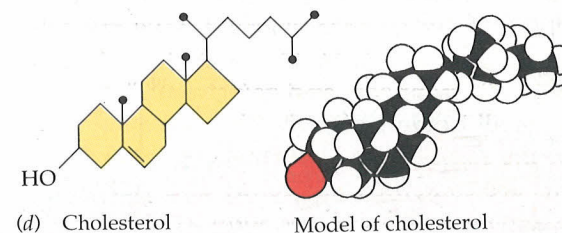
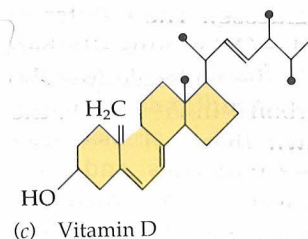
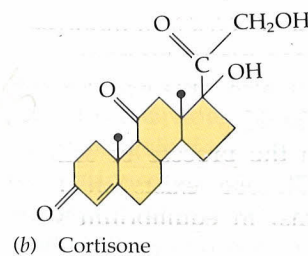
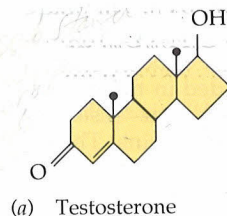
as ether, chloroform, or benzene. Some other compounds with these properties (and hence classifiable as lipids) are the carotenoids and the steroids.

The **carotenoids** are a family of light-absorbing pigments found in both plants and animals (Figure 3.7). Beta-carotene ( $\beta$ -carotene) is one of the pigments used to trap light energy in leaves to power the process of photosynthesis (Chapter 8). It is  $\beta$ -carotene that causes plants to grow toward or away from light (a behavior called phototropism, discussed in Chapter 32). In humans, a molecule of  $\beta$ -carotene can be broken down into two vitamin A molecules, from which we make the pigment rhodopsin that is required for vision (Chapter 37). Carotenoids are responsible for the color of carrots, tomatoes, pumpkins, egg yolks, and butter.

The **steroids** are a family of organic compounds based on a multiple ring structure in which the rings share carbons (Figure 3.8). Some steroids are important constituents of membranes. Others are among the hormones, chemical signals that carry messages from one part of the body to another (Chapter 34). Testosterone (Figure 3.8) is a steroid hormone that regulates sexual development in male vertebrates (animals with backbones), and the chemically similar estrogens play a similar role in females. Cortisone is one of a family of hormones that play a wide variety of regulatory roles in the digestion of carbohydrates and proteins, salt and water balance, and sexual development. Vitamin D is a steroid that regulates the absorption of calcium from the intestines. It is necessary for the proper deposition of calcium in bones; a deficiency of vitamin D leads to rickets, a bone-softening disease. Vitamin D is produced in human skin when certain other steroids are irradiated with sunlight or ultraviolet light.

Cholesterol (also shown in Figure 3.8) is synthesized in the liver. In all cells except those of bacteria, cholesterol stiffens membranes. It is also the starting material for making testosterone and several other steroid hormones and for the bile salts that help to get fats into solution so they can be digested. Cholesterol is absorbed from foods such as milk, butter, and animal fats. When there is too much cholesterol in the blood, it is deposited in the arteries (along with other substances), a condition that may lead to arteriosclerosis and heart attack.

Chemically the lipids are quite varied, as you can see by glancing back at Figures 3.3 through 3.8. Their diversity matches the variety of their functions in living things: energy storage, digestion, membrane structure, bone formation, vision, and chemical signaling. Most lipids can be synthesized in the bodies of animals; the synthesis and storage of fats is an important means of locking energy away until it is needed. The few lipids that cannot be synthesized



### 3.8 Examples of Steroids

Among the important steroids in vertebrates are (a) the male sex hormone testosterone, (b) the hormone cortisone, (c) vitamin D, and (d) cholesterol. All of these steroids have a similar ring structure (orange).

must be obtained in small amounts from the diet. For humans, the diet must include three particular unsaturated fatty acids and the fat-soluble vitamins: A, D, E, and K.

## CARBOHYDRATES

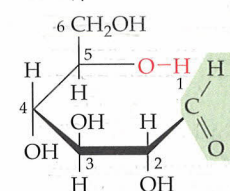
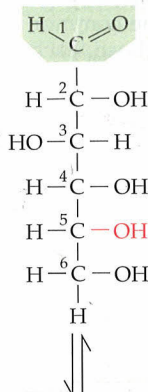
**Carbohydrates** are a diverse group of compounds with molecular weights ranging from less than 100 to hundreds of thousands. They fall into three categories: the **monosaccharides**, or *simple sugars*, which are monomers; the **oligosaccharides**, made up of a few monosaccharides linked together; and the **polysaccharides**, polymeric carbohydrates that include starches, glycogen, cellulose, and many other important biological materials. (*Mono-* means "single," *oligo-* means "few," and *poly-* means "many"; *saccharide* means "sugar.") There is no clear dividing line between a large oligosaccharide and a small polysaccharide, for these are simply terms of convenience used to separate "classes" within what is really a continuum of compounds of various sizes. All share a general formula of approximately  $C_nH_{2m}O_m$ ; that is, there are twice as many hydrogen as oxygen atoms, and the number of carbon atoms is not always the same as the number of oxygen atoms.

### Monosaccharides

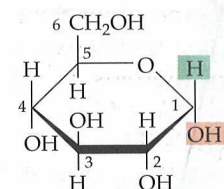
All living cells contain **glucose**,  $C_6H_{12}O_6$ , a monosaccharide. It is produced in green plants by photosynthesis (Chapter 8), and it is also obtained by the digestion of certain polysaccharides. In cells it is metabolized to yield energy in the process of cellular respiration (Chapter 7). Glucose exists in both straight-chain and ring forms, in equilibrium with each other (Figure 3.9). There are two distinct ring forms of glucose ( $\alpha$ - and  $\beta$ -glucose). These differ in the placement of the  $-H$  and  $-OH$  groups attached to a particular carbon atom in the molecule (see the carbon atom identified as carbon 1 in Figure 3.9; the numbering convention shown there will be used throughout this book).  $\alpha$ - and  $\beta$ -glucose are chemically and physically distinct substances, but they constantly interconvert in aqueous solution.

A number of other simple sugars are illustrated in Figure 3.10. Many monosaccharides have the same formula as glucose,  $C_6H_{12}O_6$ , including **fructose** ("fruit sugar"), mannose, and galactose. These compounds are all isomers of each other—they are composed of the same kinds and numbers of atoms, but the atoms are combined differently and yield different arrangements such as those shown in Figure 3.10. The six-carbon sugars are referred to collectively as **hexoses**. There are also a number of five-carbon sugars, called **pentoses**. Some pentoses are found primarily in the cell walls of plants, as are several of the hexoses. Two pentoses are of particular importance:

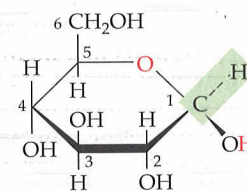
(a) Straight-chain form



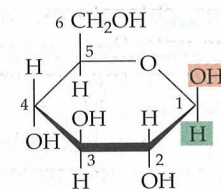
(b) Intermediate form



(d)  $\alpha$ -Glucose



(c) Ring form  
( $\alpha$ -Glucose)



(e)  $\beta$ -Glucose

### 3.9 Forms of Glucose

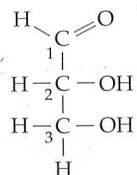
Glucose exists in several interconverting chemical forms when dissolved in water. The straight-chain form (a) has an aldehyde group at carbon 1 (shaded in green). A reaction between the aldehyde group and the hydroxyl group at carbon 5 (b) gives rise to one of the ring forms (c). The ring form is usually represented as in (d), where the darker lines at the bottom imply that that edge of the molecule extends toward you and the upper edge extends back into the page. Depending on the orientation of the aldehyde group at carbon 1 when the ring closes, either of two rapidly and spontaneously interconverting forms of glucose,  $\alpha$ -glucose (d) or  $\beta$ -glucose (e) is formed.  $\alpha$ -Glucose and  $\beta$ -glucose differ only at carbon position 1.

**ribose** and **deoxyribose** (Figure 3.10), which form part of the backbones of RNA and of DNA, respectively. Ribose and deoxyribose differ by one oxygen atom associated with one of the carbon atoms, carbon 2.

### Disaccharides

Larger carbohydrates are made by the combination of two or more monosaccharide molecules. The monosaccharides may be covalently coupled to form specific oligosaccharides and polysaccharides. The smallest oligosaccharides are the disaccharides and the trisaccharides, which are made up of two and three

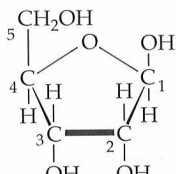


**Three-carbon sugar**

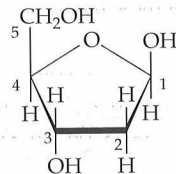
Glyceraldehyde

**3.10 Monosaccharides**

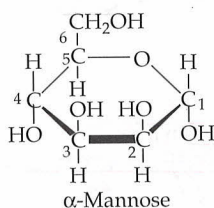
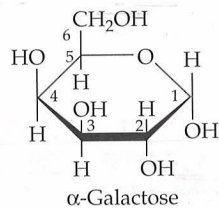
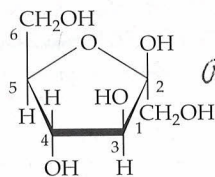
The three-carbon sugar (triose) glyceraldehyde has the formula  $\text{C}_3\text{H}_6\text{O}_3$ ; it is shown in the common straight-chain form. The pentoses, including ribose and deoxyribose, each have five carbons. The three hexoses (six-carbon sugars) shown here all have the formula  $\text{C}_6\text{H}_{12}\text{O}_6$ , but they are chemically and biologically distinct from one another.

