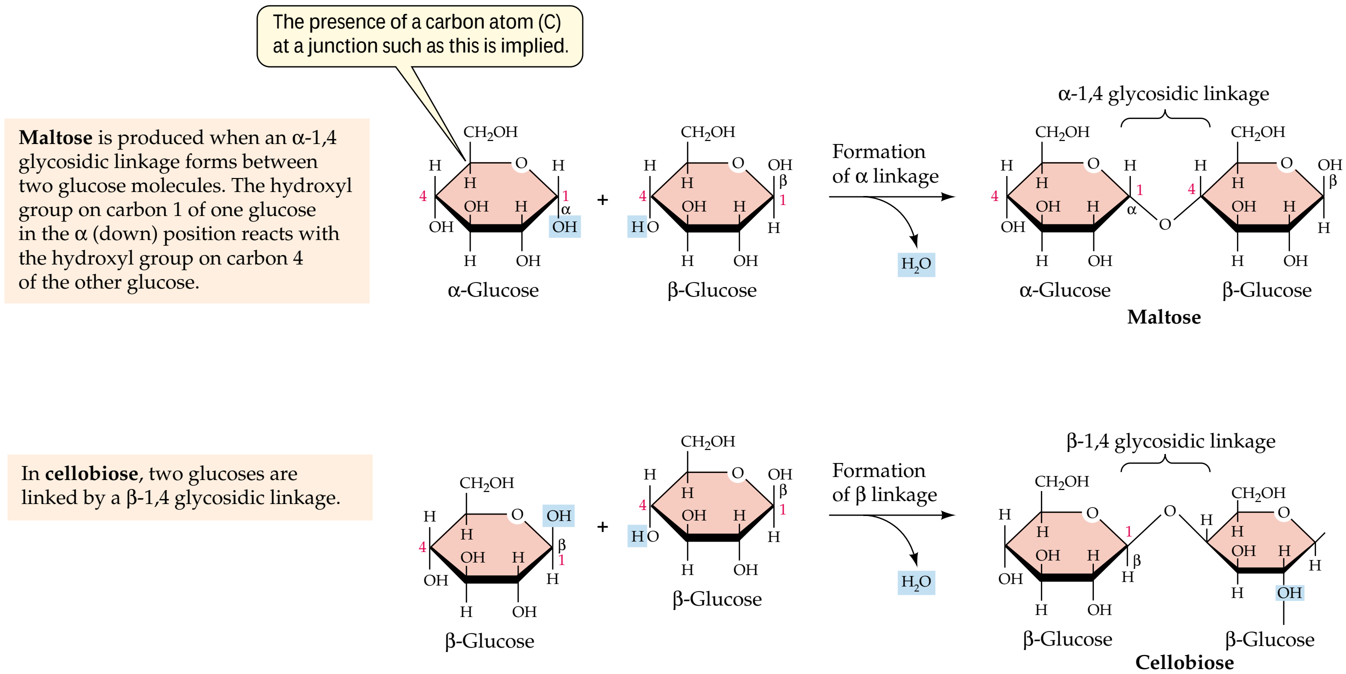


3.15 Disaccharides Are Formed by Glycosidic Linkages
Glycosidic linkages between two monosaccharides create many different disaccharides. Which disaccharide is formed depends on which monosaccharides are linked, and on the site (which carbon atom is linked) and form (α or β) of the linkage.

Polysaccharides serve as energy stores or structural materials

Polysaccharides are giant polymers of monosaccharides connected by glycosidic linkages (Figure 3.16).

- **Starch** is a polysaccharide of glucose with α-glycosidic linkages.
- **Glycogen** is a highly branched polysaccharide of glucose.
- **Cellulose** is also a polysaccharide of glucose, but its individual monosaccharides are connected by β-glycosidic linkages.

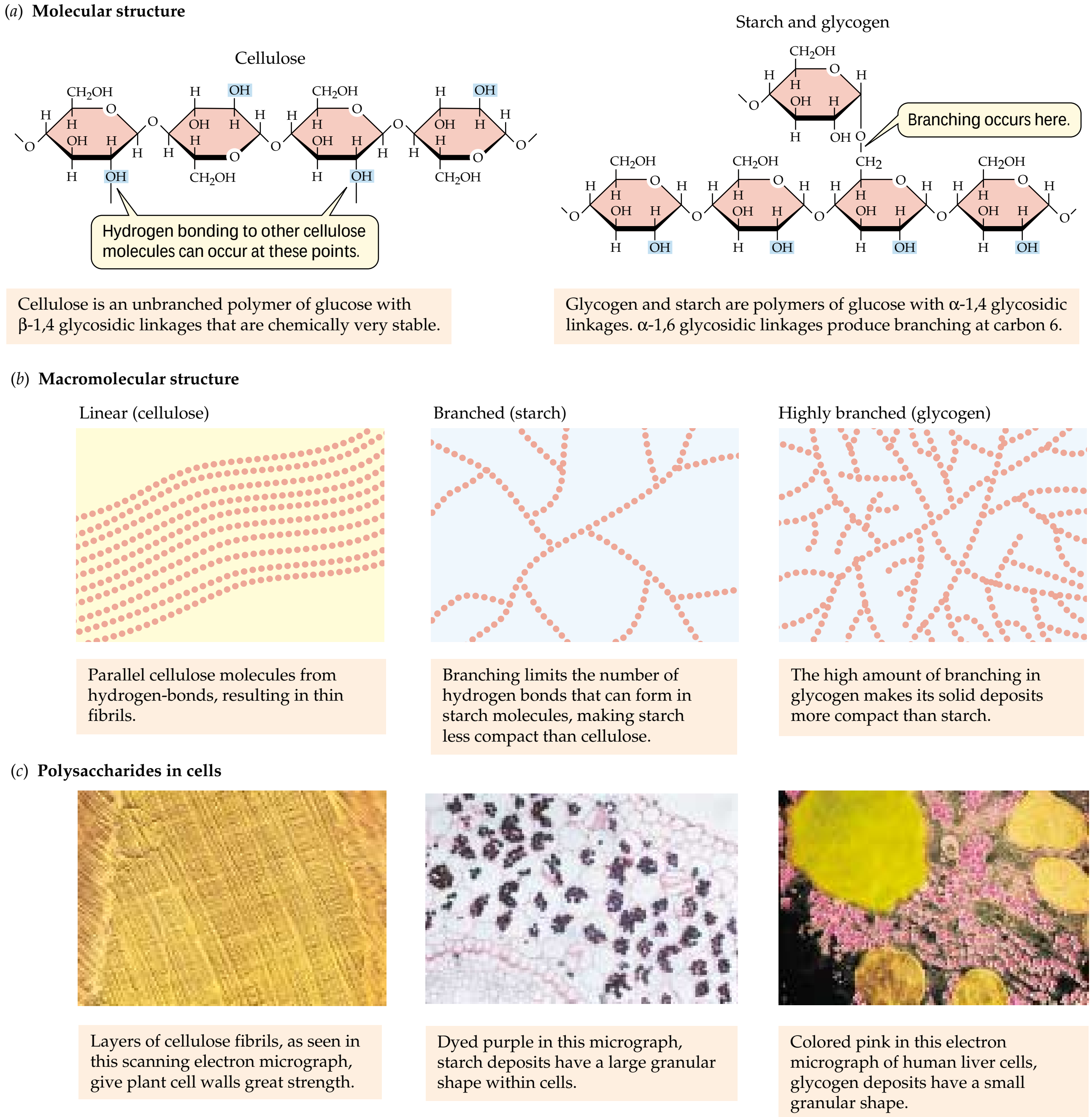
Starch actually comprises a large family of giant molecules of broadly similar structure. While all starches are large polymers of glucose with α linkages (Figure 3.16*a*), the different starches can be distinguished by the amount of branching that occurs at carbons 1 and 6 (Figure 3.16*b*). Some plant starches are unbranched, as in plant amylose; others are moderately branched, as in plant amylopectin. Starch readily binds water, and when that water is removed, unbranched starch tends to form hydrogen bonds between the polysaccharide chains, which then aggregate. This is what causes bread to become hard and stale. Adding water and gentle heat separates the chains and the bread becomes softer.

