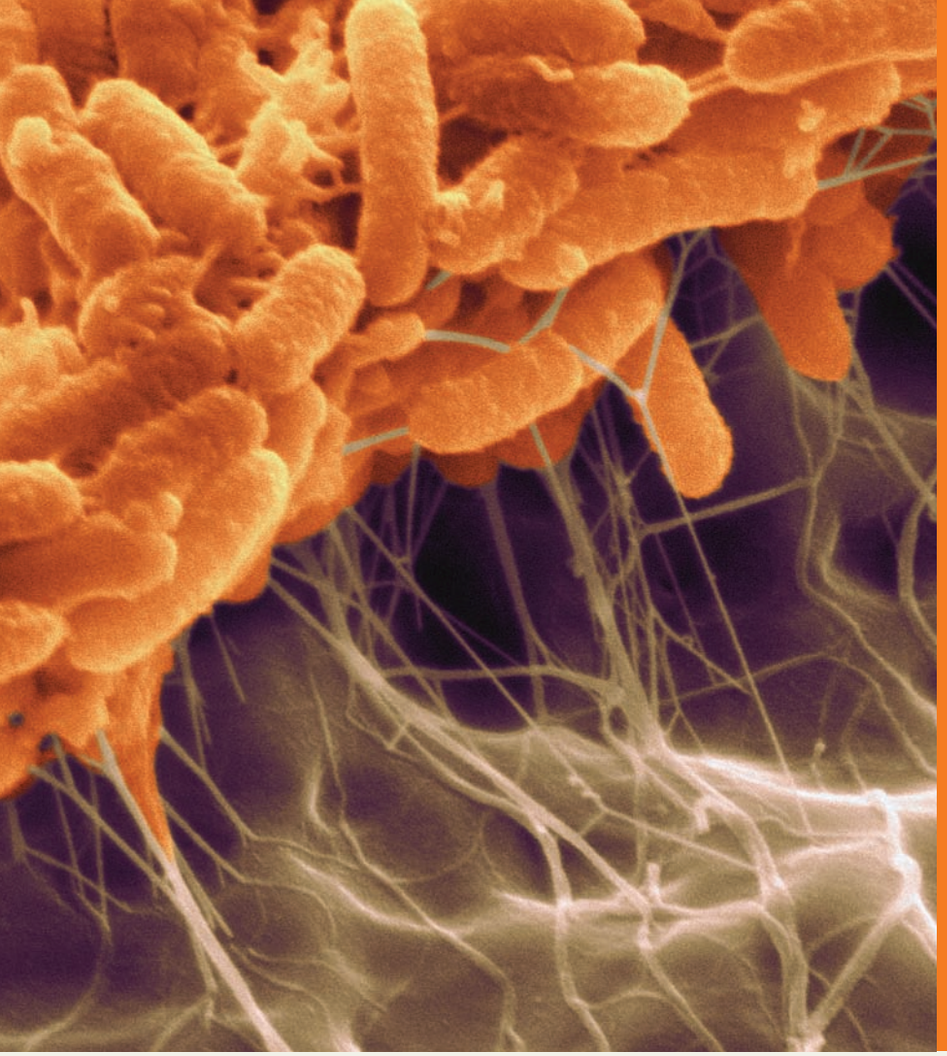

# 4

# Functional Anatomy of Prokaryotic and Eukaryotic Cells

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Despite their complexity and variety, all living cells can be classified into two groups, prokaryotes and eukaryotes, based on certain structural and functional characteristics. In general, prokaryotes are structurally simpler and smaller than eukaryotes. The DNA (genetic material) of prokaryotes is usually a single, circularly arranged chromosome and is not surrounded by a membrane; the DNA of eukaryotes is found in multiple chromosomes in a membrane-enclosed nucleus. Prokaryotes lack membrane-enclosed organelles, specialized structures that carry on various activities.

Plants and animals are entirely composed of eukaryotic cells. In the microbial world, bacteria and archaea are prokaryotes. Other cellular microbes—fungi (yeasts and molds), protozoa, and algae—are eukaryotes. Both eukaryotic and prokaryotic cells can have a sticky glycocalyx surrounding them. In nature, most bacteria are found sticking to solid surfaces including other cells rather than free-floating. The glycocalyx is the glue that holds the cells in place. The *Serratia* bacteria in the photograph are attached to plastic; the sticky glycocalyx dried into filaments during microscopic examination. An example of the problem posed by biofilms in hospital water supplies is described in the Clinical Case.

## Comparing Prokaryotic and Eukaryotic Cells: An Overview

### LEARNING OBJECTIVE

**4-1** Compare and contrast the overall cell structure of prokaryotes and eukaryotes.

Prokaryotes and eukaryotes are chemically similar, in the sense that they both contain nucleic acids, proteins, lipids, and carbohydrates. They use the same kinds of chemical reactions to metabolize food, build proteins, and store energy. It is primarily the structure of cell walls and membranes, and the absence of *organelles* (specialized cellular structures that have specific functions), that distinguish prokaryotes from eukaryotes.

The chief distinguishing characteristics of **prokaryotes** (from the Greek words meaning prenucleus) are as follows:

### Clinical Case: Infection Detection

Irene Matthews, an infection control nurse in a hospital in Atlanta, Georgia, is in a quandary. Three patients in her hospital have all contracted postprocedure bacterial septicemia. All three have a fever and dangerously low blood pressure. These three patients are in separate areas of the hospital, in different units, and they have all undergone different procedures. The first patient, Joe, a 32-year-old construction worker, is recovering from rotator cuff surgery. He is in relatively good health, otherwise. The second patient, Jessie, a 16-year-old student in intensive care, is in critical condition following an automobile accident. She is on a ventilator and cannot breathe on her own. The third patient, Maureen, a 57-year-old grandmother, is recovering from coronary artery bypass surgery. As far as Irene can tell, the only thing these patients have in common is the infectious agent—*Klebsiella pneumoniae*.

**How can three patients in different parts of a hospital contract *Klebsiella pneumoniae*? Read on to find out.**

76 86 88 95 97

1. Their DNA is not enclosed within a membrane and is usually a singular circularly arranged chromosome. (Some bacteria, such as *Vibrio cholerae,* have two chromosomes, and some bacteria have a linearly arranged chromosome.)
2. Their DNA is not associated with histones (special chromosomal proteins found in eukaryotes); other proteins are associated with the DNA.
3. They lack membrane-enclosed organelles.
4. Their cell walls almost always contain the complex polysaccharide peptidoglycan.
5. They usually divide by **binary fission.** During this process, the DNA is copied, and the cell splits into two cells. Binary fission involves fewer structures and processes than eukaryotic cell division.

**Eukaryotes** (from the Greek words meaning true nucleus) have the following distinguishing characteristics:

1. Their DNA is found in the cell's nucleus, which is separated from the cytoplasm by a nuclear membrane, and the DNA is found in multiple chromosomes.
2. Their DNA is consistently associated with chromosomal proteins called histones and with nonhistones.
3. They have a number of membrane-enclosed organelles, including mitochondria, endoplasmic reticulum, Golgi complex, lysosomes, and sometimes chloroplasts.
4. Their cell walls, when present, are chemically simple.
5. Cell division usually involves mitosis, in which chromosomes replicate and an identical set is distributed into each of two nuclei. This process is guided by the mitotic spindle, a football-shaped assembly of microtubules. Division of the cytoplasm and other organelles follows so that the two cells produced are identical to each other.

Additional differences between prokaryotic and eukaryotic cells are listed in Table 4.2, page 100. Next we describe, in detail, the parts of the prokaryotic cell.

### CHECK YOUR UNDERSTANDING

✓ What is the main feature that distinguishes prokaryotes from eukaryotes? **4-1**

## The Prokaryotic Cell

The members of the prokaryotic world make up a vast heterogeneous group of very small unicellular organisms. Prokaryotes include bacteria and archaea. The majority of prokaryotes, including the photosynthesizing cyanobacteria, are bacteria. Although bacteria and archaea look similar, their chemical composition is different, as will be described later. The thousands of species of bacteria are differentiated by many factors, including morphology (shape), chemical composition (often detected by staining reactions), nutritional requirements, biochemical activities, and sources of energy (sunlight or chemicals). It is estimated that 99% of the bacteria in nature exist in biofilms (see pages 56 and 160).