**Five-carbon sugars**

Ribose



Deoxyribose

**Six-carbon sugars** $\alpha$ -Mannose $\alpha$ -Galactose

Fructose

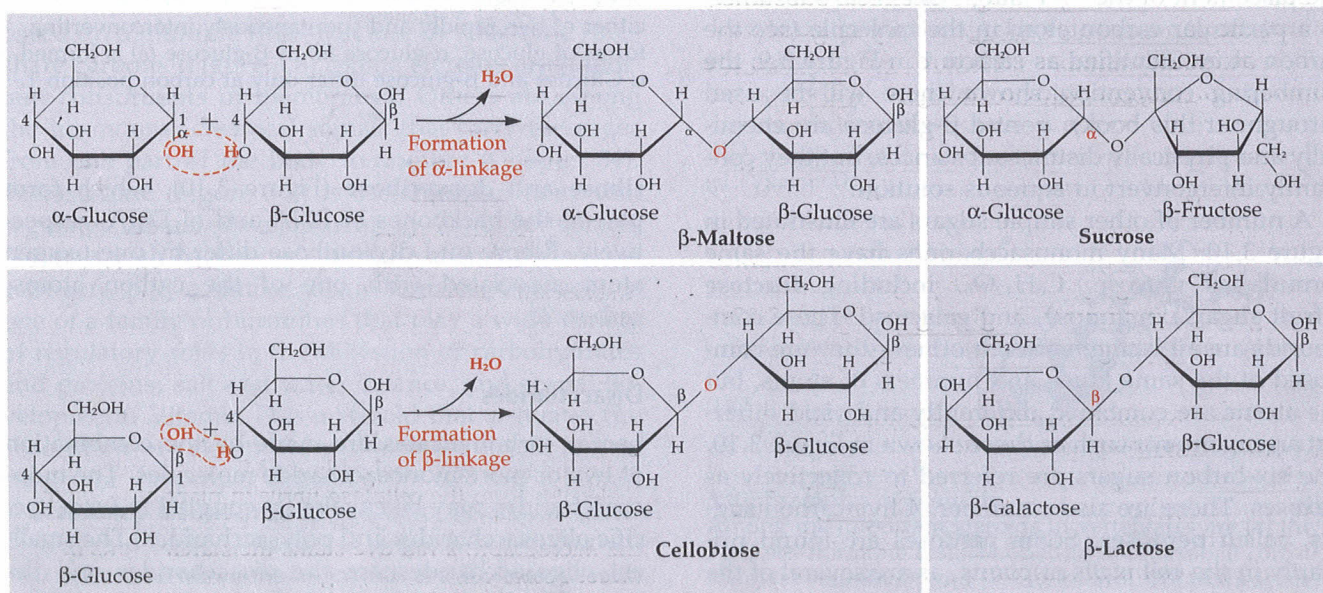
simple sugars, respectively. If one glucose molecule combines with another, as shown in Figure 3.11, the disaccharide product must be one of two types:  $\alpha$ -linked or  $\beta$ -linked, depending on whether it is  $\alpha$ -glucose or  $\beta$ -glucose that reacts. An  $\alpha$  linkage with carbon 4 of a second glucose molecule gives us **maltose**, whereas a  $\beta$  linkage gives **cellobiose**. Both maltose and cellobiose are disaccharides; both have the formula  $\text{C}_{12}\text{H}_{22}\text{O}_{11}$ ; both are composed of two glucose molecules (minus one molecule of water), but they are different compounds—they are recognized by different enzymes and undergo different chemical reactions. Two other commonly occurring disaccharides are **sucrose** and **lactose** (Figure 3.11). Sucrose (common table sugar; also  $\text{C}_{12}\text{H}_{22}\text{O}_{11}$ ) is made from one molecule of glucose and one of fructose. Lactose (milk sugar) consists of glucose and galactose.

**Polysaccharides**

As we saw in Figure 3.11, maltose consists of two glucose units connected by an  $\alpha$ -linkage. Imagine a trisaccharide (three glucose units), a tetrasaccharide

**3.11 Disaccharides**

A disaccharide is composed of two monosaccharides. As shown in the reaction at the top left (a simplified version of the actual reaction in nature), maltose is produced when an  $\alpha$ -1,4 linkage forms between two glucose molecules, while in cellobiose (bottom left) the two glucoses are linked  $\beta$ -1,4. Lactose (bottom right) is made by a  $\beta$  linkage between carbon 1 of galactose and carbon 4 of glucose. In sucrose (top right), carbon 1 of glucose is joined by an  $\alpha$ -1,2 linkage to carbon 2 of fructose.



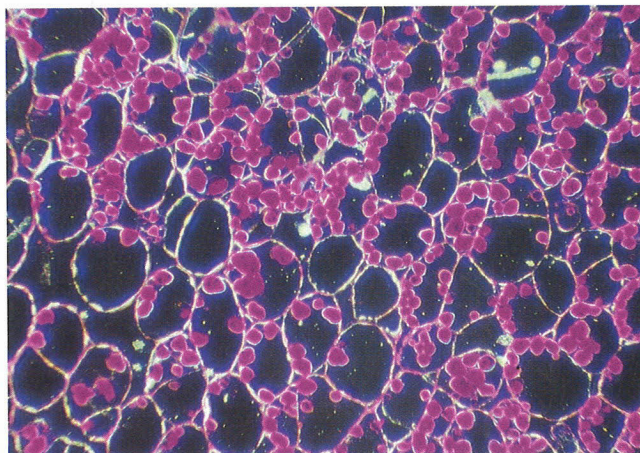
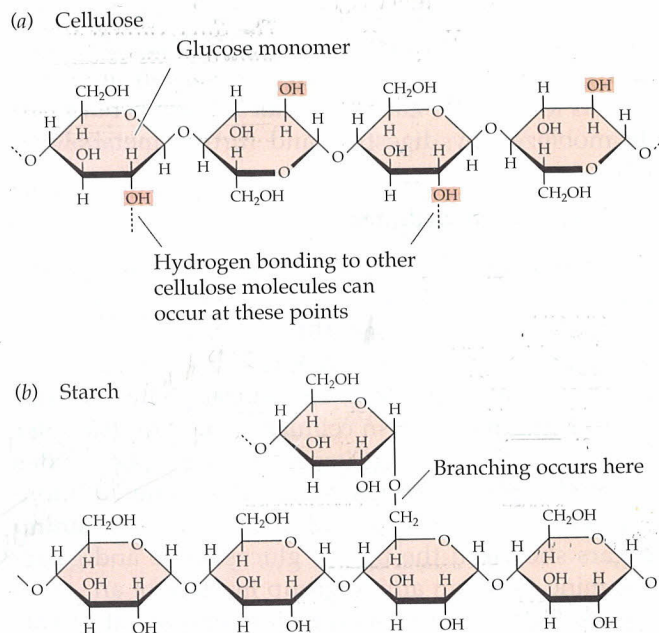
(four glucose units), and finally a giant polysaccharide consisting of hundreds or thousands of glucose units, each connected to the next by an  $\alpha$  linkage from carbon 1 of one unit to carbon 4 of the next. This polymer is **starch**, an important storage compound in the plant kingdom (Figure 3.12*b*).

Similarly, there is a giant polysaccharide made up solely of glucose but with the individual units connected by  $\beta$  linkages. This is **cellulose**, the predominant component of plant cell walls (Figure 3.12*a*). Both starch and cellulose are composed of nothing but glucose (when depolymerized, they yield only glucose), yet their biological functions and chemical and physical properties are entirely different. Enzymes that digest one will not affect the other at all. Aggregated starch forms a shapeless solid that crumbles readily, whereas cellulose is largely crystalline and has an impressive ability to withstand longitudinal pulling without breaking. Starch is primarily a storage compound in plants, holding in reserve energy and carbon that can be made available upon digestion. Cellulose is a key structural element in plant cell walls; for example, it provides much of the strength of wood. Humans have enzymes for the digestion of starch but not for the digestion of cellulose. The enzymes of many bacteria, fungi, and snails readily digest cellulose.

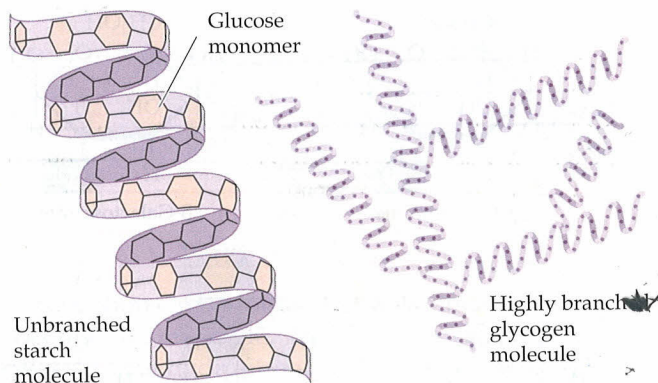
Cotton is more than 90 percent cellulose and is a familiar example of this polysaccharide and its properties. Cellulose is the standard building material for woody stalks, fibers, and all types of cell walls in plants. These rigid structures owe almost all their physical strength to cellulose, which is their toughest component and which usually makes up more than one-fourth of the plant cell wall. Cellulose is by far the most common organic compound on this planet, accounting for more than half the carbon present in plant life.