The polysaccharide glycogen stores glucose in animal livers and muscles. Starch and glycogen serve as energy storage compounds for plants and animals, respectively. These polysaccharides are readily hydrolyzed to glucose monomers, which in turn can be further degraded to liberate their stored energy and convert it to forms that can be used for cellular activities. If it is glucose that is actually needed for fuel, why must it be stored as a polymer? The reason is that 1,000 glucose molecules would exert 1,000 times the osmotic pressure (causing water to enter the cells; see Chapter 5) of a single glycogen molecule. If it were not for polysaccharides, many organisms would expend a lot of time and energy expelling excess water.

Cellulose is the predominant component of plant cell walls, and is by far the most abundant **organic** (carbon-containing) compound on Earth. Starch can be easily degraded by the actions of chemicals or enzymes. Cellulose, however, is chemically more stable because of its β-glycosidic linkages (Figure 3.16*a*). Thus starch is a good storage medium that can be easily broken down to supply glucose for energy-producing reactions, while cellulose is an excellent structural material that can withstand harsh environmental conditions without changing.

Chemically modified carbohydrates contain other groups

Some carbohydrates are chemically modified by the addition of functional groups, such as phosphate and amino groups

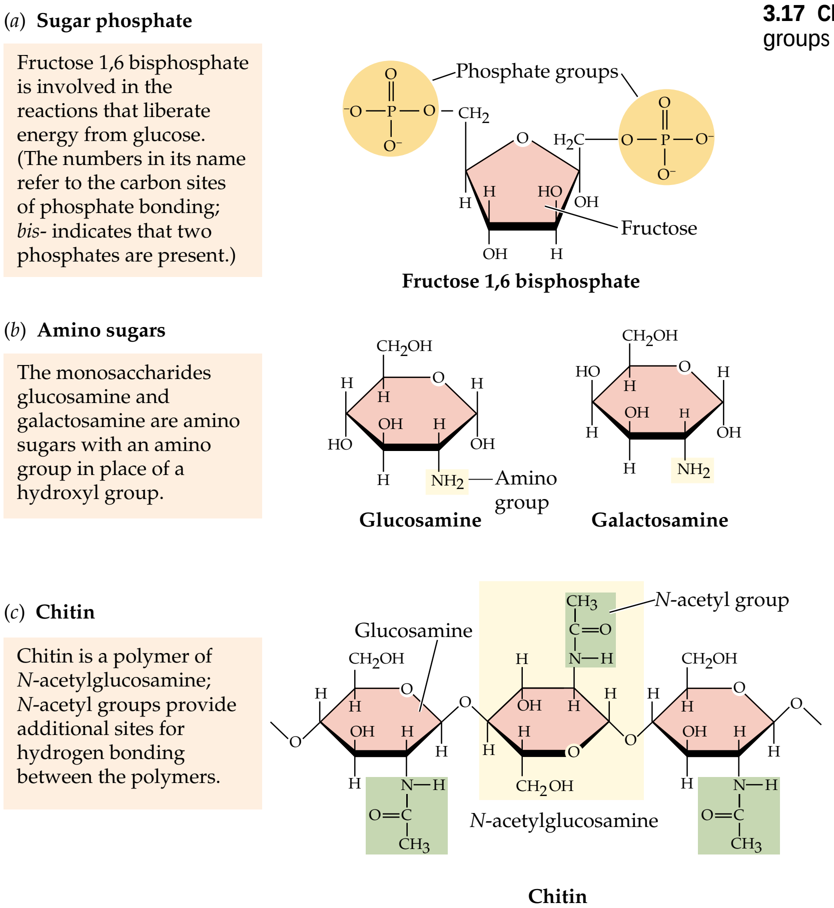


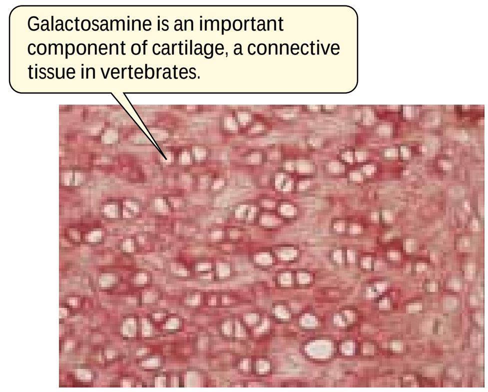
3.16 Representative Polysaccharides Cellulose, starch, and glycogen demonstrate different levels of branching and compaction in polysaccharides.

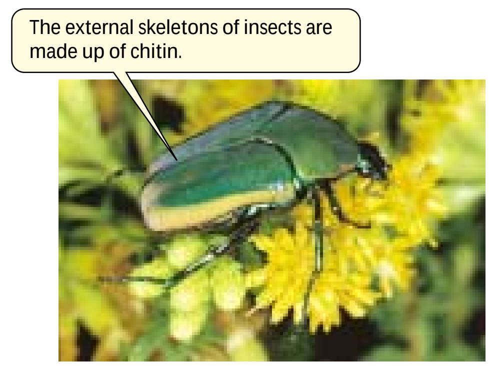
(Figure 3.17). For example, carbon 6 in glucose may be oxidized from —CH_2OH to a carboxyl group (—COOH), producing glucuronic acid. Or a phosphate group may be added to one or more of the —OH sites. Some of the resulting *sugar phosphates*, such as fructose 1,6-bisphosphate, are important intermediates in cellular energy reactions.

When an amino group is substituted for an —OH group, *amino sugars*, such as glucosamine and galactosamine, are produced. These compounds are important in the extracellular matrix, where they form parts of proteins involved in keeping tissues together. 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. A derivative of glucosamine produces the polymer *chitin*, which is the principal structural polysaccharide in the skele-

3.17 Chemically Modified Carbohydrates Added functional groups modify the form and properties of a carbohydrate.







tons of insects, 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 so chitin is one of the most abundant substances on Earth.

Lipids: Water-Insoluble Molecules

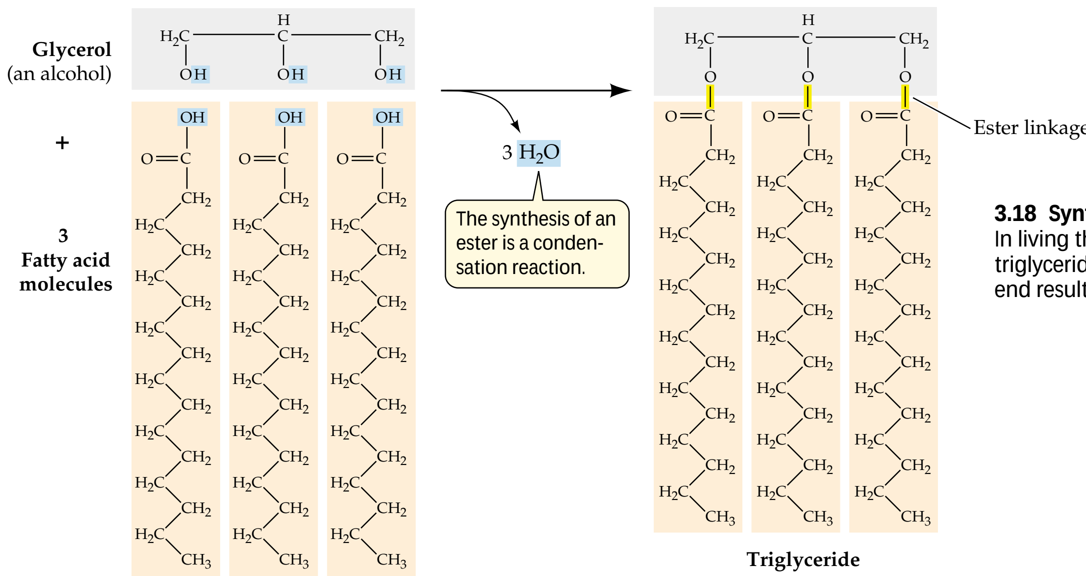
The **lipids** are a chemically diverse group of hydrocarbons. The property they all share is insolubility in water, which is due to the presence of many nonpolar covalent bonds. As we saw in Chapter 2, nonpolar hydrocarbon molecules are hydrophobic and preferentially aggregate among themselves, away from water, which is polar. When these nonpolar molecules are sufficiently close together, weak but additive van der Waals forces hold them together. These huge macromolecular aggregations are not polymers in a strict chemical sense, since their units (lipid molecules) are not held together by covalent bonds, as are, for example, the amino acids in proteins. But they can be considered polymers of individual lipid units.