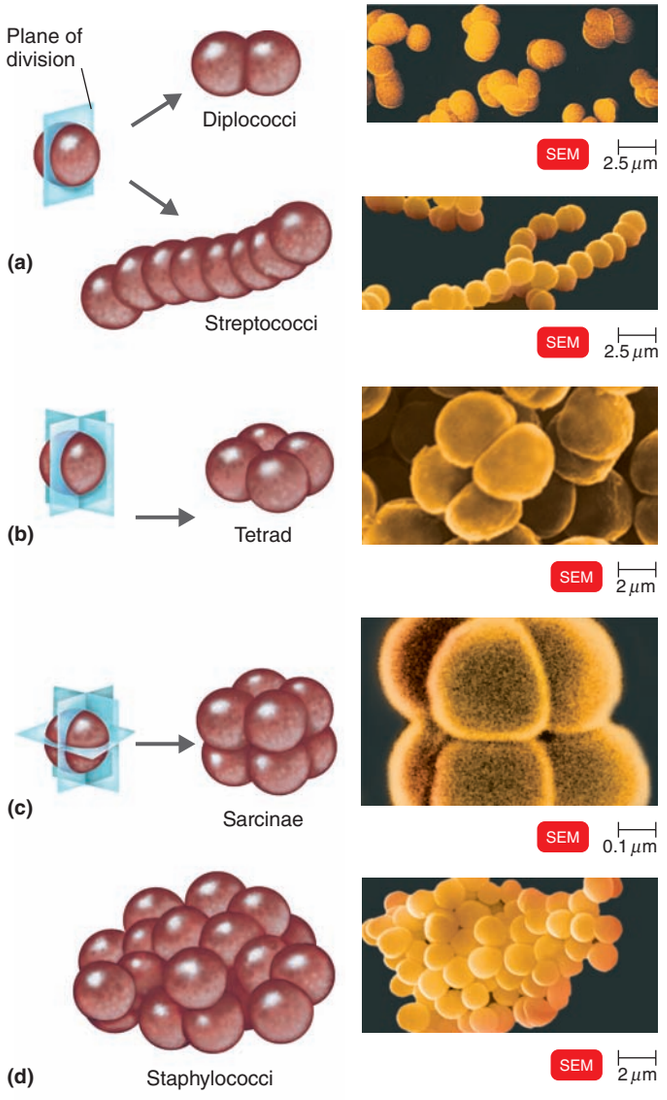



**Figure 4.1 Arrangements of cocci.** (**a**) Division in one plane produces diplococci and streptococci. (**b**) Division in two planes produces tetrads. (**c**) Division in three planes produces sarcinae, and (**d**) division in multiple planes produces staphylococci.

Q How do the planes of division determine the arrangement of cells?

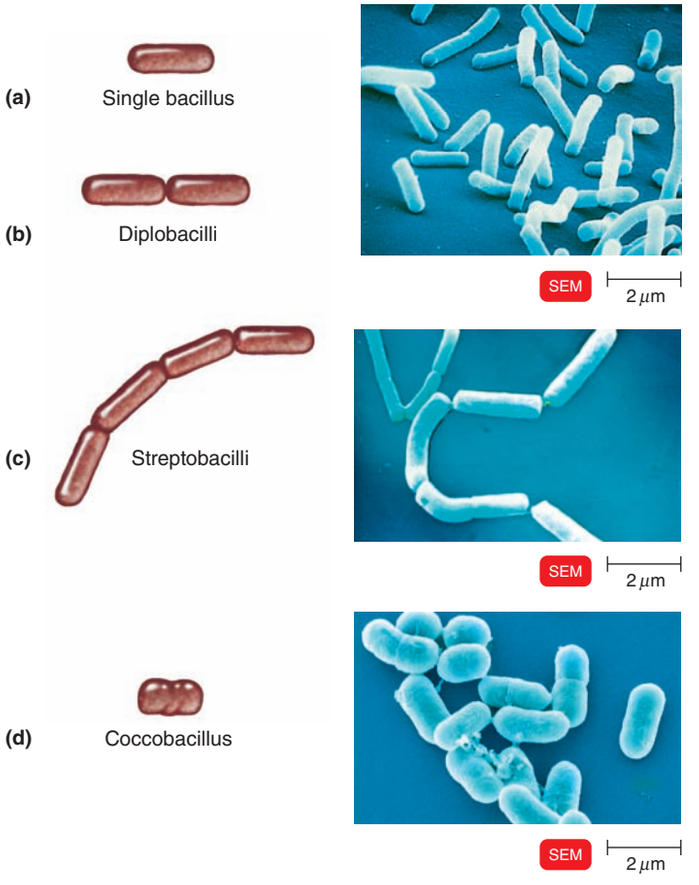



**Figure 4.2 Bacilli.** (**a**) Single bacilli. (**b**) Diplobacilli. In the top micrograph, a few joined pairs of bacilli could serve as examples of diplobacilli. (**c**) Streptobacilli. (**d**) Coccobacilli.

Q Why don't bacilli form tetrads or clusters?

# The Size, Shape, and Arrangement of Bacterial Cells

## LEARNING OBJECTIVE

**4-2** Identify the three basic shapes of bacteria.

Bacteria come in a great many sizes and several shapes. Most bacteria range from 0.2 to 2.0 μm in diameter and from 2 to 8 μm in length. They have a few basic shapes: spherical **coccus** (plural: **cocci,** meaning berries), rod-shaped **bacillus** (plural: **bacilli,** meaning little staffs), and **spiral.**

Cocci are usually round but can be oval, elongated, or flattened on one side. When cocci divide to reproduce, the cells can remain attached to one another. Cocci that remain in pairs after dividing are called **diplococci;** those that divide and remain attached in chainlike patterns are called **streptococci** (Figure 4.1a). Those that divide in two planes and remain in groups of four are known as **tetrads** (Figure 4.1b). Those that divide in three planes and remain attached in cubelike groups of eight are called **sarcinae** (Figure 4.1c). Those that divide in multiple planes and form grapelike clusters or broad sheets are called **staphylococci** (Figure 4.1d). These group characteristics are frequently helpful in identifying certain cocci.

Bacilli divide only across their short axis, so there are fewer groupings of bacilli than of cocci. Most bacilli appear as single rods, called **single bacilli.** (Figure 4.2a). **Diplobacilli** appear in pairs after division (Figure 4.2b), and **streptobacilli** occur in chains (Figure 4.2c). Some bacilli look like straws. Others have tapered ends, like cigars. Still others are oval and look so much like cocci that they are called **coccobacilli** (Figure 4.2d).

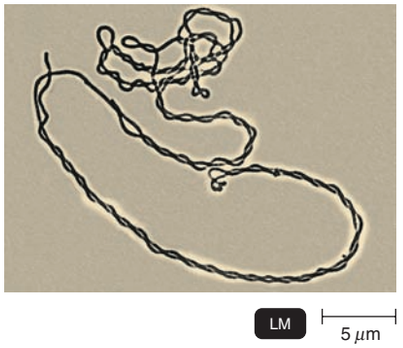



**Figure 4.3** **A double-stranded helix formed by *Bacillus subtilis*.**

Q What is the difference between the term bacillus and *Bacillus*?

"Bacillus" has two meanings in microbiology. As we have just used it, bacillus refers to a bacterial shape. When capitalized and italicized, it refers to a specific genus. For example, the bacterium *Bacillus anthracis* is the causative agent of anthrax. Bacillus cells often form long, twisted chains of cells (Figure 4.3).

Spiral bacteria have one or more twists; they are never straight. Bacteria that look like curved rods are called **vibrios** (Figure 4.4a). Others, called **spirilla,** have a helical shape, like a corkscrew, and fairly rigid bodies (Figure 4.4b). Yet another group of spirals are helical and flexible; they are called **spirochetes** (Figure 4.4c). Unlike the spirilla, which use propeller-like external appendages called flagella to move, spirochetes move by means of axial filaments, which resemble flagella but are contained within a flexible external sheath.

In addition to the three basic shapes, there are star-shaped cells (genus *Stella;* Figure 4.5a); rectangular, flat cells (halophilic archaea) of the genus *Haloarcula* (Figure 4.5b); and triangular cells.

The shape of a bacterium is determined by heredity. Genetically, most bacteria are **monomorphic;** that is, they maintain a single shape. However, a number of environmental conditions can alter that shape. If the shape is altered, identification becomes difficult. Moreover, some bacteria, such as *Rhizobium* (rī-zō′bē-um) and *Corynebacterium* (kō-rī-nē-bak-ti′rē-um), are genetically **pleomorphic,** which means they can have many shapes, not just one.

The structure of a typical prokaryotic cell is shown in Figure 4.6. We will discuss its components according to the following organization: (1) structures external to the cell wall, (2) the cell wall itself, and (3) structures internal to the cell wall.