Starch is not actually a single chemical substance; rather, the term denotes a large family of giant molecules of broadly similar structure. All starches are polymers of glucose with  $\alpha$  linkages. All are large, but some are enormous, containing tens of thousands of glucose units. An important variable is the degree of branching: Many starches have highly branched chains (Figure 3.12*b*). The starches that store glucose in plants are called **amylose** and are not highly branched. The highly branched polysaccharide that stores glucose in animals is **glycogen** (Figure 3.12*c*). Animals use glycogen to store energy in liver and muscle.

What do we mean when we say that starch and glycogen are storage compounds for energy? Very simply, these compounds can readily be depolymerized to yield glucose monomers. Glucose, in turn, can be further digested, or metabolized—that is, it can undergo chemical reactions—to yield energy for cellular work. Alternatively, glucose can be metabo-



(c) Branched and unbranched polysaccharides



### 3.12 Representative Carbohydrates

(a) Cellulose is an unbranched polymer of glucose; hydrogen bonding to other cellulose molecules can occur, as indicated here with dashed lines. Many adjacent cellulose molecules form the cellulose fibrils in plant cells. (b) In starch, branching may occur at the position indicated. In the micrograph, a red dye stains the starch grains in sweet potato cells. (c) Glycogen differs from starch in plants only in being more extensively branched.

lized so that its carbon atoms are rearranged to form the skeletons of other compounds. Thus glycogen and starch are storage depots for carbon atoms as well as for energy. Each is chemically stable but readily mobilized by digestion and further metabolism.

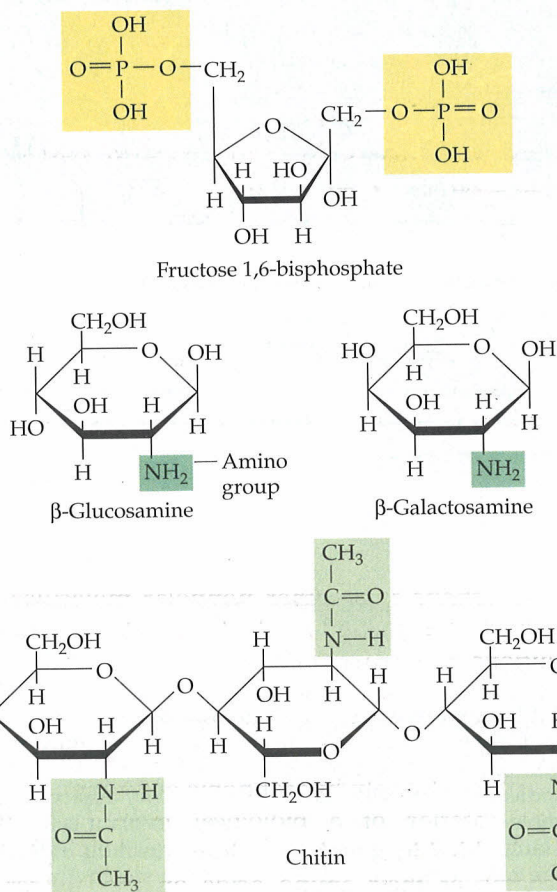
### Derivative Carbohydrates

**Derivative carbohydrates** deviate from the general formula  $C_nH_{2m}O_m$  by containing other elements. Figure 3.13 shows a sugar phosphate, amino sugars, and chitin as examples. A number of **sugar phosphates**, such as fructose 1,6-bisphosphate, are important intermediates in cellular respiration (Chapter 7) and photosynthesis (Chapter 8). Sugar phosphates have phosphate groups attached to one or more —OH groups of the parent sugar. The two **amino sugars** shown in the figure, glucosamine and galactosamine, have an amino group in place of an —OH group. Galactosamine is a major component of cartilage, the material that forms caps on the ends of bones and stiffens the protruding parts of the ears and nose. The polymer chitin is made from a derivative of glucosamine. Chitin is the principal structural polysaccharide in the skeletons of insects and their

relatives such as crabs and lobsters, as well as in the cell walls of fungi. Fungi and insects (and their relatives) constitute more than 80 percent of the species ever described, and chitin is another of the most abundant substances on Earth.

### PROTEINS

In Chapter 2 we considered the **amino acids**. These are the monomers from which a fascinating set of polymers are formed—the **proteins**. The proteins account for many of the mechanical elements of living things, from parts of subcellular membranes to skin, bones, and tendons. In vertebrates, other proteins, the immunoglobulins (including the antibodies), form a major line of defense against foreign organisms. The specialized molecules needed to bring about all biochemical reactions are a major class of proteins called enzymes. Our every movement results from the contraction and relaxation of muscles, resulting in turn from the delicately regulated sliding of particular proteins in muscle cells past one another. Still other proteins act as adjustable channels through which sodium ions ( $Na^+$ ), potassium ions ( $K^+$ ), and other ions are passed from one side of a nerve-cell membrane to the other, resulting in phenomena such as the transmission of electric signals along a nerve. To understand this stunning variety of functions, we must first see and appreciate the structure of these molecules.



### Amino Acids

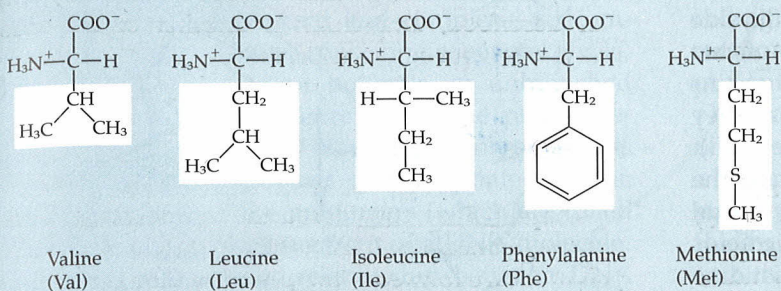
Twenty different amino acids are found in proteins. The **side chains** of amino acids show a wide variety of chemical properties. Side chains control the function of a protein—they are the reactive groups in proteins. Despite their importance, side chains are commonly left out of structural formulas, where they are represented simply by "R" (for "residue"); they are thus sometimes called R groups. Side chains are included, highlighted in color, in the structural formulas in Table 3.1.

### 3.13 Derivative Carbohydrates

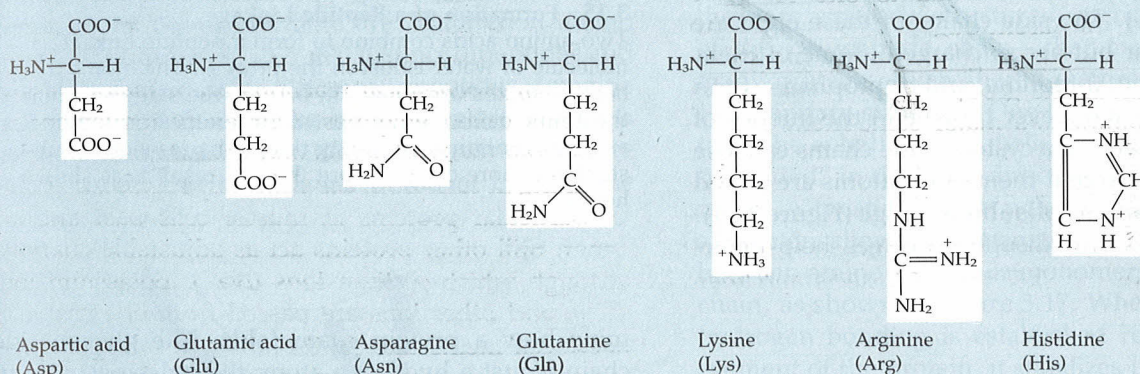
Fructose 1,6-bisphosphate is a sugar phosphate; the numbers in its name refer to the bonding of the phosphate groups (shaded in color) to the number 1 and number 6 carbon atoms of the sugar. The amino groups (—NH<sub>2</sub>) on the amino sugars  $\alpha$ -glucosamine and  $\beta$ -galactosamine are also shown in color; recall that the  $\beta$  refers to the position of the —OH group on the number 1 carbon. Chitin is a polymer of *N*-acetylglucosamine; *N*-acetyl groups are shown in color.