In this section, we will describe the different types of lipids. Lipids have a number of roles in living organisms:

- Fats and oils store energy.
- Phospholipids play important structural roles in cell membranes.
- The carotenoids help plants capture light energy.
- Steroids and modified fatty acids play regulatory roles as hormones and vitamins.
- The fat in animal bodies serves as thermal insulation.
- A lipid coating around nerves acts as electrical insulation.
- Oil or wax on the surfaces of skin, fur, and feathers repels water.

Fats and oils store energy

Chemically, fats and oils are **triglycerides**, also known as *simple lipids*. Triglycerides that are solid at room temperature (20°C) are called *fats;* those that are liquid at room temperature are called *oils*. Triglycerides are composed of two types of building blocks: fatty acids and glycerol. *Glycerol* is a small molecule with three hydroxyl (—OH) groups (an alcohol). A *fatty acid* is made up of a long nonpolar hydrocarbon chain and a polar carboxyl group (—COOH). A triglyceride contains three fatty acid molecules and one molecule of glycerol.



3.18 Synthesis of a Triglyceride In living things, the reaction that forms triglycerides is more complex, but the end result is as shown here.

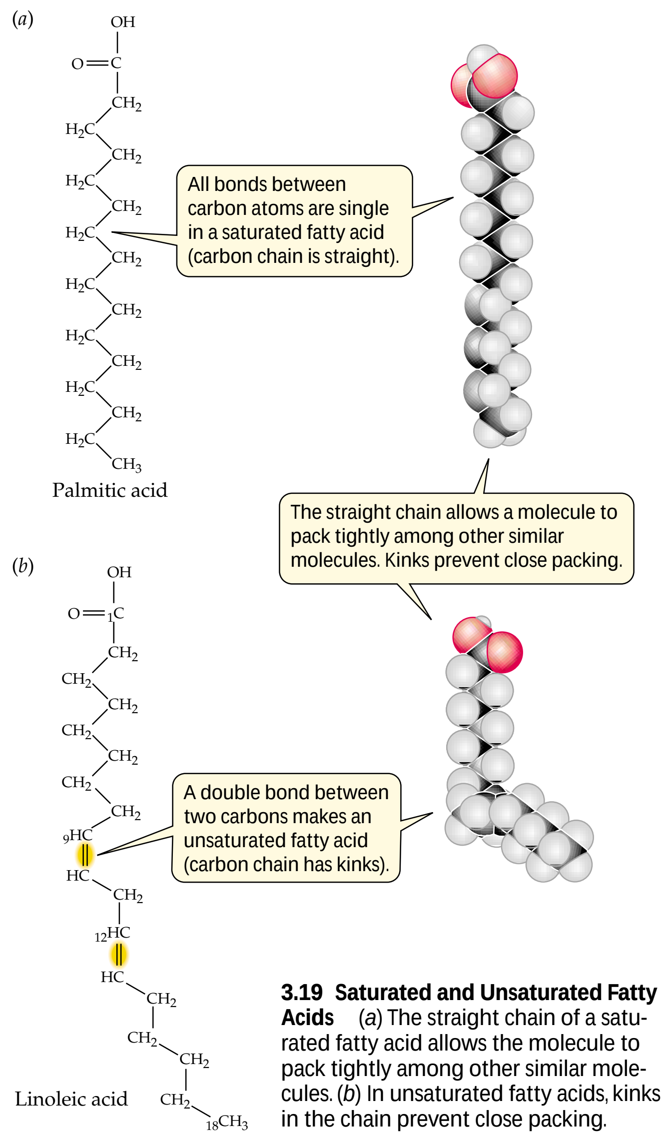
The carboxyl group of a fatty acid can form a covalent bond with the hydroxyl group of glycerol, resulting a functional group called an *ester* and water (Figure 3.18).

The three fatty acids in a triglyceride molecule need not all have the same hydrocarbon chain length or structure:

- In **saturated** fatty acids, all the bonds between the carbon atoms in the hydrocarbon chain are single bonds—there are no double bonds. That is, all the bonds are saturated with hydrogen atoms (Figure 3.19*a*). These fatty acid molecules are relatively rigid and straight, and they pack together tightly, like pencils in a box.
- In **unsaturated** fatty acids, the hydrocarbon chain contains one or more double bonds. Oleic acid, for example, is a *monounsaturated* fatty acid that has one double bond near the middle of the hydrocarbon chain, which causes a kink in the molecule (Figure 3.19*b*). Some fatty acids have more than one double bond—are *polyunsaturated*—and have multiple kinks. These kinks prevent the molecules from packing together tightly.

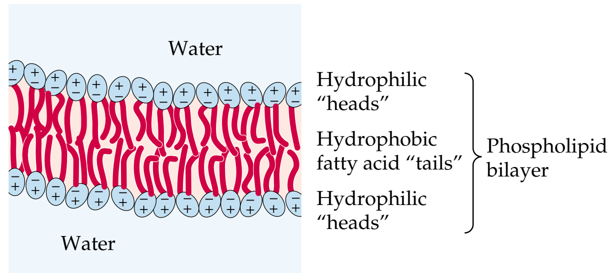
The kinks in fatty acid molecules are important in determining the fluidity and melting point of a lipid. The triglycerides of animal fats tend to have many long-chain saturated fatty acids, packed tightly together; these fats are usually solids at room temperature and have a high melting point. The triglycerides of plants, such as corn oil, tend to have short or unsaturated fatty acids. Because of their kinks, these fatty acids pack together poorly and have a low melting point, and these triglycerides are usually liquids at room temperature.

Fats and oils are marvelous storehouses for energy. When they take in excess food, many animal species deposit fat droplets in their cells as a means of storing energy. Some plant species, such as olives, avocados, sesame, castor beans, and all nuts, have substantial amounts of lipids in their seeds



3.19 Saturated and Unsaturated Fatty Acids (*a*) The straight chain of a saturated fatty acid allows the molecule to pack tightly among other similar molecules. (*b*) In unsaturated fatty acids, kinks in the chain prevent close packing.

or fruits that serve as energy reserves for the next generation. This energy can be tapped by people who eat these plant oils or use them for fuel. Indeed, the famous German engineer Rudolf Diesel used peanut oil to power one of his early automobile engines in 1900.