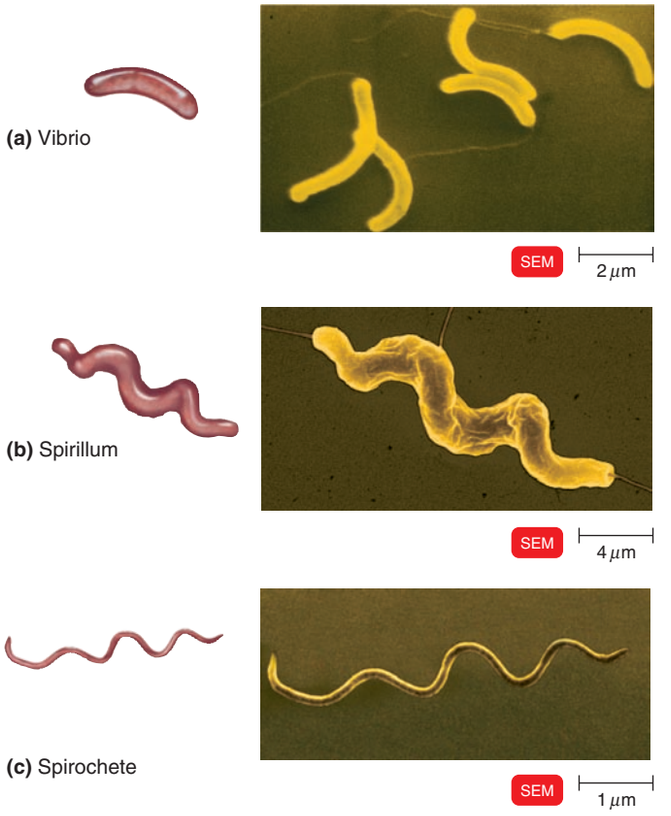



**Figure 4.4** **Spiral bacteria.** (**a**) Vibrios. (**b**) Spirillum. (**c**) Spirochete.

Q What is the distinguishing feature of spirochete bacteria?

### CHECK YOUR UNDERSTANDING

✓ How would you be able to identify streptococci through a microscope? 4-2

## Structures External to the Cell Wall

### LEARNING OBJECTIVES

**4-3** Describe the structure and function of the glycocalyx

**4-4** Differentiate flagella, axial filaments, fimbriae, and pili.

Among the possible structures external to the prokaryotic cell wall are the glycocalyx, flagella, axial filaments, fimbriae, and pili.

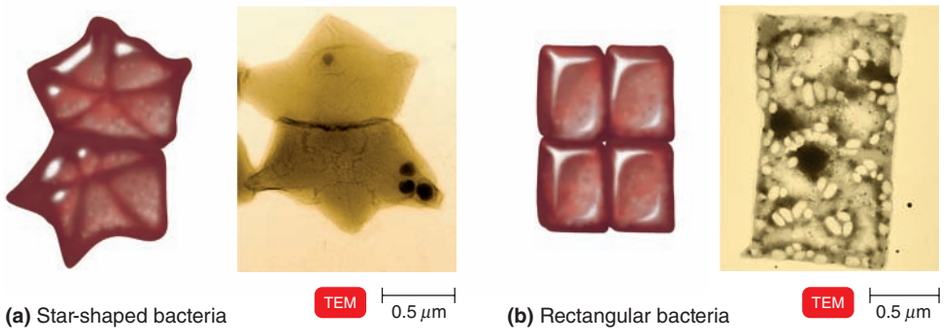


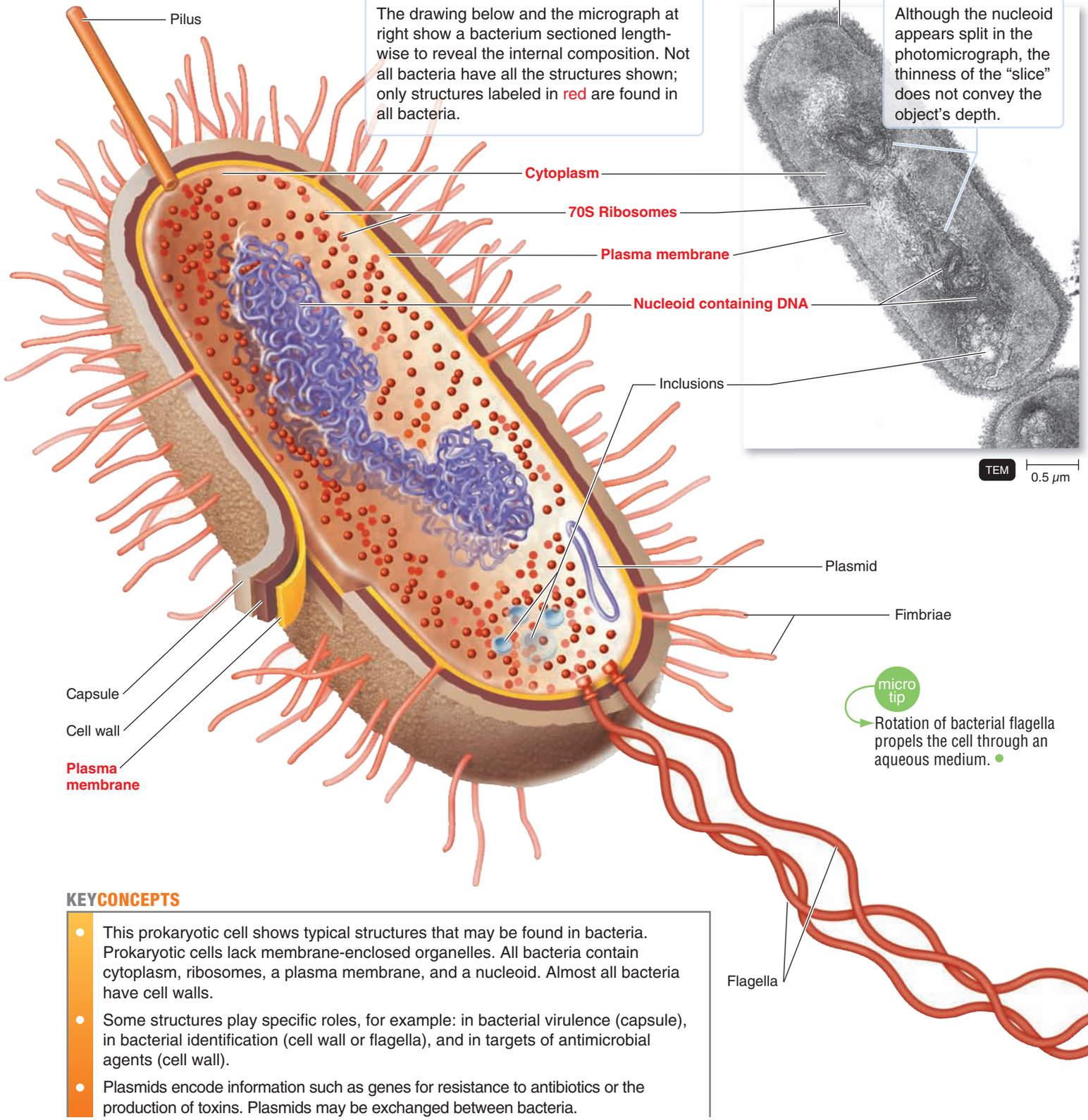

**Figure 4.5** **Star-shaped and rectangular prokaryotes.** (**a**) *Stella* (star-shaped). (**b**) *Haloarcula,* a genus of halophilic archaea (rectangular cells).

Q What are the common bacterial shapes?

FOUNDATION FIGURE **4.6**

# The Structure of a Prokaryotic Cell

The drawing below and the micrograph at right show a bacterium sectioned lengthwise to reveal the internal composition. Not all bacteria have all the structures shown; only structures labeled in red are found in all bacteria.







Although the nucleoid appears split in the photomicrograph, the thinness of the "slice" does not convey the object's depth.

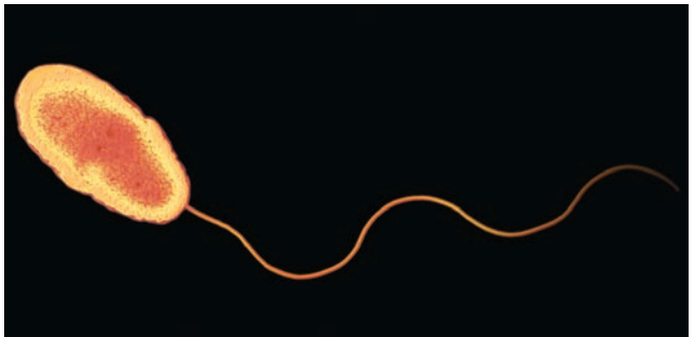
micro tip

Rotation of bacterial flagella propels the cell through an aqueous medium.

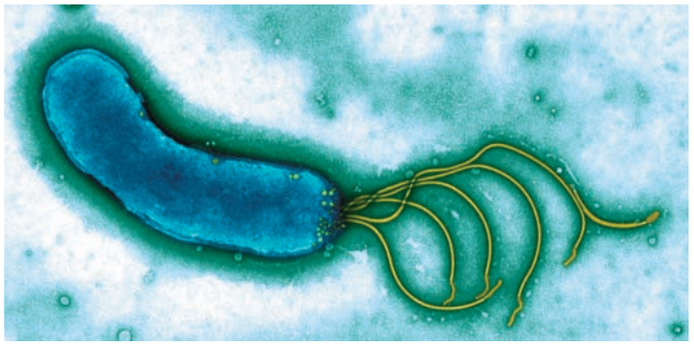
## KEY CONCEPTS

- This prokaryotic cell shows typical structures that may be found in bacteria. Prokaryotic cells lack membrane-enclosed organelles. All bacteria contain cytoplasm, ribosomes, a plasma membrane, and a nucleoid. Almost all bacteria have cell walls.
- Some structures play specific roles, for example: in bacterial virulence (capsule), in bacterial identification (cell wall or flagella), and in targets of antimicrobial agents (cell wall).
- Plasmids encode information such as genes for resistance to antibiotics or the production of toxins. Plasmids may be exchanged between bacteria.