TABLE 3.1  
Twenty amino acids found in proteins

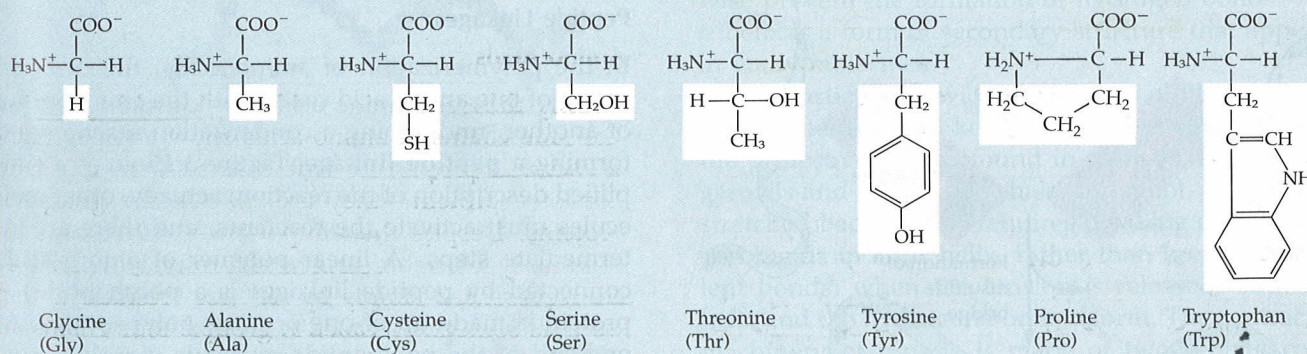
A. Amino acids with hydrophobic R groups



B. Amino acids with hydrophilic groups



C. Amino acids that occur both on the surface and in the interior of proteins



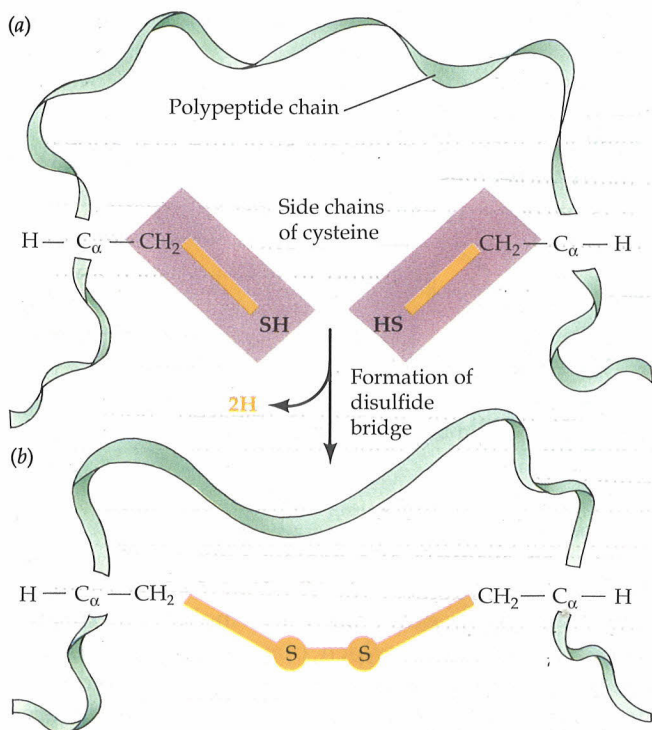
The order of a protein's amino acids determines how it folds into a three-dimensional configuration; we will discuss this folding later. One useful classification of amino acids is based on whether they are usually found on the *inside* of a folded protein molecule, on the protein's *surface*, or in *both* places. The side chains of valine, leucine, isoleucine, phenylalanine, and methionine are all either hydrocarbons or very close relatives thereof, so these side chains are hydrophobic (Table 3.1A). They form hydrophobic

interactions with other nonpolar molecules. In enzymes, for example, which operate in aqueous solutions, the hydrophobic side chains tend to fold into the interior of the molecule. (These side chains are the protein analogues of the hydrocarbon tails of phospholipids; Figure 3.6.) Other proteins function in other strongly hydrophobic environments such as the interior of a biological membrane. Proteins embedded in membranes have the hydrophobic side chains of their amino acids on the *exterior* of the

molecule, where they interact with hydrophobic portions of lipids; they may have hydrophilic side chains on the inside.

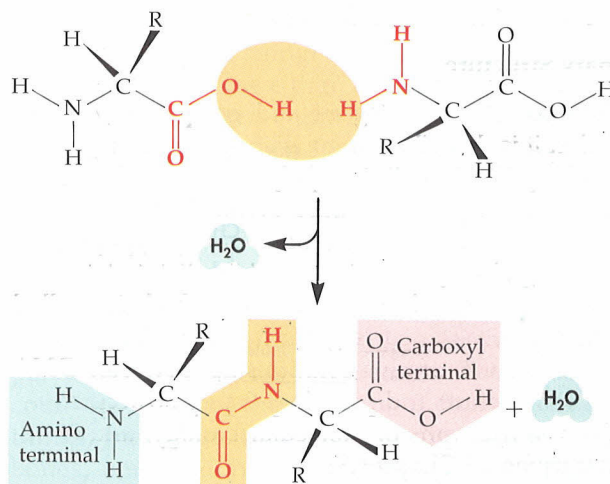
Seven amino acids have strongly hydrophilic side chains, so their behavior is just the opposite of that of the hydrophobic chains. The hydrophilic chains are either electrically charged or so polar that they associate readily with water molecules (Table 3.1B). In aqueous solution they tend to orient toward the outside of the molecule. At the pH typically found in cells (around pH 7), aspartic and glutamic acids have negative charges; lysine, arginine, and histidine have positive charges; and asparagine and glutamine are neutral but polar.

Eight amino acids of a third class can be either on the surface of a molecule or in its interior with equal ease (Table 3.1C). The side chains of these eight are moderately polar but are uncharged. Some of them—serine, tyrosine, threonine, and tryptophan—form hydrogen bonds whenever they lie in the interior of a protein molecule. Two cysteine side chains can lose hydrogen atoms so that their sulfur atoms are joined by a covalent bond in a **disulfide bridge** (Figure 3.14). Hydrogen bonds and disulfide bridges help deter-



### 3.14 Formation of a Disulfide Bridge

The SH groups on two cysteine side chains (a) in a chain of amino acids can react to form a linkage between the two sulfur atoms (b). Such disulfide bridges are important in maintaining the proper three-dimensional shapes of protein molecules.



### 3.15 Formation of a Peptide Linkage

Two amino acids combine to form a peptide linkage; a molecule of water is lost in the process. The atoms that become linked are shown in orange; the side chains on the amino acids are not shown but are designated by R, as is conventional. (In living things the reaction is substantially more complex, but the end result is as shown here.)

mine how a protein chain folds. The glycine side chain is just a hydrogen atom; thus glycines may fit into tight corners in the interior of a protein molecule, where a larger side chain could not fit.

### Peptide Linkages

In the polymerization of amino acids, the carboxyl group of one amino acid reacts with the amino group of another, undergoing a condensation reaction and forming a **peptide linkage**. Figure 3.15 gives a simplified description of the reaction; actually, other molecules must activate the reactants, and there are intermediate steps. A linear polymer of amino acids connected by peptide linkages is a **polypeptide**. A protein is made up of one or more polypeptides. At one end of the polypeptide molecule there is a free amino group, and at the other end a free carboxyl group; the other amino and carboxyl groups are bound in peptide linkages. Thus there is a directionality to a protein; the dipeptide glycine-alanine, in which glycine has the free amino group, differs from alanine-glycine, in which alanine has the free amino group.

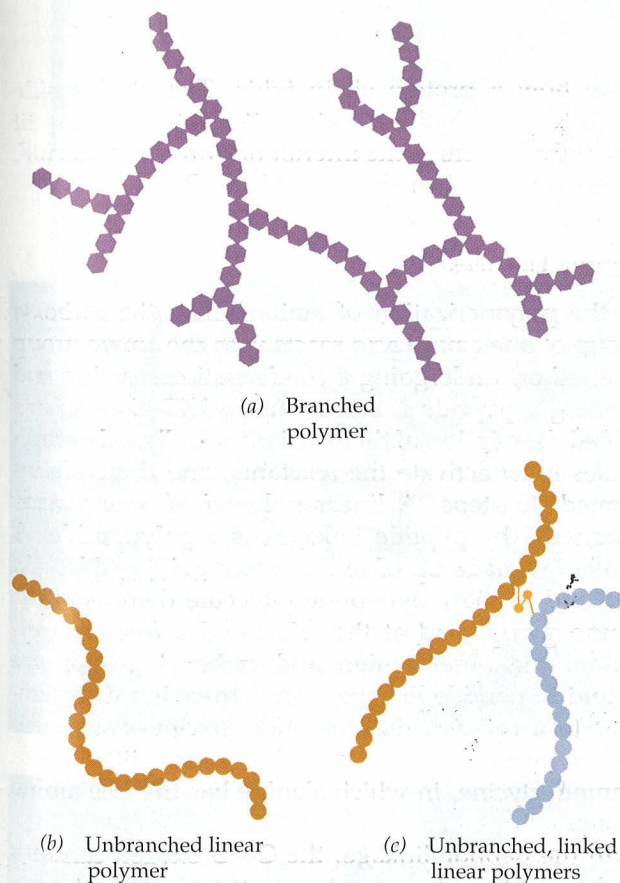
In the peptide linkage, the C=O oxygen carries a slight negative charge, whereas the N-H hydrogen is slightly positive. This asymmetry of charge favors hydrogen bonding (Chapter 2) within the protein molecule itself and with other molecules, contributing to both the structure and the function of many proteins.

## LEVELS OF PROTEIN STRUCTURE

### Primary Structure

Protein structure is elegant and complex—so complex that it is described as consisting of several levels. A polypeptide is a linear polymer, or unbranched chain of amino acids (Figure 3.16). The precise sequence of these building blocks in a polypeptide is called its **primary structure** and is dictated by the precise sequence of the monomers (which are called nucleotides) in a linear segment of a DNA molecule. The elucidation of this relationship between DNA primary structure and protein primary structure was one of the triumphs of molecular biology, and it will be described in Chapter 11.

The theoretical number of possible different proteins is enormous. As there are 20 different amino acids, there are  $20 \times 20 = 400$  distinct dipeptides and  $20 \times 20 \times 20 = 8000$  different tripeptides. Imagine this process of multiplying by 20 extended to even a small protein made up of 100 monomers—there could be  $20^{100}$  of these small proteins. Each of the



### 3.16 Branched versus Linear Polymers

(a) Some biological polymers, such as the carbohydrate glycogen (Figure 3.12c) are highly branched, as depicted in the generalized molecule here. Proteins, however, are unbranched (b), although the chains of amino acids may be linked together, as shown in (c).

different possible proteins has its own distinctive primary structure.