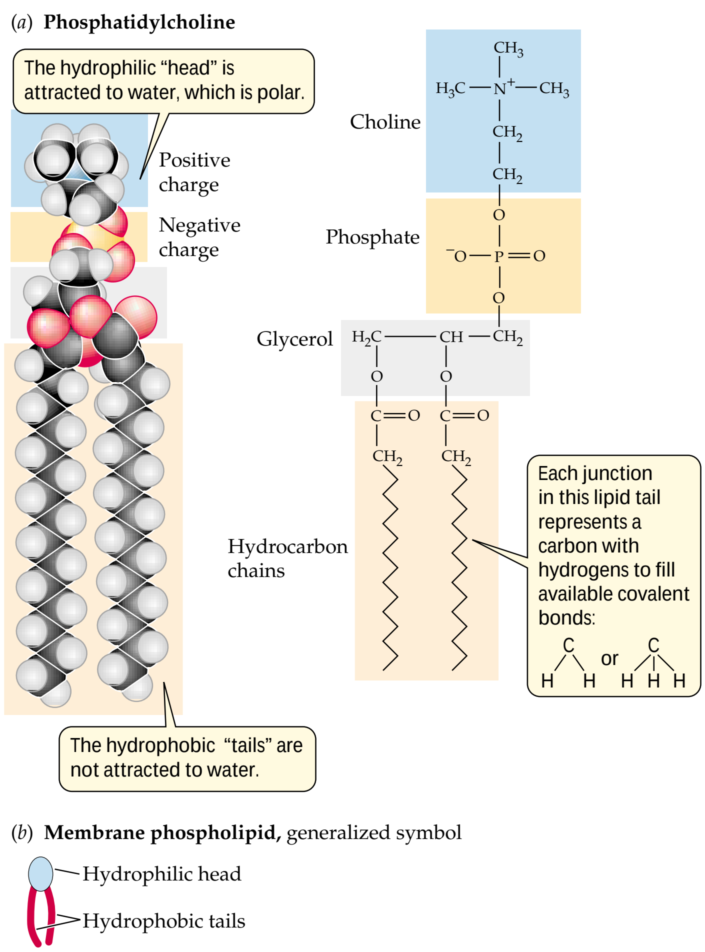
3.21 Phospholipids Form a Bilayer In an aqueous environment, hydrophobic interactions bring the "tails" of phospholipids together in the interior of a phospholipid bilayer. The hydrophilic "heads" face outward on both sides of the bilayer, where they interact with the surrounding water molecules.

Phospholipids form the core of biological membranes

Because lipids and water do not interact, a mixture of water and lipids forms two distinct layers. Many biologically important substances—such as ions, sugars, and free amino acids—that are soluble in water are insoluble in lipids.

Like triglycerides, **phospholipids** contain fatty acids bound to glycerol by ester linkages. In phospholipids, however, any one of several phosphate-containing compounds replaces one of the fatty acids (Figure 3.20). The phosphate functional group has a negative electric charge, so this portion of the molecule is hydrophilic, attracting polar water molecules. But the two fatty acids are hydrophobic, so they tend to aggregate away from water.

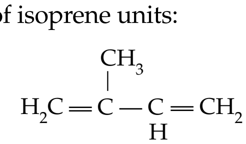
In an aqueous environment, phospholipids line up in such a way that the nonpolar, hydrophobic "tails" pack tightly together and the phosphate-containing "heads" face outward, where they interact with water. The phospholipids thus form a *bilayer*, a sheet two molecules thick, with water excluded from the core (Figure 3.21). Biological membranes have this kind of phospholipid bilayer structure, and we will devote all of Chapter 5 to their biological functions.



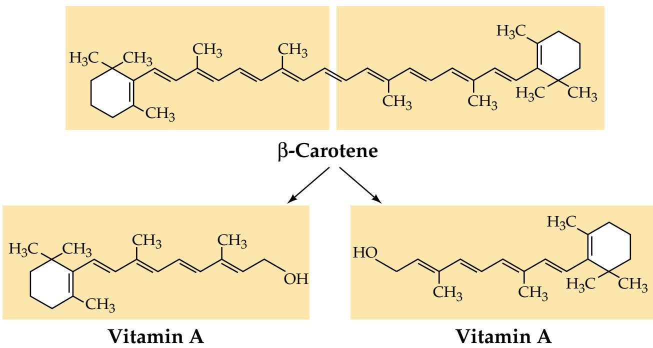
3.20 Phospholipid Structure (*a*) Phosphatidylcholine (lecithin) demonstrates the structure of a phospholipid molecule. In other phospholipids, the amino acid serine, the sugar alcohol inositol, or other compounds replace choline. (*b*) This generalized symbol is used throughout this book to represent a membrane phospholipid.

Carotenoids and steroids

The next two lipid classes we'll discuss—the carotenoids and the steroids—have chemical structures very different from those of triglycerides and phospholipids and from each other. Both carotenoids and steroids are synthesized by covalent linking and chemical modification of isoprene to form a series of isoprene units:



CAROTENOIDS TRAP LIGHT ENERGY. The **carotenoids** are a family of light-absorbing pigments found in plants and animals. Beta-carotene (β-carotene) is one of the pigments that traps light energy in leaves during photosynthesis. In humans, a molecule of β-carotene can be broken down into two vitamin A molecules (Figure 3.22), from which we make the pigment rhodopsin, which is required for vision. Carotenoids are responsible for the colors of carrots, tomatoes, pumpkins, egg yolks, and butter.



3.22 β-Carotene is the Source of Vitamin A The carotenoid β-carotene is symmetrical around its central double bond; when split, β-carotene becomes two vitamin A molecules. The simplified structural formula used here is standard chemical shorthand for large organic molecules with many carbon atoms. Structural formulas are simplified by omitting the C (indicating a carbon atom) at the intersections of the lines representing covalent bonds. Hydrogen atoms (H) to fill all the available bonding sites on each C are assumed.

STEROIDS ARE SIGNAL MOLECULES. The **steroids** are a family of organic compounds whose multiple rings share carbons (Figure 3.23). The steroid cholesterol is an important constituent of membranes. Other steroids function as hormones, chemical signals that carry messages from one part of the body to another. Testosterone and the estrogens are steroid hormones that regulate sexual development in vertebrates. Cortisol and related hormones play many regulatory roles in the digestion of carbohydrates and proteins, in the maintenance of salt balance and water balance, and in sexual development.

Cholesterol is synthesized in the liver and is the starting material for making testosterone and other steroid hormones, as well as the bile salts that help break down dietary fats so that they can be digested. Cholesterol is absorbed from foods such as milk, butter, and animal fats.

Some lipids are vitamins

Vitamins are small molecules that are not synthesized by the body, but are necessary for its normal functioning. Vitamins must be acquired from dietary sources.

- *Vitamin A* is formed from the β-carotene found in green and yellow vegetables (see Figure 3.22). In humans, a deficiency of vitamin A leads to dry skin, eyes, and internal body surfaces, retarded growth and development, and night blindness, which is a diagnostic symptom for the deficiency.
- *Vitamin D* regulates the absorption of calcium from the intestines. It is necessary for the proper deposition of calcium in bones; a deficiency of vitamin D can lead to rickets, a bone-softening disease.
- *Vitamin E* seems to protect cells from the damaging effects of oxidation–reduction reactions. For example, it has an important role in preventing unhealthy changes in the double bonds in the unsaturated fatty acids of membrane phospholipids. Commercially, vitamin E is added to some foods to slow spoilage.
- *Vitamin K* is found in green leafy plants and is also synthesized by bacteria normally present in the human intestine. This vitamin is essential to the formation of blood clots.

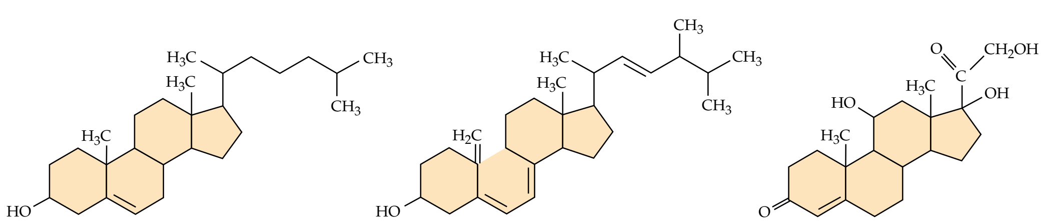
Inadequate vitamin intake can lead to deficiency diseases.

Wax coatings repel water

The sheen on human hair is not there only for cosmetic purposes. Glands in the skin secrete a waxy coating that repels water and keeps the hair pliable. Birds that live near water have a similar waxy coating on their feathers. The shiny leaves of holly plants, familiar during winter holidays, also have a waxy coating. Finally, bees make their honeycombs out of wax.