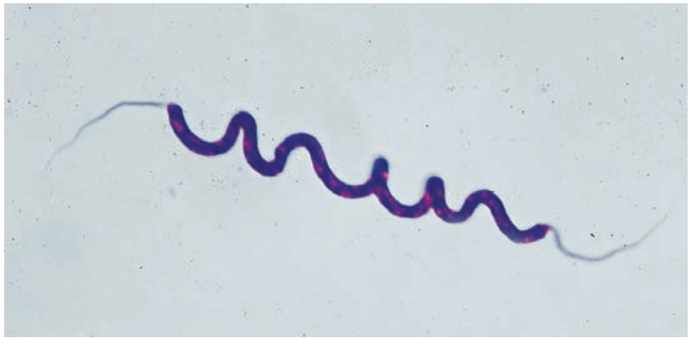

**(a)** Peritrichous




**(b)** Monotrichous and polar




**(c)** Lophotrichous and polar




**(d)** Amphitrichous and polar

**Figure 4.7 Arrangements of bacterial flagella.** (**a**) Peritrichous. (**b**)–(**d**) Polar.

Not all prokaryotic cells have flagella. What are bacteria without flagella called?

## Glycocalyx

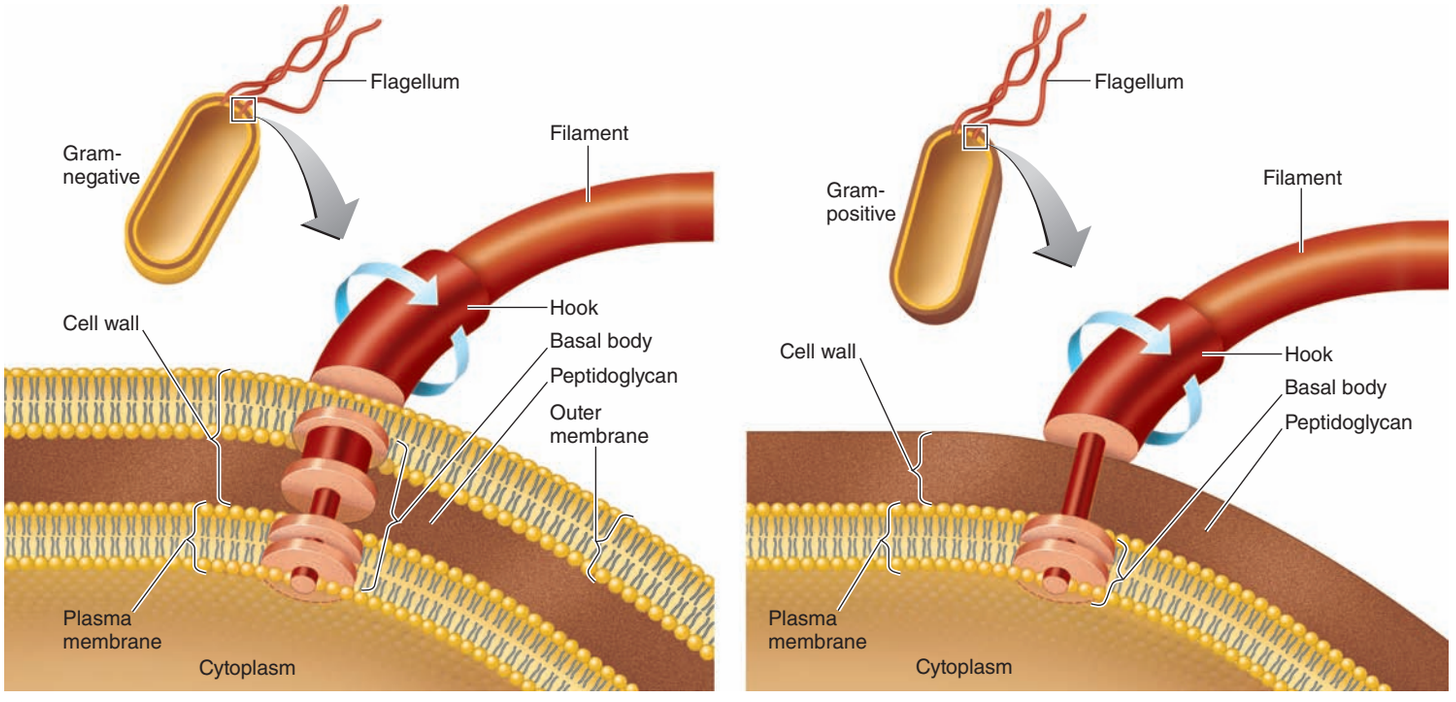
Many prokaryotes secrete on their surface a substance called glycocalyx. **Glycocalyx** (meaning sugar coat) is the general term used for substances that surround cells. The bacterial glycocalyx is a viscous (sticky), gelatinous polymer that is external to the cell wall and composed of polysaccharide, polypeptide, or both. Its chemical composition varies widely with the species. For the most part, it is made inside the cell and secreted to the cell surface. If the substance is organized and is firmly attached to the cell wall, the glycocalyx is described as a **capsule.** The presence of a capsule can be determined by using negative staining, described in Chapter 3 (see Figure 3.14a, page 70). If the substance is unorganized and only loosely attached to the cell wall, the glycocalyx is described as a **slime layer.**

In certain species, capsules are important in contributing to bacterial virulence (the degree to which a pathogen causes disease). Capsules often protect pathogenic bacteria from phagocytosis by the cells of the host. (As you will see later, phagocytosis is the ingestion and digestion of microorganisms and other solid particles.) For example, *Bacillus anthracis* produces a capsule of D-glutamic acid. (Recall from Chapter 2 that the D forms of amino acids are unusual.) Because only encapsulated *B. anthracis* causes anthrax, it is speculated that the capsule may prevent its being destroyed by phagocytosis.

Another example involves *Streptococcus pneumoniae* (streptō-kok′kus nü-mō′nē-ī), which causes pneumonia only when the cells are protected by a polysaccharide capsule. Unencapsulated *S. pneumoniae* cells cannot cause pneumonia and are readily phagocytized. The polysaccharide capsule of *Klebsiella* (kleb-sē-el′lä) also prevents phagocytosis and allows the bacterium to adhere to and colonize the respiratory tract.

The glycocalyx is a very important component of biofilms (see page 160). A glycocalyx that helps cells in a biofilm attach to their target environment and to each other is called an **extracellular polymeric substance (EPS).** The EPS protects the cells within it, facilitates communication among them, and enables the cells to survive by attaching to various surfaces in their natural environment.

Through attachment, bacteria can grow on diverse surfaces such as rocks in fast-moving streams, plant roots, human teeth, medical implants, water pipes, and even other bacteria. *Streptococcus mutans* (mū′tans), an important cause of dental caries, attaches itself to the surface of teeth by a glycocalyx. *S. mutans* may use its capsule as a source of nutrition by breaking it down and utilizing the sugars when energy stores are low. *Vibrio cholerae* (vib′-rē-o kol′-er-ī), the cause of cholera, produces a glycocalyx that helps it attach to the cells of the small intestine. A glycocalyx also can protect a cell against dehydration, and its viscosity may inhibit the movement of nutrients out of the cell.




**(a)** Parts and attachment of a flagellum of a gram-negative bacterium

**(b)** Parts and attachment of a flagellum of a gram-positive bacterium

**Figure 4.8 The structure of a prokaryotic flagellum.** The parts and attachment of a flagellum of a gram-negative bacterium and gram-positive bacterium are shown in these highly schematic diagrams.

Q How do the basal bodies of gram-negative and gram-positive bacteria differ?