The higher levels of protein structure—from local coiling and folding to the overall shape of the entire molecule—all derive from the primary structure. By presenting side chains of differing character (hydrophilic or hydrophobic, for example) in a specific and unique order, the precise sequence of amino acids in a given protein determines the ways in which the polypeptide chain can twist and fold. By twisting and folding, each specific protein adopts a specific structure that distinguishes it from every other protein.

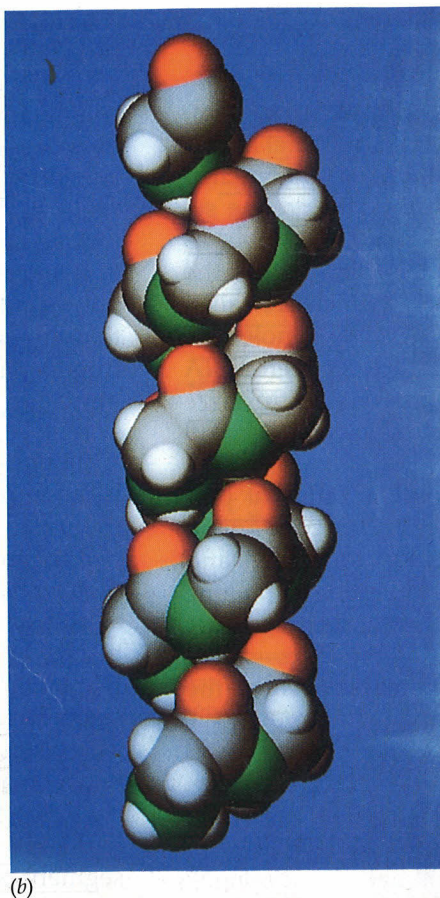
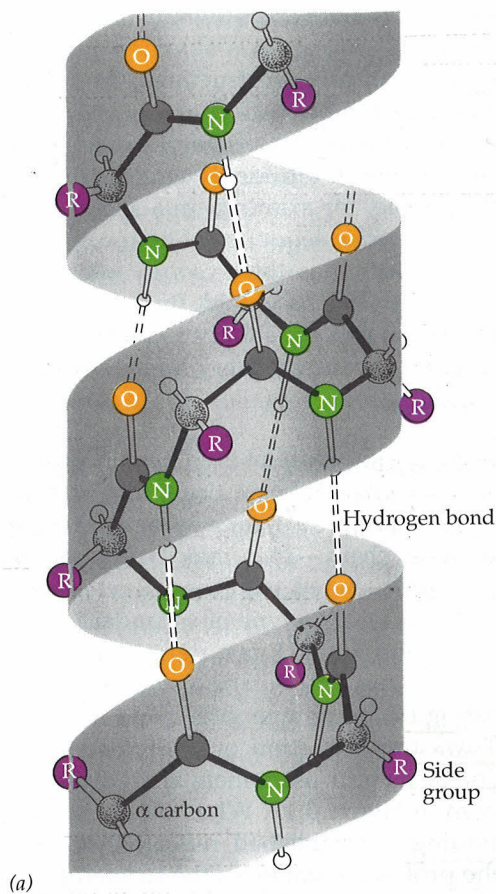
### Secondary Structure

Although the overall structure of each kind of protein is absolutely distinctive, above the primary level there are aspects of structure—such as regular coiling of the polypeptide chain—that may be shared by many proteins. Such shared features are referred to as **secondary structure**. One type of secondary structure, the  $\alpha$  helix (alpha helix), is a right-handed coil “threaded” in the same direction as a standard wood screw. A twisting of the polypeptide chain about its axis often allows the formation of hydrogen bonds between amino acids four monomers apart along the chain, as shown in Figure 3.17. When this pattern of hydrogen bonding is established repeatedly over a segment of the protein, it stabilizes the twisted form, resulting in an  $\alpha$  helix. The ability to form an  $\alpha$  helix depends upon the primary structure: Certain amino acids have side chains that distort the coil or otherwise prevent the formation of hydrogen bonds. The  $\alpha$  helix is a form of secondary structure that appears in many molecules.

It is particularly evident in a class of fibrous structural proteins called keratins. These include most of the protective tissues found in animals, such as fingernails and claws, skin, hair, and wool. Hair can be stretched because this requires breaking only hydrogen bonds in an  $\alpha$  helix, rather than breaking covalent bonds; when the tension is released, both the helix and the hydrogen bonds reform. The contractile machinery of muscle is made of two protein components, actin and myosin (Chapter 38), with the myosin arranged in an  $\alpha$ -helical secondary structure.

Silk is an example of a protein with another type of secondary structure, the  **$\beta$ -pleated sheet** (Figure 3.18). Here the protein chains are almost completely extended and are bound into sheets by hydrogen bonds connecting one chain to another. In many proteins, regions of  $\beta$ -pleated sheet are formed by bonding between different parts of the same polypeptide chain.

A third type of secondary structure, the triple helix, is found in collagen (Figure 3.19). This important protein, found in cartilage, tendons, the underlayers of the skin, and the cornea of the eye, consists of



### 3.17 The $\alpha$ Helix

The  $\alpha$  helix is an important form of secondary structure in many proteins. (a) A ball-and-stick drawing of an  $\alpha$  helix. The right-handed coil of the helix can be seen by following the black bonds in the backbone of the polypeptide. The atoms in the relatively rigid plane of the peptide linkages between amino acid residues are in color, and the hydrogen bonds that stabilize the helix are drawn as dashed lines. (b) The actual positions of the atoms in relationship to one another are realistically rendered in this computer drawing of the  $\alpha$  helix. Side chains of the amino acids have been omitted. Carbons are shown in gray, oxygens in red, hydrogens in white, and nitrogens in green. (See Figure 3.20c for the appearance of several lengths of an  $\alpha$  helix in a complete protein molecule.)

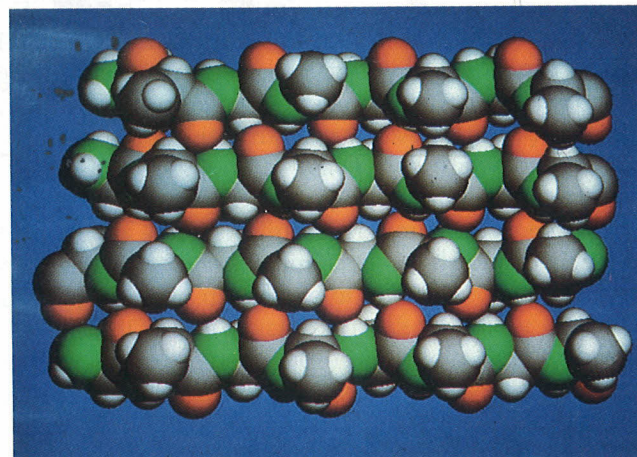
three polypeptide chains twisted around one another like the strands of a cable. Hydrogen bonds connect the chains, resulting in a structure that is strong, rigid, and unstretchable. The tail of a rat, under the skin, is almost pure collagen.

### Tertiary Structure

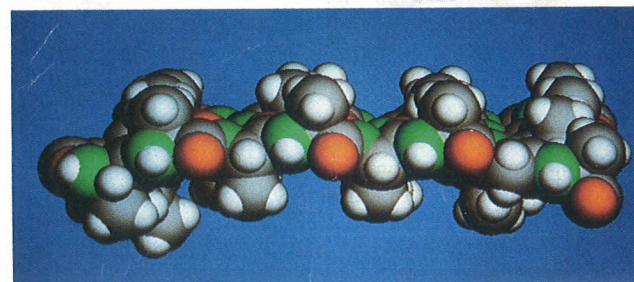
The  $\alpha$  helices and  $\beta$ -pleated sheets sometimes predominate throughout the bulk of a protein molecule, as in the examples cited above. More frequently, however, these secondary structures are found in only limited portions of the molecule and thus do not dominate its overall shape, or **tertiary structure**. A complete description of the tertiary structure specifies the location of every atom in the molecule in

### 3.18 The $\beta$ -Pleated Sheet

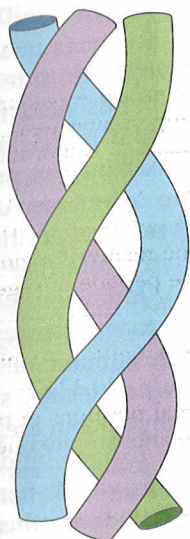
(a) This computer drawing shows a localized  $\beta$ -pleated sheet area of a protein. We see four parallel strands of the polypeptide running horizontally in the figure. These strands are joined by hydrogen bonds, forming a sheet. Atoms are colored by the conventions of Figure 3.17. (b) The same material shown in (a), but viewed from the bottom edge to emphasize the "pleats" in the sheet.