All waxes have the same basic structure: They are formed by an ester linkage between a saturated, long-chain fatty acid and a saturated, long-chain alcohol. The result is a very long

3.23 All Steroids Have the Same Ring Structure The steroids shown here, all important in vertebrates, are composed of carbon and hydrogen and are highly hydrophobic. However, small chemical variations, such as the presence or absence of a methyl or hydroxyl group, can produce enormous functional differences.



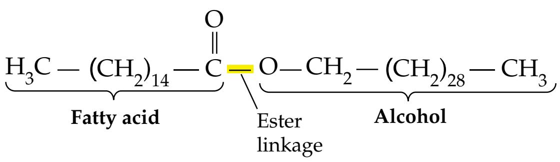
Cholesterol is a constituent of membranes and is the source of steroid hormones.

Vitamin D_2 can be produced in the skin by the action of light on a cholesterol derivative.

Cortisol is a hormone secreted by the adrenal glands.

Testosterone is a male sex hormone.

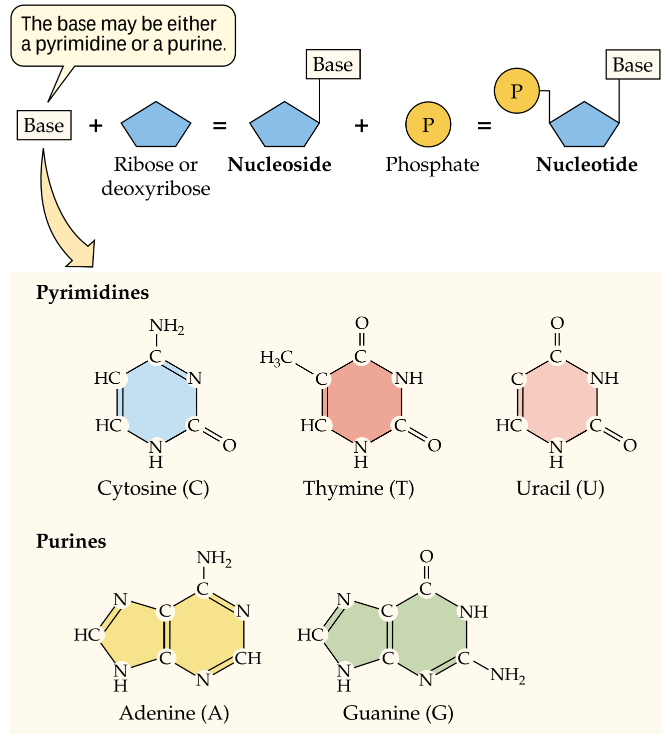
molecule, with 40–60 CH_2 groups. For example, here is the structure of beeswax:



This highly nonpolar structure accounts for the impermeability of wax to water.

Nucleic Acids: Informational Macromolecules That Can Be Catalytic

The **nucleic acids** are polymers specialized for the storage, transmission, and use of information. There are two types of nucleic acids: **DNA** (deoxyribonucleic acid) and **RNA** (ribonucleic acid). DNA molecules are giant polymers that encode hereditary information and pass it from generation to generation. Through an RNA intermediate, the information encoded in DNA is also used to specify the amino acid sequence of proteins. Information flows from DNA to DNA in reproduction, but in the nonreproductive activities of the cell, information flows from DNA to RNA to proteins, which ultimately carry out these functions. In addition, certain RNAs act as catalysts for important reactions in cells.



3.24 Nucleotides Have Three Components A nucleotide consists of a phosphate group, a pentose sugar (ribose or deoxyribose), and a nitrogen-containing base, all linked together by covalent bonds. The nitrogenous bases fall into two categories: Purines have two fused rings, and the smaller pyrimidines have a single ring.

The nucleic acids have characteristic chemical properties

Nucleic acids are composed of monomers called **nucleotides**, each of which consists of a pentose sugar, a phosphate group, and a nitrogen-containing **base**—either a pyrimidine or a purine (Figure 3.24). (Molecules consisting of a pentose sugar and a nitrogenous base, but no phosphate group, are called **nucleosides**.) In DNA, the pentose sugar is deoxyribose, which differs from the ribose found in RNA by one oxygen atom (see Figure 3.14).

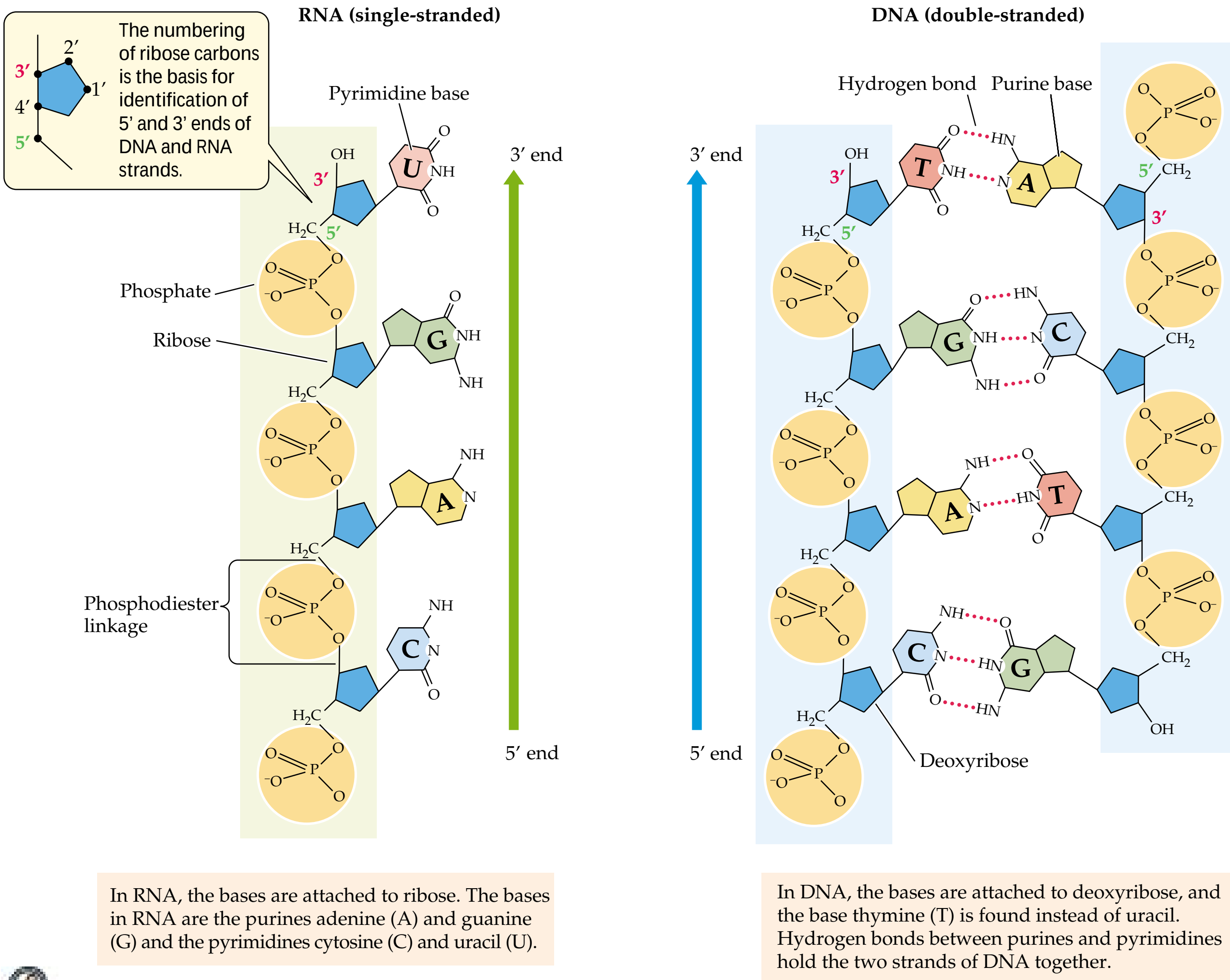
In both RNA and DNA, the backbone of the macromolecule consists of alternating pentose sugars and phosphates (sugar—phosphate—sugar—phosphate). The bases are attached to the sugars and project from the chain (Figure 3.25). The nucleotides are joined by *phosphodiester linkages* between the sugar of one nucleotide and the phosphate of the next (-*diester* refers to the two covalent bonds formed by —OH groups reacting with acidic phosphate groups). The phosphate groups link carbon 3 in one pentose sugar to carbon 5 in the adjacent sugar.