## Flagella

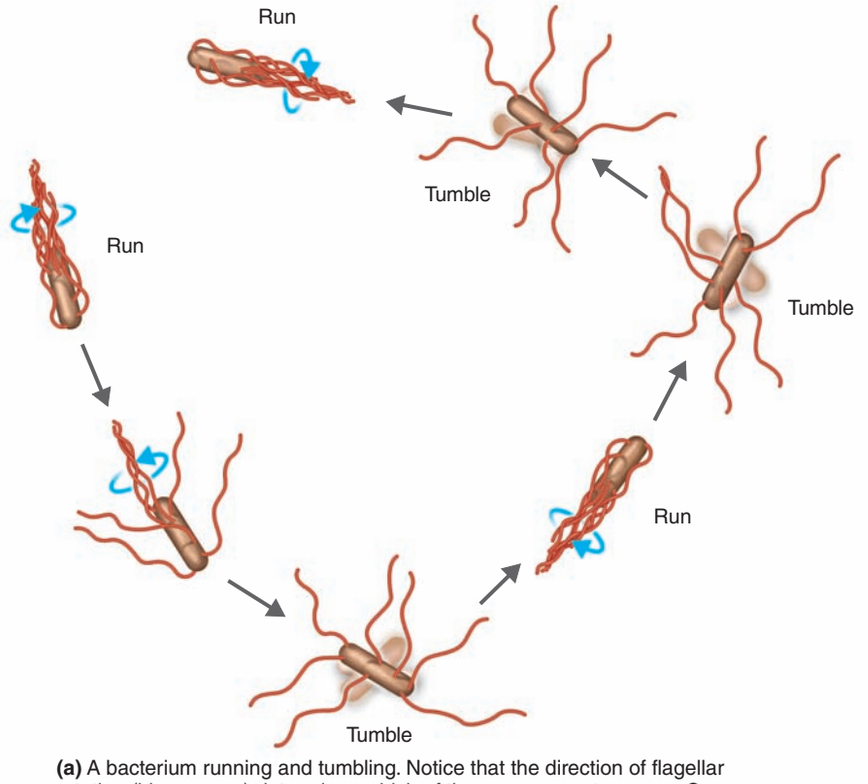
Some prokaryotic cells have **flagella** (singular: **flagellum**), which are long filamentous appendages that propel bacteria. Bacteria that lack flagella are referred to as **atrichous** (without projections). Flagella may be **peritrichous** (distributed over the entire cell; Figure 4.7a) or **polar** (at one or both poles or ends of the cell). If polar, flagella may be **monotrichous** (a single flagellum at one pole; Figure 4.7b), **lophotrichous** (a tuft of flagella coming from one pole; Figure 4.7c), or **amphitrichous** (flagella at both poles of the cell; Figure 4.7d).

A flagellum has three basic parts (Figure 4.8). The long outermost region, the *filament,* is constant in diameter and contains the globular (roughly spherical) protein *flagellin* arranged in several chains that intertwine and form a helix around a hollow core. In most bacteria, filaments are not covered by a membrane or sheath, as in eukaryotic cells. The filament is attached to a slightly wider *hook,* consisting of a different protein. The third portion of a flagellum is the *basal body,* which anchors the flagellum to the cell wall and plasma membrane.

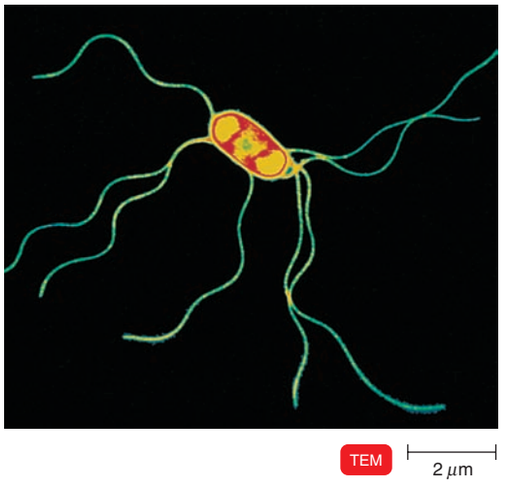
The basal body is composed of a small central rod inserted into a series of rings. Gram-negative bacteria contain two pairs of rings; the outer pair of rings is anchored to various portions of the cell wall, and the inner pair of rings is anchored to the plasma membrane. In gram-positive bacteria, only the inner pair is present. As you will see later, the flagella (and cilia) of eukaryotic cells are more complex than those of prokaryotic cells.

Each prokaryotic flagellum is a semirigid, helical structure that moves the cell by rotating from the basal body. The rotation of a flagellum is either clockwise or counterclockwise around its long axis. (Eukaryotic flagella, by contrast, undulate in a wavelike motion.) The movement of a prokaryotic flagellum results from rotation of its basal body and is similar to the movement of the shaft of an electric motor. As the flagella rotate, they form a bundle that pushes against the surrounding liquid and propels the bacterium. Flagellar rotation depends on the cell's continuous generation of energy.

Bacterial cells can alter the speed and direction of rotation of flagella and thus are capable of various patterns of **motility,** the ability of an organism to move by itself. When a bacterium moves in one direction for a length of time, the movement is called a "run" or "swim." "Runs" are interrupted by periodic, abrupt, random changes in direction called "tumbles." Then, a "run" resumes. "Tumbles" are caused by a reversal of flagellar rotation (Figure 4.9a). Some species of bacteria endowed with many flagella—*Proteus* (prō′tē-us), for example (Figure 4.9b)—can "swarm," or show rapid wavelike movement across a solid culture medium.




**(a)** A bacterium running and tumbling. Notice that the direction of flagellar rotation (blue arrows) determines which of these movements occurs. Gray arrows indicate direction of movement of the microbe.




**(b)** A *Proteus* cell in the swarming stage may have more than 1000 peritrichous flagella.

**Figure 4.9 Flagella and bacterial motility.**

Do bacterial flagella push or pull a cell?

One advantage of motility is that it enables a bacterium to move toward a favorable environment or away from an adverse one. The movement of a bacterium toward or away from a particular stimulus is called **taxis.** Such stimuli include chemicals (**chemotaxis**) and light (**phototaxis**). Motile bacteria contain receptors in various locations, such as in or just under the cell wall. These receptors pick up chemical stimuli, such as oxygen, ribose, and galactose. In response to the stimuli, information is passed to the flagella. If the chemotactic signal is positive, called an *attractant,* the bacteria move toward the stimulus with many runs and few tumbles. If the chemotactic signal is negative, called a *repellent,* the frequency of tumbles increases as the bacteria move away from the stimulus.

The flagellar protein called **H antigen** is useful for distinguishing among **serovars,** or variations within a species, of gram-negative bacteria (see page 310). For example, there are at least 50 different H antigens for *E. coli.* Those serovars identified as *E. coli* O157:H7 are associated with foodborne epidemics (see Chapter 1, page 19). **Animations** Motility; Flagella: Structure, Movement, Arrangement

## Axial Filaments

Spirochetes are a group of bacteria that have unique structure and motility. One of the best-known spirochetes is *Treponema pallidum* (tre-pō-nē′mä pal′li-dum), the causative agent of syphilis. Another spirochete is *Borrelia burgdorferi* (bôr′-rel-ē-a burg-dor′fer-ē), the causative agent of Lyme disease. Spirochetes move by means of **axial filaments,** or **endoflagella,** bundles of fibrils that arise at the ends of the cell beneath an outer sheath and spiral around the cell (**Figure 4.10**).

Axial filaments, which are anchored at one end of the spirochete, have a structure similar to that of flagella. The rotation of the filaments produces a movement of the outer sheath that propels the spirochetes in a spiral motion. This type of movement is similar to the way a corkscrew moves through a cork. This corkscrew motion probably enables a bacterium such as *T. pallidum* to move effectively through body fluids. **Animation** Spirochetes