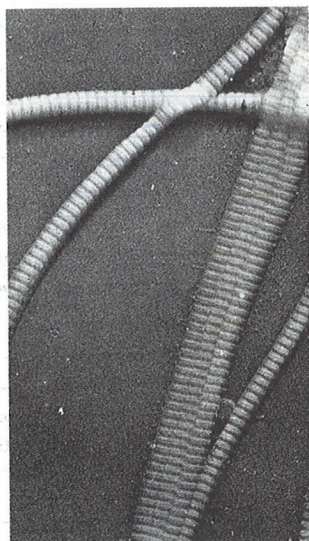
(a)



(b)



(a) Secondary structure of collagen

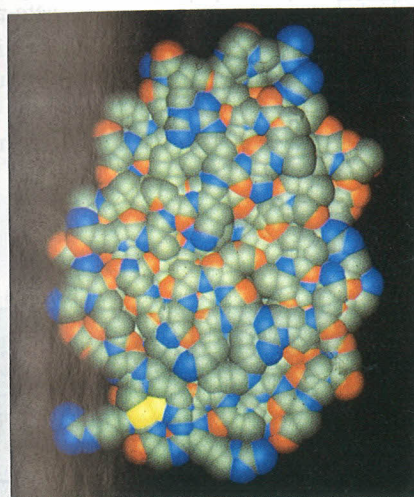


(b) Collagen fibril

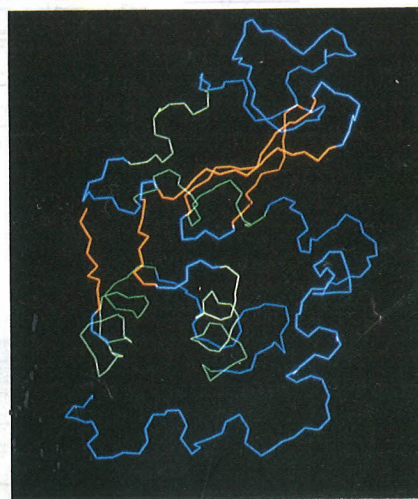
### 3.19 Collagen

(a) The secondary structure of the protein collagen consists of a triple helix of polypeptide chains in this pattern. Such a triple helix is called tropocollagen. (b) A number of triple helices of tropocollagen join in parallel fashion to create a strong, flexible collagen fibril; several collagen fibrils are shown here, magnified about 20,000 times. The spacing between black bands corresponds to the length of a single tropocollagen molecule.

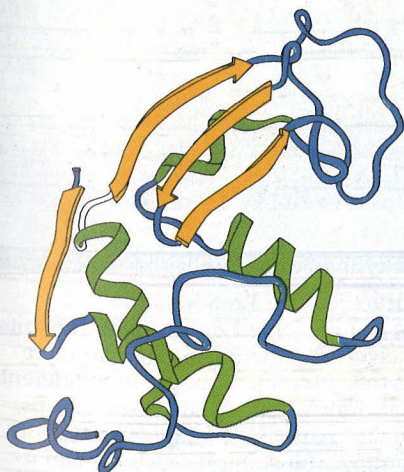
three-dimensional space, in relation to all the other atoms. The tertiary structure of the protein lysozyme is shown in various representations in Figure 3.20. Bear in mind that this tertiary structure and the secondary structure emphasized in Figure 3.20c derive entirely from the protein's primary structure. If lysozyme is heated carefully, causing the tertiary structure to break down, the protein will return to its normal tertiary structure when it is cooled. The only



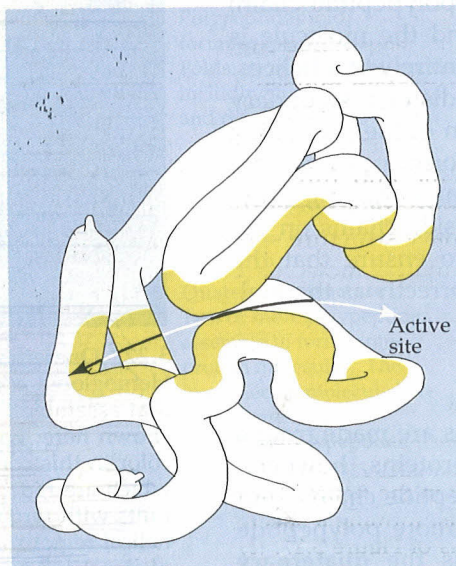
(a)



(b)



(c)

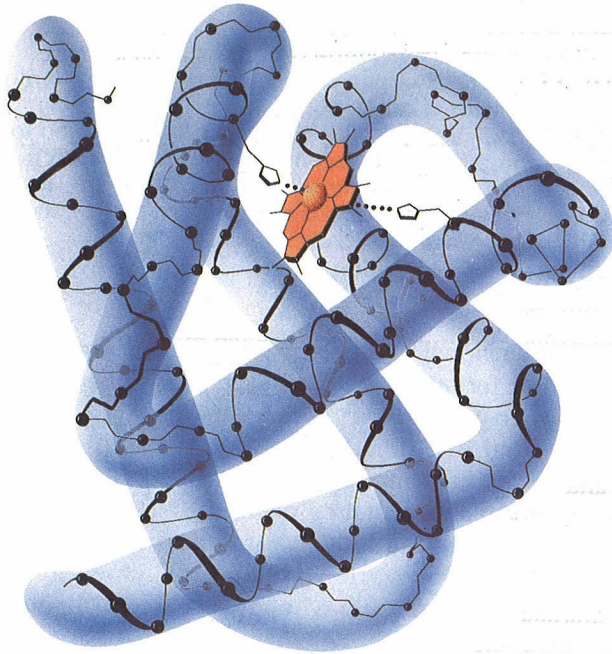


(d)

### 3.20 Four Representations of Lysozyme

The tertiary structure of the enzyme lysozyme is shown in four different representations that emphasize different aspects of the structure. All are similarly oriented, although (c) and (d) are slightly rotated relative to the others. (a) This computer-generated, space-filling representation gives the most realistic impression of lysozyme's tertiary structure, which is densely packed. (b) This computer-drawn representation emphasizes the backbone of the folded polypeptide. Regions in green have  $\alpha$ -helical secondary structure; those in red constitute a  $\beta$ -pleated sheet. (c) The ribbon representation also emphasizes the secondary structure of certain parts of the molecule; the coiled regions are  $\alpha$ -helices and the  $\beta$ -pleated sheet is indicated by the arrows. (d) The "sausage" representation gives a crude picture of the folding of the polypeptide chain. Note the position (shown in yellow) of the active site—the part of the enzyme molecule that binds reactant molecules. From its position in (d), you can infer the position of the active site in the other three representations.





### 3.21 Tertiary Structure of a Protein

Tertiary structure—the exact three-dimensional folding of a protein molecule—is illustrated for the protein myoglobin. The individual atoms are not shown, nor are the individual amino acids, which form the coiled polypeptide chain. The chain is  $\alpha$  helical throughout most of its length. The purple shading shows the overall tertiary configuration of the molecule. The red structure in the upper part of the drawing is an iron-containing heme group.

information needed to specify the unique shape of the lysozyme molecule is the information contained in its primary structure.

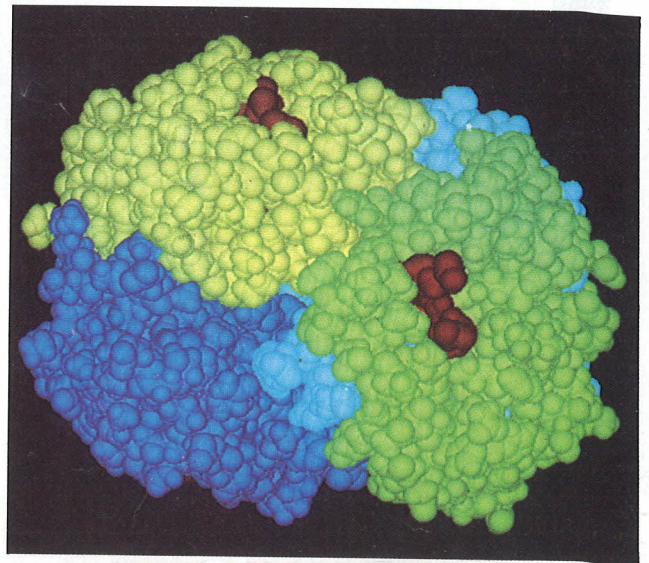
Myoglobin is an important protein (Figure 3.21). Its function—to store oxygen in certain animal tissues—will be discussed in Chapter 39. Myoglobin has 153 amino acids in its single polypeptide chain; there are no disulfide bridges, and the molecule is unusual in that it consists almost entirely of  $\alpha$  helices. (Most proteins do not show a distinct secondary structure over such a large fraction of the molecule.) The eight helices in myoglobin form a pocket that encloses a **heme group**: an iron-containing ring structure that binds  $O_2$ . Hydrophobic side chains on the inner sides of the helices help to ensure that the helices fold against one another correctly as the molecule is formed.

### Quaternary Structure

Myoglobin and most other proteins are made from a single polypeptide chain. Some proteins, however, are made from two or more polypeptide chains, and the configuration of those two or more polypeptide chains in the protein molecule is the **quaternary structure** of the protein. Hemoglobin, a protein that

brings oxygen from the lungs to the tissues and delivers it to myoglobin for storage, illustrates quaternary structure (Figure 3.22). Hydrophobic interactions, hydrogen bonds, and ionic bonds hold four polypeptide chains together to make a hemoglobin molecule. There are two each of two kinds of polypeptides. As the molecule takes up or releases oxygen, its four subunits shift their relative positions slightly, changing the quaternary structure (the relative arrangement of the subunits). Ionic bonds are broken, exposing buried side chains that enhance the binding of molecular oxygen. Each subunit of hemoglobin is folded like a myoglobin molecule, suggesting that both hemoglobin and myoglobin are evolutionary descendants of the same oxygen-binding ancestral protein. But on the surfaces where hemoglobin's subunits come in contact with each other—regions that on myoglobin are exposed to aqueous surroundings—hemoglobin has hydrophobic side chains where myoglobin has hydrophilic ones. Again, the chemical nature of side chains on individual amino acids, as specified by DNA, determines how the molecule folds and packs in three dimensions. Proteins having more than one polypeptide chain function only after they form appropriate quaternary structures.