Most RNA molecules consist of only one polynucleotide chain. DNA, however, is usually double-stranded; it has two polynucleotide strands held together by hydrogen bonding between their nitrogenous bases. The two strands of DNA run in opposite directions. You can see what this means by drawing an arrow through the phosphate group from carbon 5′ to carbon 3′ in the next ribose. If you do this for both strands of the DNA in Figure 3.25, the arrows will point in opposite directions. This antiparallel orientation is necessary for the strands to fit together in three-dimensional space.

The uniqueness of a nucleic acid resides in its nucleotide sequence

Only four nitrogenous bases—and thus only four nucleotides—are found in DNA. The DNA bases and their abbreviations are adenine (A), cytosine (C), guanine (G), and thymine (T). A key to understanding the structure and function of nucleic acids is the principle of **complementary base pairing**. In double-stranded DNA, adenine and thymine always pair (A-T), and cytosine and guanine always pair (C-G).

Base pairing is complementary because of three factors: the sites for for hydrogen bonding on each base, the geometry of the sugar–phosphate backbone, which brings opposite bases near each other, and the molecular sizes of the paired bases. Adenine and guanine are both purines, consisting of two fused rings. Thymine and cytosine are both pyrimidines, consisting of only one ring. The pairing of a large purine with



3.25 Distinguishing Characteristics of DNA and RNA
RNA is usually a single strand. DNA usually consists of two strands running in opposite directions.

a small pyrimidine ensures stability and consistency in the double-stranded molecule of DNA.

Ribonucleic acids are also made up of four different monomers, but their nucleotides differ from those of DNA. In RNA the nucleotides are termed *ribonucleotides* (the ones in DNA are *deoxyribonucleotides*). They contain ribose rather than deoxyribose, and instead of the base thymine, RNA uses the base uracil (U) (Table 3.3). The other three bases are the same as in DNA.

Although RNA is generally single-stranded, complementary hydrogen bonding between ribonucleotides can take place. These bonds play important roles in determining the shapes of some RNA molecules and in associations between RNA molecules during protein synthesis (Figure 3.26). When the base sequence of DNA is copied in the synthesis of RNA, complementary base pairing also takes place between ribonucleotides and deoxyribonucleotides. In RNA, guanine and cytosine pair (G-C), as in DNA, but adenine pairs with uracil (A-U). Adenine in an RNA strand can pair either with uracil (in another RNA strand) or with thymine (in a DNA strand).

3.3 Distinguishing RNA from DNA

NUCLEIC ACID	SUGAR	BASES
RNA	Ribose	Adenine Cytosine Guanine Uracil
DNA	Deoxyribose	Adenine Cytosine Guanine Thymine

DNA is a purely *informational* molecule. The information in DNA is encoded in the sequence of bases carried in its strands—the information encoded in the sequence TCAG is different from the information in the sequence CCAG. The information can be read easily and reliably, in a specific order.

The three-dimensional appearance of DNA is strikingly uniform. The segment shown in Figure 3.27 could be from any DNA molecule. The variations in DNA—the different sequences of bases—are strictly "internal." Through hydrogen bonding, the two complementary polynucleotide strands pair and twist to form a double helix. When compared with the complex and varied tertiary structures of different proteins, this uniformity is surprising. But this structural contrast makes sense in terms of the functions of these two classes of macromolecules.

It is their different and unique shapes that permit proteins to recognize specific "target" molecules. The unique three-dimensional form of each protein matches at least a portion of the surface of the target molecule. In other words, structural diversity in the molecules to which proteins bind requires corresponding diversity in the structure of the proteins themselves.

In DNA, then, the information is in the sequence of the bases; in proteins, the information is in the shape of the molecule.

DNA is a guide to evolutionary relationships

Because DNA carries hereditary information between generations, a theoretical series of DNA molecules with changes in base sequences stretches back through evolutionary time. Of course, we cannot study all of these DNA molecules, because many of their organisms have become extinct. However, we can study the DNA of living organisms, which are judged to have changed little over millions of years. Comparisons and contrasts of these DNA molecules can be added to evidence from fossils and other sources to reveal the evolutionary record, as we will see in Chapter 24.

Closely related living species should have more similar base sequences than species judged by other criteria to be more distantly related. The examination of base sequences has confirmed many of the evolutionary relationships that have been inferred from the more traditional study of body structures, biochemistry, and physiology. For example, the closest living relative of humans (*Homo sapiens*) is the chimpanzee (genus *Pan*

DNA studies revealed a close evolutionary relationship between starlings and mockingbirds that was not expected on the basis of their anatomy or behavior.

DNA studies support the division of the prokaryotes into two domains, Bacteria and Archaea. Each of these two groups of prokaryotes is as distinct from the other as either is from the Eukarya, the third domain into which living things are classified (see Chapter 1). In addition, DNA comparisons support the hypothesis that certain subcellular compartments of eukaryotes (the organelles called mitochondria and chloroplasts) evolved from early bacteria that established a stable and mutually beneficial way of life inside larger cells.

RNA may have been the first biological catalyst

The three-dimensional structure of a folded RNA molecule presents a unique surface to the external environment (see Figure 3.26). These surfaces are every bit as specific as those of proteins. We noted above that an important role of proteins in biology is to act as catalysts, speeding up reactions that would ordinarily take place too slowly to be biologically useful, and that the spatial property of proteins is vital to this role.

As we will see, certain RNA molecules can also act as catalysts, using their three-dimensional shapes and other chemical properties. They can catalyze reactions on their own nucleotides as well as in other cellular substances. These catalytic RNAs are called **ribozymes**. Their discovery had implications for theories of the origin of life.

The Miller-Urey experiment and other such experiments in prebiotic chemistry yielded both amino acids and nucleotides. Organisms can synthesize both RNA and proteins from these monomers. As we noted above, in current organisms on Earth, protein synthesis requires DNA and RNA, and nucleic acid synthesis requires proteins (as enzymes). So the question is, when life originated, which came first, the proteins or the nucleic acids?

The discovery of catalytic RNAs provided a solution to this dilemma and led to the hypothesis that early life was part of an "RNA world." RNA can be informational (in its nucleotide sequence) as well as catalytic. So when RNA was first made, it could have acted as a catalyst for its own replication, as well as for the synthesis of proteins. Then DNA could have eventually evolved by being made from RNA. There is some laboratory evidence supporting this scenario:

- RNAs of different sequences have been put in a test tube and made to replicate on their own. Such self-replicating ribozymes speed up the synthesis of RNA 7 million-fold.
- In living organisms today, the formation of peptide linkages (see Figure 3.5) is catalyzed by a ribozyme.
- In certain viruses called retroviruses, there is an enzyme called reverse transcriptase that catalyzes the synthesis of DNA from RNA.

Nucleotides have other important roles

Nucleotides are more than just the building blocks of nucleic acids. As we will see in later chapters, there are several nucleotides with other functions:

- ATP (adenosine triphosphate) acts as an energy transducer in many biochemical reactions (see Chapter 6).
- GTP (guanosine triphosphate) serves as an energy source, especially in protein synthesis. It also has a role in the transfer of information from the environment to the body tissues (see Chapters 12 and 15).
- cAMP (cyclic adenosine monophosphate), a special nucleotide in which a bond forms between the sugar and phosphate groups within adenosine monophosphate, is essential in many processes, including the actions of hormones and the transmission of information by the nervous system (see Chapter 15).