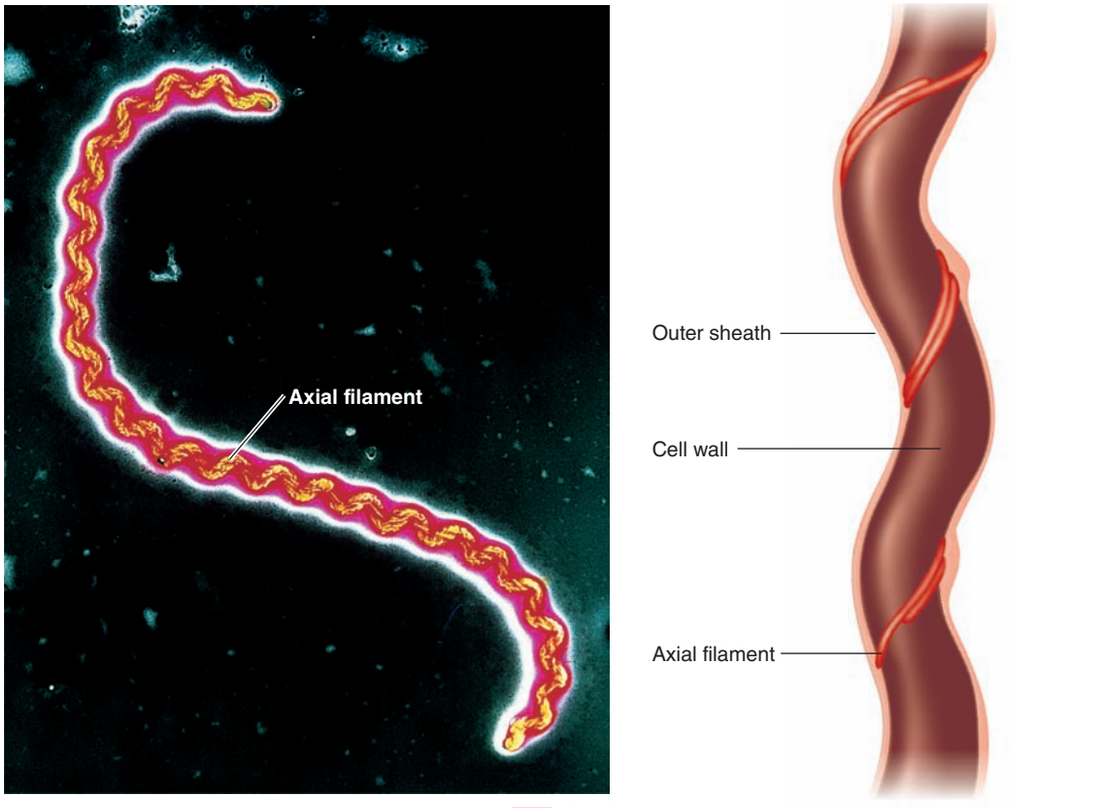
## Fimbriae and Pili

Many gram-negative bacteria contain hairlike appendages that are shorter, straighter, and thinner than flagella and are used for attachment and transfer of DNA rather than for motility. These structures, which consist of a protein called *pilin* arranged helically around a central core, are divided into two types, fimbriae and pili, having very different functions. (Some microbiologists use the two terms interchangeably to refer to all such structures, but we distinguish between them.)

**Fimbriae** (singular: **fimbria**) can occur at the poles of the bacterial cell or can be evenly distributed over the entire surface of the cell. They can number anywhere from a few to several

**Figure 4.10** **Axial filaments.**

Q How are endoflagella different from flagella?




**(a)** A photomicrograph of the spirochete *Leptospira,* showing an axial filament

**(b)** A diagram of axial filaments wrapping around part of a spirochete (see Figure 11.26a for a cross section of axial filaments)

hundred per cell (**Figure 4.11**). Fimbriae have a tendency to adhere to each other and to surfaces. As a result, they are involved in forming biofilms and other aggregations on the surfaces of liquids, glass, and rocks. Fimbriae can also help bacteria adhere to epithelial surfaces in the body. For example, fimbriae on the bacterium *Neisseria gonorrhoeae* (nī-se′rē-ä go-nôr-rē′ī), the causative agent of gonorrhea, help the microbe colonize mucous membranes. Once colonization occurs, the bacteria can cause disease. The fimbriae of *E. coli* O157 enable this bacterium to adhere to the lining of the small intestine, where it causes a severe watery diarrhea. When fimbriae are absent (because of genetic mutation), colonization cannot happen, and no disease ensues.

**Pili** (singular: **pilus**) are usually longer than fimbriae and number only one or two per cell. Pili are involved in motility and DNA transfer. In one type of motility, called **twitching motility,** a pilus extends by the addition of subunits of pilin, makes contact with a surface or another cell, and then retracts (powerstroke) as the pilin subunits are disassembled. This is called the *grappling hook model* of twitching motility and results in short, jerky, intermittent movements. Twitching motility has been observed in *Pseudomonas aeruginosa*, *Neisseria gonorrhoeae*, and some strains of *E. coli.* The other type of motility associated with pili is **gliding motility,** the smooth gliding movement of myxobacteria. Although the exact mechanism is unknown for most myxobacteria, some utilize pilus retraction. Gliding motility provides a means for microbes to travel in environments with a low water content, such as biofilms and soil.


**Figure 4.11** **Fimbriae.** The fimbriae seem to bristle from this *E. coli* cell, which is beginning to divide.

Q Why are fimbriae necessary for colonization?

Some pili are used to bring bacteria together allowing the transfer of DNA from one cell to another, a process called conjugation. Such pili are called **conjugation (sex) pili** (see page 234). In this process, the conjugation pilus of one bacterium called an $F^+$ cell connects to receptors on the surface of another bacterium of its own species or a different species. The two cells make physical contact, and DNA from the $F^+$ cell is transferred to the other cell. The exchanged DNA can add a new function to the recipient cell, such as antibiotic resistance or the ability to digest its medium more efficiently.

### CHECK YOUR UNDERSTANDING

- Why are bacterial capsules medically important? **4-3**
- How do bacteria move? **4-4**

# The Cell Wall

### LEARNING OBJECTIVES

**4-5** Compare and contrast the cell walls of gram-positive bacteria, gram-negative bacteria, acid-fast bacteria, archaea, and mycoplasmas.

**4-6** Compare and contrast archaea and mycoplasmas.

**4-7** Differentiate *protoplast, spheroplast,* and *L form.*

The **cell wall** of the bacterial cell is a complex, semirigid structure responsible for the shape of the cell. The cell wall surrounds the underlying, fragile plasma (cytoplasmic) membrane and protects it and the interior of the cell from adverse changes in the outside environment (see Figure 4.6). Almost all prokaryotes have cell walls.

The major function of the cell wall is to prevent bacterial cells from rupturing when the water pressure inside the cell is greater than that outside the cell (see Figure 4.18d, page 92). It also helps maintain the shape of a bacterium and serves as a point of anchorage for flagella. As the volume of a bacterial cell increases, its plasma membrane and cell wall extend as needed. Clinically, the cell wall is important because it contributes to the ability of some species to cause disease and is the site of action of some antibiotics. In addition, the chemical composition of the cell wall is used to differentiate major types of bacteria.

Although the cells of some eukaryotes, including plants, algae, and fungi, have cell walls, their walls differ chemically from those of prokaryotes, are simpler in structure, and are less rigid.

## Composition and Characteristics

The bacterial cell wall is composed of a macromolecular network called **peptidoglycan** (also known as *murein*), which is present either alone or in combination with other substances. Peptidoglycan consists of a repeating disaccharide attached by polypeptides to form a lattice that surrounds and protects the entire cell. The disaccharide portion is made up of monosaccharides called N-acetylglucosamine (NAG) and N-acetylmuramic acid (NAM) (from *murus,* meaning wall), which are related to glucose. The structural formulas for NAG and NAM are shown in **Figure 4.12**.

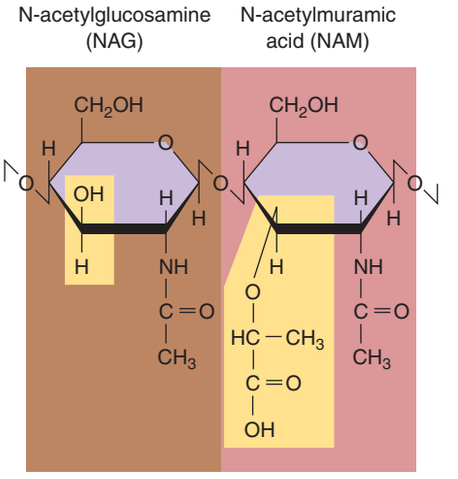



**Figure 4.12 N-acetylglucosamine (NAG) and N-acetylmuramic acid (NAM) joined as in a peptidoglycan.** The gold areas show the differences between the two molecules. The linkage between them is called a β-1,4 linkage.

Q What kind of molecules are these: carbohydrates, lipids, or proteins?

The various components of peptidoglycan are assembled in the cell wall (**Figure 4.13a**). Alternating NAM and NAG molecules are linked in rows of 10 to 65 sugars to form a carbohydrate "backbone" (the glycan portion of peptidoglycan). Adjacent rows are linked by **polypeptides** (the peptide portion of peptidoglycan). Although the structure of the polypeptide link varies, it always includes *tetrapeptide side chains,* which consist of four amino acids attached to NAMs in the backbone. The amino acids occur in an alternating pattern of D and L forms (see Figure 2.13, page 43). This is unique because the amino acids found in other proteins are L forms. Parallel tetrapeptide side chains may be directly bonded to each other or linked by a *peptide cross-bridge,* consisting of a short chain of amino acids.

Penicillin interferes with the final linking of the peptidoglycan rows by peptide cross-bridges (see Figure 4.13a). As a result, the cell wall is greatly weakened and the cell undergoes **lysis,** destruction caused by rupture of the plasma membrane and the loss of cytoplasm.

### Gram-Positive Cell Walls

In most gram-positive bacteria, the cell wall consists of many layers of peptidoglycan, forming a thick, rigid structure (**Figure 4.13b**). By contrast, gram-negative cell walls contain only a thin layer of peptidoglycan (**Figure 4.13c**).