The four levels of protein structure are summarized in Figure 3.23.



### 3.22 Quaternary Structure of a Protein

Hemoglobin consists of four folded polypeptide subunits that assemble themselves into the quaternary structure shown here. Each of the subunits is shown in a different color in this computer drawing. Note the heme groups, which are red. The quaternary assemblage includes subunits with tertiary folding, the subunits each contain  $\alpha$ -helical regions of secondary structure, and all these levels of structural organization are ultimately dependent on the primary sequence of amino acids in the polypeptides.

## NUCLEIC ACIDS

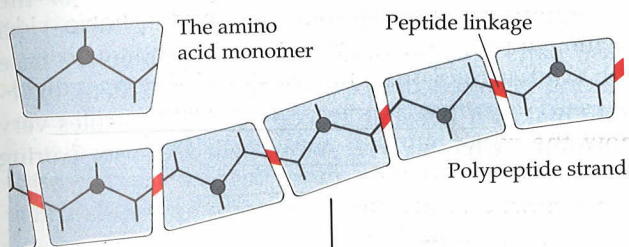
The proteins of today exist because of the structures and activities of various **nucleic acids**. One group of these, the **DNAs**, or **deoxyribonucleic acids**, are giant polymers that carry the instructions for making proteins; another, the **RNAs**, or **ribonucleic acids**, interpret and carry out the instructions coded in the DNAs.

Nucleic acids form from monomers called **nucleotides**, each of which consists of a simple pentose

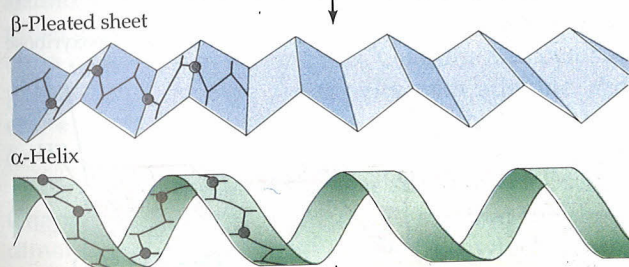
sugar, a phosphate group, and another portion called a nitrogenous (nitrogen-containing) base (Figure 3.24). Molecules consisting of a pentose sugar and a nitrogenous base, but no phosphate group, are called **nucleosides**. In DNA, the sugar is deoxyribose, which differs from the ribose found in RNA by one oxygen atom (Figure 3.10). As shown in Figure 3.25, the "backbones" of both polymers consist of alternating sugars and phosphates; the bases, which are attached to the sugars, project from the chain. Most RNA molecules are single stranded: Each molecule consists

### 3.23 Four Levels of Protein Structure

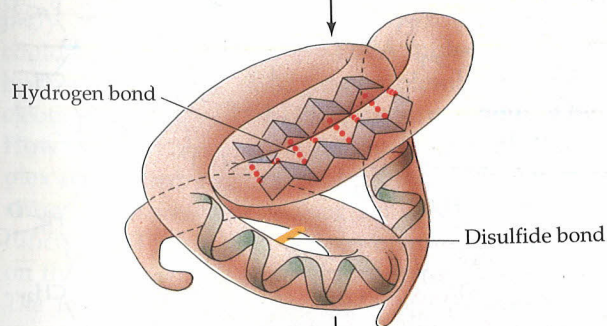
The four levels of protein structure—primary, secondary, tertiary, and quaternary—are summarized here. Secondary, tertiary, and quaternary structure all arise from the primary structure of the protein.



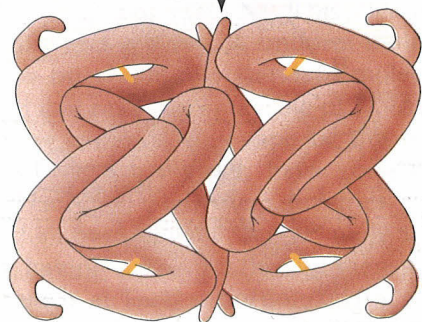
**Primary structure**  
Amino acid monomers are joined by peptide linkages, forming **polypeptide strands**.



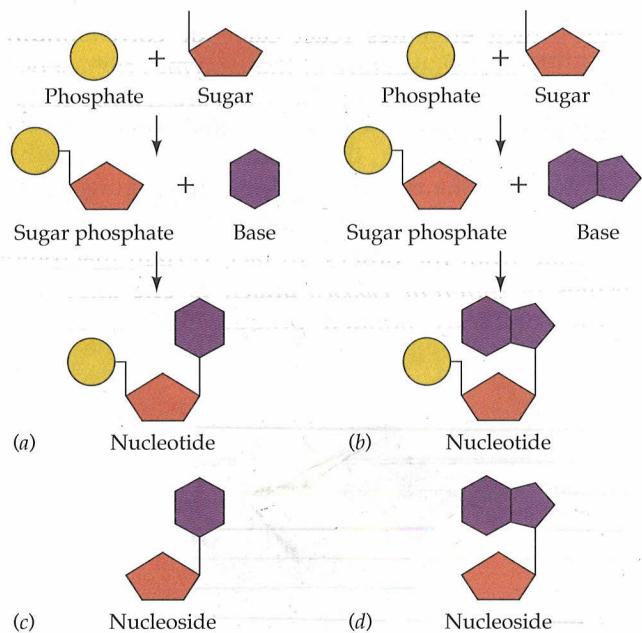
**Secondary structure**  
Polypeptide strands may form  $\beta$ -pleated sheets or  $\alpha$  helices.



**Tertiary structure**  
Polypeptides fold, forming specific shapes. Folds are stabilized by bonds, including hydrogen and disulfide bonds



**Quaternary structure**  
Two or more polypeptides assemble to form larger protein molecules. The hypothetical molecule here is a tetramer, made up of four polypeptides.

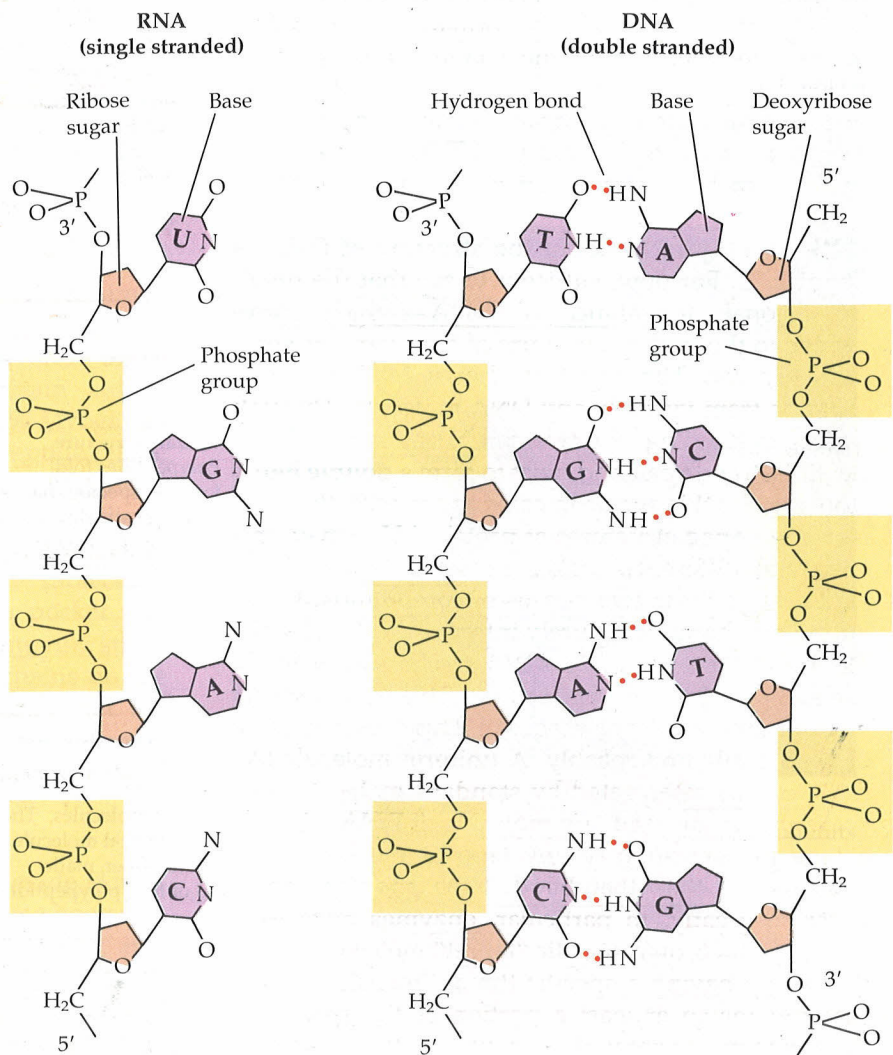


### 3.24 Components of a Nucleotide

A sugar and a phosphate form a sugar phosphate (either ribose phosphate or deoxyribose phosphate). In nucleotide synthesis, a nitrogen-containing base is then built on the sugar phosphate in several steps not depicted here, forming the complete nucleotide monomer. The four bases fall into two categories, as indicated here by their shapes in (a) and (b). A nucleoside consists of a sugar (*not* a sugar phosphate) and a base (c and d).