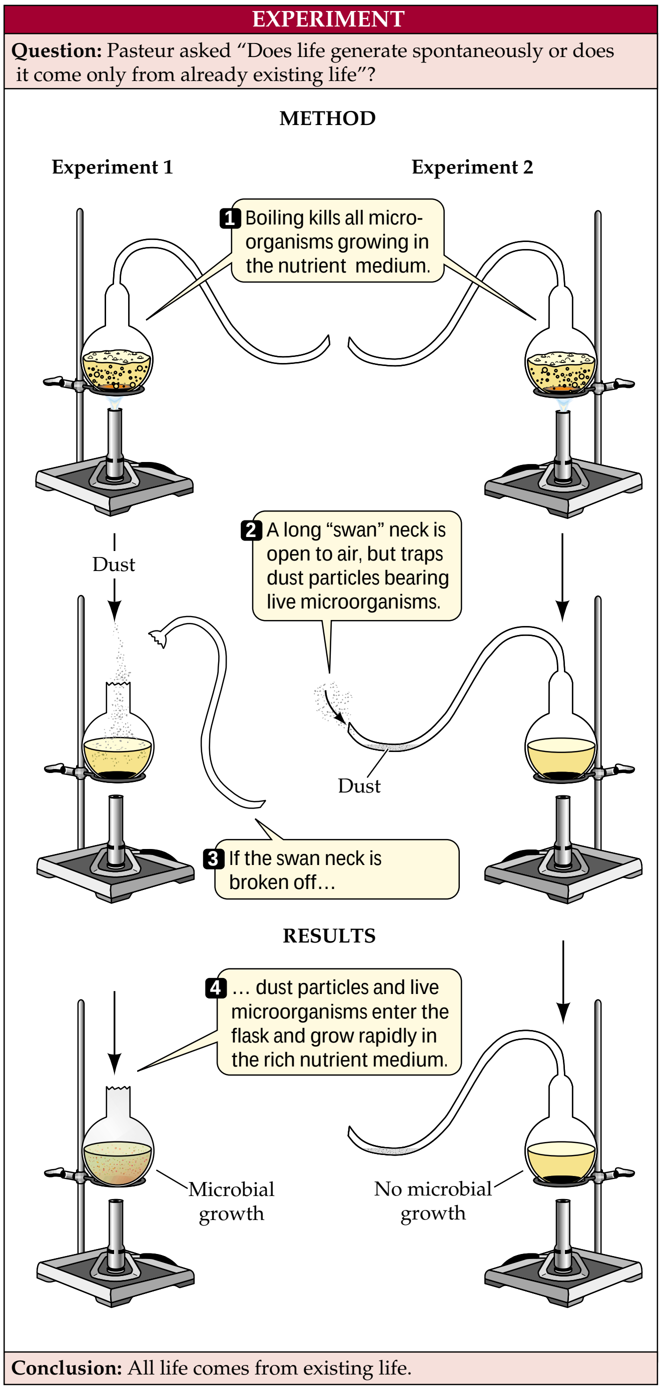
All Life from Life

The concepts conveyed throughout this chapter—that large molecules obey the mechanistic laws of physics and chemistry, and that life could have arisen from inanimate, self-replicating macromolecules—have come to be generally accepted by the scientific community. So should we expect to see new life forms arise at any time from the biochemical environment?

During the Renaissance (a period from about 1350 to 1700 A.D., marked by the birth of modern science), most people thought that at least some forms of life arose directly from inanimate or decaying matter by *spontaneous generation*. For instance, it was suggested that mice arose from sweaty clothes placed in dim light, frogs came from moist soil, and flies were produced from meat. These ideas were attacked by scientists such as the Italian doctor and poet Francisco Redi using the relatively new idea of using experiments to test an idea. In 1668, Redi proposed that flies arose not by some mysterious transformation of decaying meat, but from other flies, who laid their eggs on the meat. The eggs developed into wormlike maggots (the immature form of flies). Redi set out several jars containing chunks of meat.

- One jar contained meat exposed both to the air and to flies.
- A second jar contained meat in a container wrapped in a fine cloth so that the meat was exposed to the air, but not to flies.
- The meat in the third jar was in a sealed container and thus was not exposed to either air or flies.

As he had hypothesized, Redi found maggots, which then hatched into flies, only in the first container. The idea that a complex organism like a fly could come from a totally different substance was laid to rest.



3.28 Disproving the Spontaneous Generation of Life Louis Pasteur’s classic experiments showed that, under today’s conditions, an inanimate solution remains lifeless unless a living organism contaminates it.

With the invention of the microscope in the 1660s, a vast new biological world was unveiled. Under microscopic observation, virtually every environment on Earth was found to be teeming with tiny organisms such as bacteria. Some scientists believed that these organisms arose spontaneously from their rich chemical environment.

The experiments that disproved this idea were done by the great French scientist Louis Pasteur. His experiments showed that microorganisms come only from other microorganisms, and that an environment without life remains lifeless unless contaminated by living creatures (Figure 3.28).

These experiments by Redi, Pasteur, and others provided solid evidence that neither small (bacteria) nor large (flies) organisms come from inanimate matter, but instead come from living parent organisms.

Indeed, life on Earth no longer arises from nonliving materials. This is because the atmospheric and planetary conditions that exist on Earth today are vastly different from those on the prebiotic, anaerobic planet. The oxygen present in today’s atmosphere would break down the prebiotic molecules before they could accumulate. In addition, the necessary energy sources—including constant lightning strikes, immense volcanic eruptions, and bombardment by intense ultraviolet light—are no longer present with anything like their primeval force.

Chapter Summary

Theories of the Origin of Life

▶ Life may have come from outside Earth. The evidence for this proposal comes primarily from chemicals contained in meteorites that have landed on Earlth.

▶ The theory of chemical evolution proposes that life on Earth originated on Earth. Experiments using model systems that attempt to duplicate the ancient Earth have shown that chemical evolution could have produced the four types of macromolecules that distinguish living things. **Review Figure 3.1.** **See Web/CD Tutorial 3.1**

Macromolecules: Giant Polymers

▶ Macromolecules are polymers constructed by the formation of covalent bonds between smaller molecules called monomers. Macromolecules in living organisms include polysaccharides, proteins, and nucleic acids. **Review Figure 3.2 and Table 3.1**

▶ Macromolecules have specific, characteristic three-dimensional shapes that depend on the structure, properties, and sequence of their monomers.

▶ Different functional groups give local sites on macromolecules specific properties that are important for their biological functioning and their interactions with other macromolecules. **See Web/CD Tutorial 3.2**

Condensation and Hydrolysis Reactions

▶ Monomers are joined by condensation reactions, which release a molecule of water for each bond formed. Hydrolysis reactions use water to break polymers into monomers. **Review Figure 3.3**

Proteins: Polymers of Amino Acids

- The functions of proteins include support, protection, catalysis, transport, defense, regulation, and movement. Protein function sometimes requires an attached prosthetic group.
- There are 20 amino acids found in proteins. Each amino acid consists of an amino group, a carboxyl group, a hydrogen, and a side chain bonded to the α carbon atom. **Review Table 3.2**
- The side chains, or R groups, of amino acids may be charged, polar, or hydrophobic; there are also special cases, such as the —SH groups of cysteine, which can form disulfide bridges. The side chains give different properties to each of the amino acids. **Review Table 3.2 and Figure 3.4**
- Amino acids are covalently bonded together into polypeptide chains by peptide linkages, which form by condensation reactions between the carboxyl and amino groups. **Review Figure 3.5**
- Polypeptide chains are folded into specific three-dimensional shapes to form functional proteins. Four levels of protein structure are possible: primary, secondary, tertiary, and quaternary.
- The primary structure of a protein is the sequence of amino acids bonded by peptide linkages. This primary structure determines both the higher levels of structure and protein function. **Review Figure 3.6*a***
- The two types of secondary structure—α helices and β pleated sheets—are maintained by hydrogen bonds between atoms of the amino acid residues. **Review Figure 3.6*b,c***
- The tertiary structure of a protein is generated by bending and folding of the polypeptide chain. **Review Figures 3.6*d*, 3.7**
- The quaternary structure of a protein is the arrangement of two or more polypeptides into a single functional protein consisting of two or more polypeptide subunits. **Review Figures 3.6*e*, 3.8**
- Weak chemical interactions are important in the three-dimensional structure of proteins and in their binding to other molecules. **Review Figure 3.9, 3.10**
- Proteins denatured by heat, alterations in pH, or certain chemicals lose their tertiary and secondary structure as well as their biological function. Renaturation is not often possible. **Review Figure 3.11**
- Chaperonins assist protein folding by preventing binding to inappropriate ligands. **Review Figure 3.12**