In addition, the cell walls of gram-positive bacteria contain *teichoic acids,* which consist primarily of an alcohol (such as glycerol or ribitol) and phosphate. There are two classes of teichoic acids: *lipoteichoic acid,* which spans the peptidoglycan layer and is linked

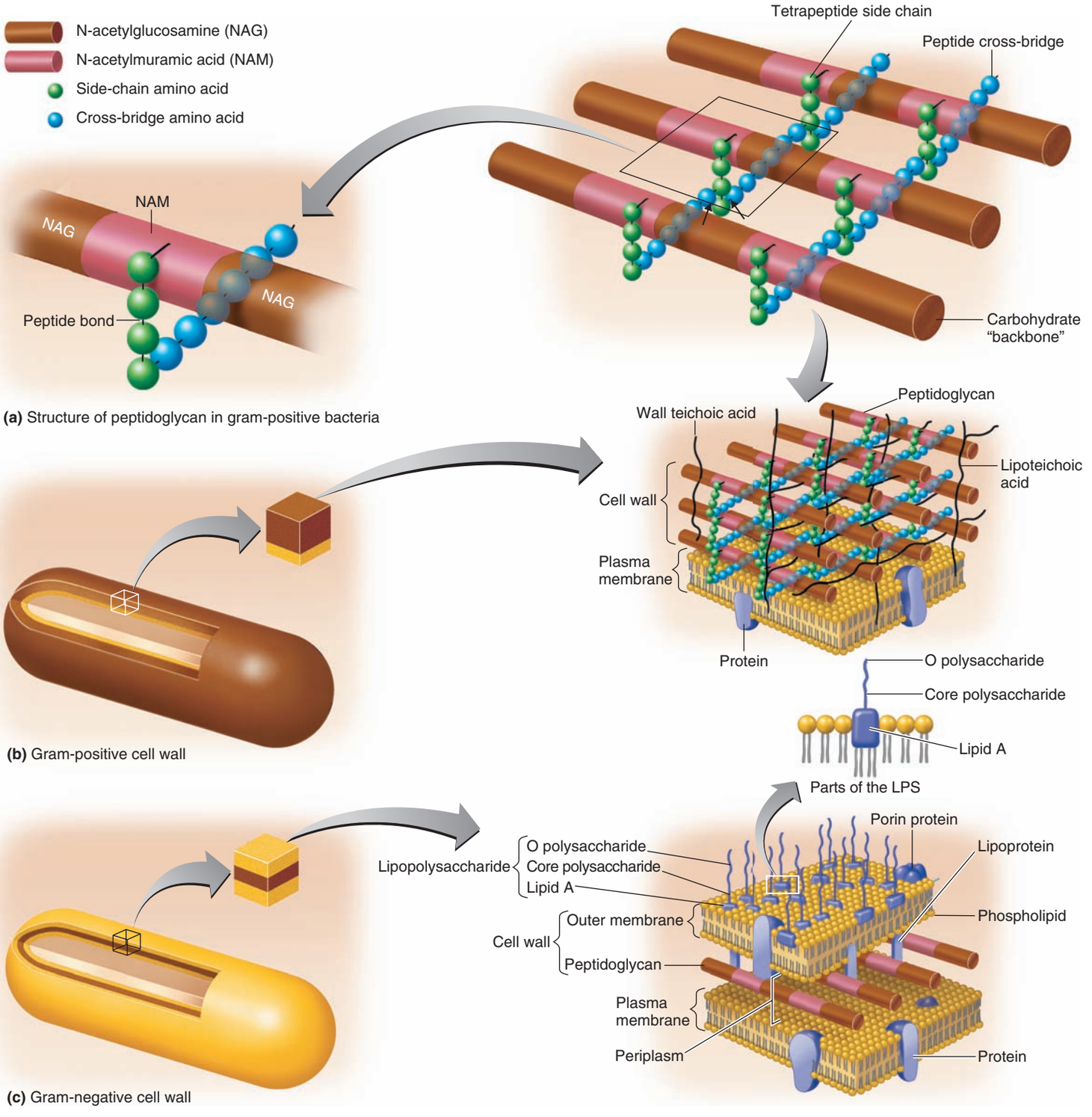



**Figure 4.13** **Bacterial cell walls.** (**a**) The structure of peptidoglycan in gram-positive bacteria. Together the carbohydrate backbone (glycan portion) and tetrapeptide side chains (peptide portion) make up peptidoglycan. The frequency of peptide cross-bridges and the number of amino acids in these bridges vary with species of bacteria. The small arrows indicate where penicillin interferes with the linkage of peptidoglycan rows by peptide cross-bridges. (**b**) A gram-positive cell wall. (**c**) A gram-negative cell wall.

Q What are the major structural differences between gram-positive and gram-negative cell walls?

to the plasma membrane, and *wall teichoic acid,* which is linked to the peptidoglycan layer. Because of their negative charge (from the phosphate groups), teichoic acids may bind and regulate the movement of cations (positive ions) into and out of the cell. They may also assume a role in cell growth, preventing extensive wall breakdown and possible cell lysis. Finally, teichoic acids provide much of the wall's antigenic specificity and thus make it possible to identify gram-positive bacteria by certain laboratory tests (see Chapter 10). Similarly, the cell walls of gram-positive streptococci are covered with various polysaccharides that allow them to be grouped into medically significant types.

### Gram-Negative Cell Walls

The cell walls of gram-negative bacteria consist of one or a very few layers of peptidoglycan and an outer membrane (see Figure 4.13c). The peptidoglycan is bonded to lipoproteins (lipids covalently linked to proteins) in the outer membrane and is in the *periplasm,* a gel-like fluid between the outer membrane and the plasma membrane. The periplasm contains a high concentration of degradative enzymes and transport proteins. Gram-negative cell walls do not contain teichoic acids. Because the cell walls of gram-negative bacteria contain only a small amount of peptidoglycan, they are more susceptible to mechanical breakage.

The *outer membrane* of the gram-negative cell consists of lipopolysaccharides (LPS), lipoproteins, and phospholipids (see Figure 4.13c). The outer membrane has several specialized functions. Its strong negative charge is an important factor in evading phagocytosis and the actions of complement (lyses cells and promotes phagocytosis), two components of the defenses of the host (discussed in detail in Chapter 16). The outer membrane also provides a barrier to certain antibiotics (for example, penicillin), digestive enzymes such as lysozyme, detergents, heavy metals, bile salts, and certain dyes.

However, the outer membrane does not provide a barrier to all substances in the environment because nutrients must pass through to sustain the metabolism of the cell. Part of the permeability of the outer membrane is due to proteins in the membrane, called **porins,** that form channels. Porins permit the passage of molecules such as nucleotides, disaccharides, peptides, amino acids, vitamin $B_{12}$, and iron.

The **lipopolysaccharide (LPS)** of the outer membrane is a large complex molecule that contains lipids and carbohydrates and consists of three components: (1) lipid A, (2) a core polysaccharide, and (3) an O polysaccharide. **Lipid A** is the lipid portion of the LPS and is embedded in the top layer of the outer membrane. When gram-negative bacteria die, they release lipid A, which functions as an endotoxin (Chapter 15). Lipid A is responsible for the symptoms associated with infections by gram-negative bacteria such as fever, dilation of blood vessels, shock, and blood clotting. The **core polysaccharide** is attached to lipid A and contains unusual sugars. Its role is structural—to provide stability. The **O polysaccharide** extends outward from the core polysaccharide and is composed of sugar molecules. The O polysaccharide functions as an antigen and is useful for distinguishing species of gram-negative bacteria. For example, the foodborne pathogen *E. coli* O157:H7 is distinguished from other serovars by certain laboratory tests that test for these specific antigens. This role is comparable to that of teichoic acids in gram-positive cells.

#### Clinical Case

Irene reviews what she knows about gram-negative *K. pneumoniae* bacteria. Although this bacterium is part of normal intestinal microbiota, outside its typical environment it can cause serious infection. *K. pneumoniae* accounts for about 8% of all health care–associated infections. Irene surmises that the bacteria had to come from the hospital somewhere.

**What is causing the patients' fever and low blood pressure?**

76 **86** 88 95 97

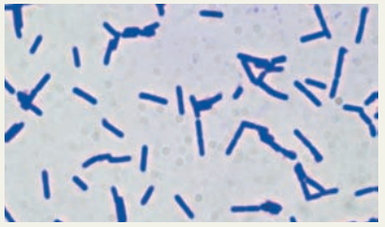
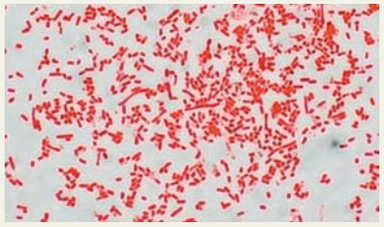
## Cell Walls and the Gram Stain Mechanism

Now that you have studied the Gram stain (in Chapter 3, page 68) and the chemistry of the bacterial cell wall (in the previous section), it is easier to understand the mechanism of the Gram stain. The mechanism is based on differences in the structure of the cell walls of gram-positive and gram-negative bacteria and how each reacts to the various reagents (substances used for producing a chemical reaction). Crystal violet, the primary stain, stains both gram-positive and gram-negative cells purple because the dye enters the cytoplasm of both types of cells. When iodine (the mordant) is applied, it forms large crystals with the dye that are too large to escape through the cell wall. The application of alcohol dehydrates the peptidoglycan of gram-positive cells to make it more impermeable to the crystal violet-iodine. The effect on gram-negative cells is quite different; alcohol dissolves the outer membrane of gram-negative cells and even leaves small holes in the thin peptidoglycan layer through which crystal violet-iodine diffuse. Because gram-negative bacteria are colorless after the alcohol wash, the addition of safranin (the counterstain) turns the cells pink or red. Safranin provides a contrasting color to the primary stain (crystal violet). Although gram-positive and gram-negative cells both absorb safranin, the pink or red color of safranin is masked by the darker purple dye previously absorbed by gram-positive cells.