### 3.25 RNA versus DNA

A ribonucleic acid (RNA) is made up of a ribose sugar-phosphate backbone with a nitrogenous base attached to each sugar, as shown on the left. On the right is a portion of a double-stranded deoxyribonucleic acid (DNA); it consists of two deoxyribose sugar-phosphate backbones, with the bases attached to the sugars between the strands. The molecule is held together by hydrogen bonds between opposite bases on the two strands. For the bases, A = adenine, T = thymine, G = guanine, C = cytosine, and U = uracil. Note that RNA contains U where DNA contains T.



of one polynucleotide chain. DNA, however, is usually double stranded, with two polynucleotide chains being held together by hydrogen bonding between their nitrogenous bases.

Only four nitrogenous bases—and thus only four nucleotides—are found in DNA. The DNA bases are adenine, cytosine, guanine, and thymine. A key to understanding the structures and functions of nucleic acids is the principle of **complementary base pairing**: Particular bases only pair with certain other bases. In DNA, wherever one strand carries an adenine, the other must carry thymine at the corresponding point. Wherever one chain has a cytosine, the other has guanine. The base pairing rules for DNA and RNA are shown in Table 3.2. The pairing scheme maximizes hydrogen bonding between the two strands of DNA. Because one of the larger **purine** bases (adenine or guanine) always pairs with one of the smaller **pyrimidine** bases (thymine or cytosine), all base pairs are the same size. Complementary base pairing between the two strands of the DNA molecule makes it possible to copy DNA molecules very faithfully (Chapter 11). As we will see, base pairing

TABLE 3.2  
Base Pairing Rules for the Nucleic Acids

IN DNA:	WHEN RNA AND DNA INTERACT:		WHEN RNA PAIRS WITH RNA:
	RNA	DNA	
A pairs with T	A pairs with T	A pairs with U	
T pairs with A	U pairs with A	U pairs with A	
G pairs with C	G pairs with C	G pairs with C	
C pairs with G	C pairs with G	C pairs with G	

is also important in understanding RNA functions, and it contributes in part to the structures of certain RNA molecules.

Ribonucleic acids are also composed of four different nucleotides, but the nucleotides differ from those of DNA. The **ribonucleotides** contain ribose rather than deoxyribose, and one of their four bases is different from that in DNA. The four principal bases in RNA are adenine, cytosine, guanine, and uracil (instead of thymine). Although RNA is generally single stranded, complementary associations between nucleotides are important in the formation of new RNA strands, in determining the shapes of some RNA molecules, and in associations between RNA molecules during protein synthesis. Guanine and cytosine pair as in DNA, and uracil pairs with adenine. Adenine in an RNA strand can pair with either uracil (in an RNA strand) or thymine (in a DNA strand).

We will say more about the structure of DNA in Chapter 11. For now, suffice it to say that the three-dimensional appearance of DNA—which corresponds to the tertiary structure of a protein—is strikingly regular. The segment shown in Figure 3.26 could be from virtually any DNA molecule. Through hydrogen bonding, the two complementary polynucleotide strands pair and twist to form a **double helix**. How regular this seems in comparison with the complex and varied structures of proteins! However, this structural difference makes sense in terms of the functions of these two classes of compounds. DNA, on the one hand, is a purely informational molecule. *The information carried by DNA resides simply in the sequence of bases carried in its chains.* This is, in a sense, like the tape of a tape recorder. This message must be read easily and reliably. A uniform molecule like DNA can be interpreted by standard molecular machinery that can read any molecule of DNA—just as a tape player can play any tape of the right size. Proteins, on the other hand, have good reason to differ so greatly. In particular, enzymes must each recognize their own specific “target” molecules. They do this by having a specific three-dimensional form that can match at least a portion of the surface of their targets. Structural diversity in the molecules

with which enzymes react calls for corresponding diversity in the structure of the enzymes themselves. DNAs are similar and uniform and are read by simple machinery; proteins are diverse and interact with a diversity of other compounds.

Throughout this chapter we have treated the classes of macromolecules as if each were completely separate from the others. In fact, certain macromolecules of different classes attach to one another to form covalently bonded products. Many proteins



### 3.26 The Double Helix of DNA

The backbones of the two strands in a DNA molecule are coiled in a double helix. The double helix is demonstrated with a computer drawing showing the atoms in a length of 20 base pairs. Allow your eye to follow the yellow phosphorus atoms and their attached red oxygen atoms in the two helical backbones. The paired bases are stacked in the center of the coil and should become apparent if you concentrate on the light blue nitrogen atoms and the dark blue carbon atoms. The smaller white atoms are hydrogens.

have attached carbohydrates that play roles in the functioning of the whole molecule, and other proteins have attached lipids.

## SUMMARY

Many important biological molecules are polymers: They are built from monomers. The monomers combine (polymerize) by undergoing condensations.

The characteristic structures of the lipids differ from the other molecular structures discussed in this chapter. Lipid molecules do not form true polymers. However, all lipid molecules have large hydrophobic regions. As a result, lipids present in any aqueous system tend to aggregate—like oil in water. Triglycerides may accumulate in animal cells, forming enormous fat droplets that may later function as fuel.

The phospholipids tend to aggregate to form a continuous bilayer, with their hydrophilic regions exposed to the surrounding aqueous environment. This arrangement accounts for the formation of cellular membranes. Other lipid molecules, such as cholesterol or the carotenoids, may be inserted into the phospholipid bilayer of the membrane, as may protein molecules with hydrophobic surfaces.

The monosaccharides have two principal functions: They serve as fuel, and as building blocks for polysaccharides—large polymers formed by conden-

sation reactions. The functions of polysaccharides are varied. Starch and glycogen are storage compounds in plants and animals, respectively. The individual molecules of cellulose join other cellulose molecules to form tight crystalline structures, binding the chains into a supramolecular aggregate with great tensile strength. Cellulose is the principal component of the plant cell wall.

Proteins and nucleic acids also form by condensation reactions. Protein molecules have particular tertiary structures as a result of the differing structures and properties of the side chains of the 20 amino acids that are their monomers. The three-dimensional conformation (tertiary structure) of a protein arises spontaneously, on the basis of its specific primary structure (its amino acid sequence). The differences in tertiary structure are the basis for the great specificity of such proteins as the enzymes and immunoglobulins. Local regularities such as  $\alpha$  helices and  $\beta$ -pleated sheets are forms of secondary structure. Proteins consisting of more than one polypeptide chain have specific spatial arrangements of these subunits, called quaternary structure.

In contrast to the proteins, the even larger DNA molecules are composed of only four different monomers joined by complementary base pairing. DNA molecules have a very uniform structure, but an enormous information content is based on the sequence of monomers within the polymer.

## SELF-QUIZ

- All lipids:
  - are triglycerides.
  - are polar.
  - are hydrophilic.
  - are polymers.
  - are more soluble in nonpolar solvents than in water.
- Which of the following is *not* a lipid?
  - A steroid
  - A fat
  - A triglyceride
  - A biological membrane
  - A carotenoid
- All carbohydrates:
  - are polymers.
  - are simple sugars.
  - consist of one or more simple sugars.
  - are found in biological membranes.
  - are more soluble in nonpolar solvents than in water.
- Which of the following is *not* a carbohydrate?
  - Glucose
  - Starch
  - Cellulose
  - Hemoglobin
  - Deoxyribose
- All proteins:
  - are enzymes.
  - consist of one or more polypeptides.
  - are amino acids.
  - have quaternary structures.
  - have prosthetic groups.
- Which statement is *not* true of the primary structure of a protein?
  - It may be branched.
  - It is determined by the structure of the corresponding DNA.
  - It is unique to that protein.
  - It determines the tertiary structure of the protein.
  - It is the sequence of amino acids in the protein.
- The amino acid leucine (Table 3.1):
  - is found in all proteins.
  - cannot form peptide linkages.
  - is likely to appear in that part of a membrane protein that lies within the phospholipid bilayer.
  - is likely to appear in that part of a membrane protein that lies outside the phospholipid bilayer.
  - is identical to the amino acid lysine.
- The quaternary structure of a protein:
  - consists of four subunits—hence the name *quaternary*.
  - is unrelated to the function of the protein.
  - may be  $\alpha$ ,  $\beta$ , or  $\gamma$ .
  - depends on covalent bonding among the subunits.
  - depends on the primary structures of the subunits.

9. All nucleic acids:

- are polymers of nucleotides.
- are polymers of amino acids.
- are double-stranded.
- are double-helical in structure.
- contain deoxyribose.

10. Which statement is *not* true of condensation reactions?

- Protein synthesis results from condensation reactions.
- Polysaccharide synthesis results from condensation reactions.

c. Nucleic acid synthesis results from condensation reactions.

- Condensation reactions consume water as a reactant.
- Different condensation reactions produce the different kinds of macromolecules.

## FOR STUDY

- Phospholipids make up a major part of every biological membrane; cellulose is the major constituent of the cell walls of plants. How do the chemical structures and physical properties of phospholipids and cellulose relate to their functions in cells?
- Suppose that, in a given protein, one lysine is replaced by aspartic acid (Table 3.1). Is this a change in

primary or secondary structure? How might it result in a change in tertiary structure? In quaternary structure?

- If there are 20 different amino acids commonly found in proteins, how many different dipeptides are there? How many different tripeptides? How many different polypeptides composed of 200 amino acid subunits? If there are four dif-

ferent nitrogenous bases commonly found in RNA, how many different dinucleotides are there? How many different trinucleotides? How many different single-stranded RNAs composed of 200 nucleotides?

- Contrast the structures of hemoglobin, a DNA molecule, and a protein that spans a biological membrane.

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