Carbohydrates: Sugars and Sugar Polymers

- All carbohydrates contain carbon bonded to hydrogen atoms and hydroxyl groups.
- Hexoses are monosaccharides that contain six carbon atoms. Examples of hexoses include glucose, galactose, and fructose, which can exist as chains or rings. **Review Figures 3.13, 3.14. See Web/CD Activity 3.1**
- The pentoses are five-carbon monosaccharides. Two pentoses, ribose and deoxyribose, are components of the nucleic acids RNA and DNA, respectively. **Review Figure 3.14**
- Glycosidic linkages may have either α or β orientation in space. They covalently link monosaccharides into larger units such as disaccharides, oligosaccharides, and polysaccharides. **Review Figure 3.15**
- Cellulose, a very stable glucose polymer, is the principal component of the cell walls of plants. It is formed by glucose units linked together by β-glycosidic linkages between carbons 1 and 4. Starches, less dense and less stable than cellulose, store energy in plants. Starches and glycogen are formed by α-glycosidic linkages between carbons 1 and 4 and are distinguished by the amount of branching they exhibit. **Review Figure 3.16**
- Chemically modified monosaccharides include the sugar phosphates and amino sugars. A derivative of the amino sugar glucosamine polymerizes to form the polysaccharide chitin, which is found in the cell walls of fungi and the exoskeletons of insects. **Review Figure 3.17**

Lipids: Water-Insoluble Molecules

- Although lipids can form gigantic structures, these aggregations are not chemically macromolecules because the individual units are not linked by covalent bonds.
- Fats and oils are triglycerides, composed of three fatty acids covalently bonded to a glycerol molecule by ester linkages. **Review Figure 3.18**
- Saturated fatty acids have a hydrocarbon chain with no double bonds. The hydrocarbon chains of unsaturated fatty acids have one or more double bonds that bend the chain, making close packing less possible. **Review Figure 3.29**
- Phospholipids have a hydrophobic hydrocarbon "tail" and a hydrophilic phosphate "head." **Review Figure 3.20**
- In water, the interactions of the hydrophobic tails and hydrophilic heads of phospholipids generate a phospholipid bilayer that is two molecules thick. The head groups are directed outward, where they interact with the surrounding water. The tails are packed together in the interior of the bilayer. **Review Figure 3.21**
- Carotenoids trap light energy in green plants. Carotene can be split to form vitamin A, a lipid vitamin. **Review Figure 3.22**
- Some steroids, such as testosterone, function as hormones. Cholesterol is synthesized by the liver and has a role in cell membranes, as well as in the digestion of fats. **Review Figure 3.23**
- Vitamins are substances that are required for normal functioning, but must be acquired from the diet.

Nucleic Acids: Informational Macromolecules

- DNA is the hereditary material. Both DNA and RNA play roles in the formation of proteins. Information flows from DNA to RNA to protein.
- Nucleic acids are polymers made up of nucleotides. A nucleotide consists of a phosphate group, a sugar (ribose in RNA and deoxyribose in DNA), and a nitrogen-containing base. In DNA the bases are adenine, guanine, cytosine, and thymine, but in RNA uracil substitutes for thymine. **Review Figure 3.24 and Table 3.3. See Web/CD Activity 3.2**
- In the nucleic acids, the bases extend from a sugar–phosphate backbone. The information content of DNA and RNA resides in their base sequences. RNA is single-stranded. DNA is a double-stranded helix in which there is complementary, hydrogen-bonded base pairing between adenine and thymine (A-T) and guanine and cytosine (G-C). The two strands of the DNA double helix run in opposite directions. **Review Figures 3.25, 3.27. See Web/CD Activity 3.3**
- Base pairing of single-stranded RNAs can lead to three-dimensional structures, which can be catalytic. This finding has led to the proposal that in the origin of life, RNA preceded protein. **Review Figure 3.26**
- Comparing the DNA base sequences of different living species provides information on their evolutionary relationships.

All Life from Life

- One of the earliest conclusions from biology as a modern experimental science was that even the tiniest microbe comes from others of the same type—that is, that life begets life. **Review Figure 3.28. See Web/CD Tutorial 3.3**

▶ The conditions on primeval Earth that may have enabled life to arise from inanimate self-replicating chemicals no longer exist. Today all life comes from pre-existing life.

Self-Quiz

1. The most abundant molecule in the cell is
   a. carbohydrate.
   b. lipid.
   c. nucleic acid.
   d. protein.
   e. water.
2. All lipids are
   a. triglycerides.
   b. polar.
   c. hydrophilic.
   d. polymers of fatty acids.
   e. more soluble in nonpolar solvents than in water.
3. All carbohydrates
   a. are polymers.
   b. are simple sugars.
   c. consist of one or more simple sugars.
   d. are found in biological membranes.
   e. are more soluble in nonpolar solvents than in water.
4. Which of the following is *not* a carbohydrate?
   a. Glucose
   b. Starch
   c. Cellulose
   d. Hemoglobin
   e. Deoxyribose
5. All proteins
   a. are enzymes.
   b. consist of one or more polypeptides.
   c. are amino acids.
   d. have quaternary structures.
   e. are more soluble in nonpolar solvents than in water.
6. Which of the following statements about the primary structure of a protein is *not* true?
   a. It may be branched.
   b. It is determined by the structure of the corresponding DNA.
   c. It is unique to that protein.
   d. It determines the tertiary structure of the protein.
   e. It is the sequence of amino acids in the protein.
7. The amino acid leucine (see Table 3.2)
   a. is found in all proteins.
   b. cannot form peptide linkages.
   c. is likely to appear in the part of a membrane protein that lies within the phospholipid bilayer.
   d. is likely to appear in the part of a membrane protein that lies outside the phospholipid bilayer.
   e. is identical to the amino acid lysine.
8. The quaternary structure of a protein
   a. consists of four subunits—hence the name *quaternary*.
   b. is unrelated to the function of the protein.
   c. may be either alpha or beta.
   d. depends on covalent bonding among the subunits.
   e. depends on the primary structures of the subunits.
9. All nucleic acids
   a. are polymers of nucleotides.
   b. are polymers of amino acids.
   c. are double-stranded.
   d. are double-helical.
   e. contain deoxyribose.
10. Which of the following statements about condensation reactions is *not* true?
   a. Protein synthesis results from them.
   b. Polysaccharide synthesis results from them.
   c. Nucleic acid synthesis results from them.
   d. They consume water as a reactant.
   e. Different condensation reactions produce different kinds of macromolecules.

For Discussion

1. Phospholipids make up a major part of most biological membranes; 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?
2. Suppose that, in a given protein, one lysine is replaced by aspartic acid (see Table 3.2). Does this change occur in the primary structure or in the secondary structure? How might it result in a change in tertiary structure? In quaternary structure?
3. If there are 20 different amino acids commonly found in proteins, how many different dipeptides are there? How many different tripeptides? How many different trinucleotides? How many different single-stranded RNAs composed of 200 nucleotides?
4. Contrast the following three structures, emphasizing the surfaces they present to their environment: hemoglobin; a DNA molecule; a protein that spans a biological membrane.
5. Why might RNA have preceded proteins in the evolution of biological macromolecules?