In any population of cells, some gram-positive cells will give a gram-negative response. These cells are usually dead. However, there are a few gram-positive genera that show an increasing number of gram-negative cells as the culture ages. *Bacillus* and *Clostridium* are examples and are often described as *gram-variable.*

A comparison of some of the characteristics of gram-positive and gram-negative bacteria is presented in **Table 4.1**.

**TABLE 4.1 Some Comparative Characteristics of Gram-Positive and Gram-Negative Bacteria**

| Characteristic | Gram-Positive | Gram-Negative |
|---|---|---|
| |  LM 6 μm |  LM 15 μm |
| **Gram Reaction** | Retain crystal violet dye and stain blue or purple | Can be decolorized to accept counterstain (safranin) and stain pink or red |
| **Peptidoglycan Layer** | Thick (multilayered) | Thin (single-layered) |
| **Teichoic Acids** | Present in many | Absent |
| **Periplasmic Space** | Absent | Present |
| **Outer Membrane** | Absent | Present |
| **Lipopolysaccharide (LPS) Content** | Virtually none | High |
| **Lipid and Lipoprotein Content** | Low (acid-fast bacteria have lipids linked to peptidoglycan) | High (because of presence of outer membrane) |
| **Flagellar Structure** | 2 rings in basal body | 4 rings in basal body |
| **Toxins Produced** | Exotoxins | Endotoxins and exotoxins |
| **Resistance to Physical Disruption** | High | Low |
| **Cell Wall Disruption by Lysozyme** | High | Low (requires pretreatment to destabilize outer membrane) |
| **Susceptibility to Penicillin and Sulfonamide** | High | Low |
| **Susceptibility to Streptomycin, Chloramphenicol, and Tetracycline** | Low | High |
| **Inhibition by Basic Dyes** | High | Low |
| **Susceptibility to Anionic Detergents** | High | Low |
| **Resistance to Sodium Azide** | High | Low |
| **Resistance to Drying** | High | Low |

## Atypical Cell Walls

Among prokaryotes, certain types of cells have no walls or have very little wall material. These include members of the genus *Mycoplasma* (mī-kō-plaz′mä) and related organisms (see Figure 11.20, page 320). Mycoplasmas are the smallest known bacteria that can grow and reproduce outside living host cells. Because of their size and because they have no cell walls, they pass through most bacterial filters and were first mistaken for viruses. Their plasma membranes are unique among bacteria in having lipids called *sterols*, which are thought to help protect them from lysis (rupture).

Archaea may lack walls or may have unusual walls composed of polysaccharides and proteins but not peptidoglycan. These walls do, however, contain a substance similar to peptidoglycan called *pseudomurein*. Pseudomurein contains N-acetyltalosaminuronic acid instead of NAM and lacks the D-amino acids found in bacterial cell walls. Archaea generally cannot be Gram-stained but appear gram-negative because they do not contain peptidoglycan.

### Acid-Fast Cell Walls

Recall from Chapter 3 that the acid-fast stain is used to identify all bacteria of the genus *Mycobacterium* and pathogenic species of

*Nocardia*. These bacteria contain high concentrations (60%) of a hydrophobic waxy lipid (**mycolic acid**) in their cell wall that prevents the uptake of dyes, including those used in the Gram stain. The mycolic acid forms a layer outside of a thin layer of peptidoglycan. The mycolic acid and peptidoglycan are held together by a polysaccharide. The hydrophobic waxy cell wall causes both cultures of *Mycobacterium* to clump and to stick to the walls of the flask. Acid-fast bacteria can be stained with carbolfuchsin; heating enhances penetration of the stain. The carbolfuchsin penetrates the cell wall, binds to cytoplasm, and resists removal by washing with acid-alcohol. Acid-fast bacteria retain the red color of carbolfuchsin because it is more soluble in the cell wall mycolic acid than in the acid-alcohol. If the mycolic acid layer is removed from the cell wall of acid-fast bacteria, they will stain gram-positive with the Gram stain.

## Damage to the Cell Wall

Chemicals that damage bacterial cell walls, or interfere with their synthesis, often do not harm the cells of an animal host because the bacterial cell wall is made of chemicals unlike those in eukaryotic cells. Thus, cell wall synthesis is the target for some antimicrobial drugs. One way the cell wall can be damaged is by exposure to the digestive enzyme *lysozyme*. This enzyme occurs naturally in some eukaryotic cells and is a constituent of perspiration, tears, mucus, and saliva. Lysozyme is particularly active on the major cell wall components of most gram-positive bacteria, making them vulnerable to lysis. Lysozyme catalyzes hydrolysis of the bonds between the sugars in the repeating disaccharide "backbone" of peptidoglycan. This act is analogous to cutting the steel supports of a bridge with a cutting torch: the gram-positive cell wall is almost completely destroyed by lysozyme. The cellular contents that remain surrounded by the plasma membrane may remain intact if lysis does not occur; this wall-less cell is termed a **protoplast.** Typically, a protoplast is spherical and is still capable of carrying on metabolism.

Some members of the genus *Proteus,* as well as other genera, can lose their cell walls and swell into irregularly shaped cells called **L forms,** named for the Lister Institute, where they were discovered. They may form spontaneously or develop in response to penicillin (which inhibits cell wall formation) or lysozyme (which removes the cell wall). L forms can live and divide repeatedly or return to the walled state.

When lysozyme is applied to gram-negative cells, usually the wall is not destroyed to the same extent as in gram-positive cells; some of the outer membrane also remains. In this case, the cellular contents, plasma membrane, and remaining outer wall layer are called a **spheroplast,** also a spherical structure. For lysozyme to exert its effect on gram-negative cells, the cells are first treated with EDTA (ethylenediaminetetraacetic acid). EDTA weakens ionic bonds in the outer membrane and thereby damages it, giving the lysozyme access to the peptidoglycan layer.

Protoplasts and spheroplasts burst in pure water or very dilute salt or sugar solutions because the water molecules from the surrounding fluid rapidly move into and enlarge the cell, which has a much lower internal concentration of water. This rupturing, called **osmotic lysis,** will be discussed in detail shortly.

As noted earlier, certain antibiotics, such as penicillin, destroy bacteria by interfering with the formation of the peptide cross-bridges of peptidoglycan, thus preventing the formation of a functional cell wall. Most gram-negative bacteria are not as susceptible to penicillin as gram-positive bacteria are because the outer membrane of gram-negative bacteria forms a barrier that inhibits the entry of this and other substances, and gram-negative bacteria have fewer peptide cross-bridges. However, gram-negative bacteria are quite susceptible to some β-lactam antibiotics that penetrate the outer membrane better than penicillin. Antibiotics will be discussed in more detail in Chapter 20.

### Clinical Case

The outer membrane of *K. pneumoniae*'s gram-negative cell wall contains the endotoxin, lipid A, which causes fever and capillary dilation.

Irene works with Joe's, Jessie's , and Maureen's physicians to combat this potentially deadly infection. Irene is particularly concerned about Jessie because of her already weakened respiratory condition. All three patients are treated with a β-lactam antibiotic, imipenem. *Klebsiella* bacteria are resistant to many antibiotics, but imipenem seems to be working for Joe and Maureen. Jessie, however, is getting worse.

**Why are Jessie's symptoms worsening if the bacteria are being killed?**

76 86 **88** 95 97

### CHECK YOUR UNDERSTANDING

- Why are drugs that target cell wall synthesis useful? **4-5**
- Why are mycoplasmas resistant to antibiotics that interfere with cell wall synthesis? **4-6**
- How do protoplasts differ from L forms? **4-7**

# Structures Internal to the Cell Wall

### LEARNING OBJECTIVES

**4-8** Describe the structure, chemistry, and functions of the prokaryotic plasma membrane.

**4-9** Define *simple diffusion*, *facilitated diffusion*, *osmosis*, *active transport*, and *group translocation.*

**4-10** Identify the functions of the nucleoid and ribosomes.

**4-11** Identify the functions of four inclusions.

**4-12** Describe the functions of endospores, sporulation, and endospore germination.

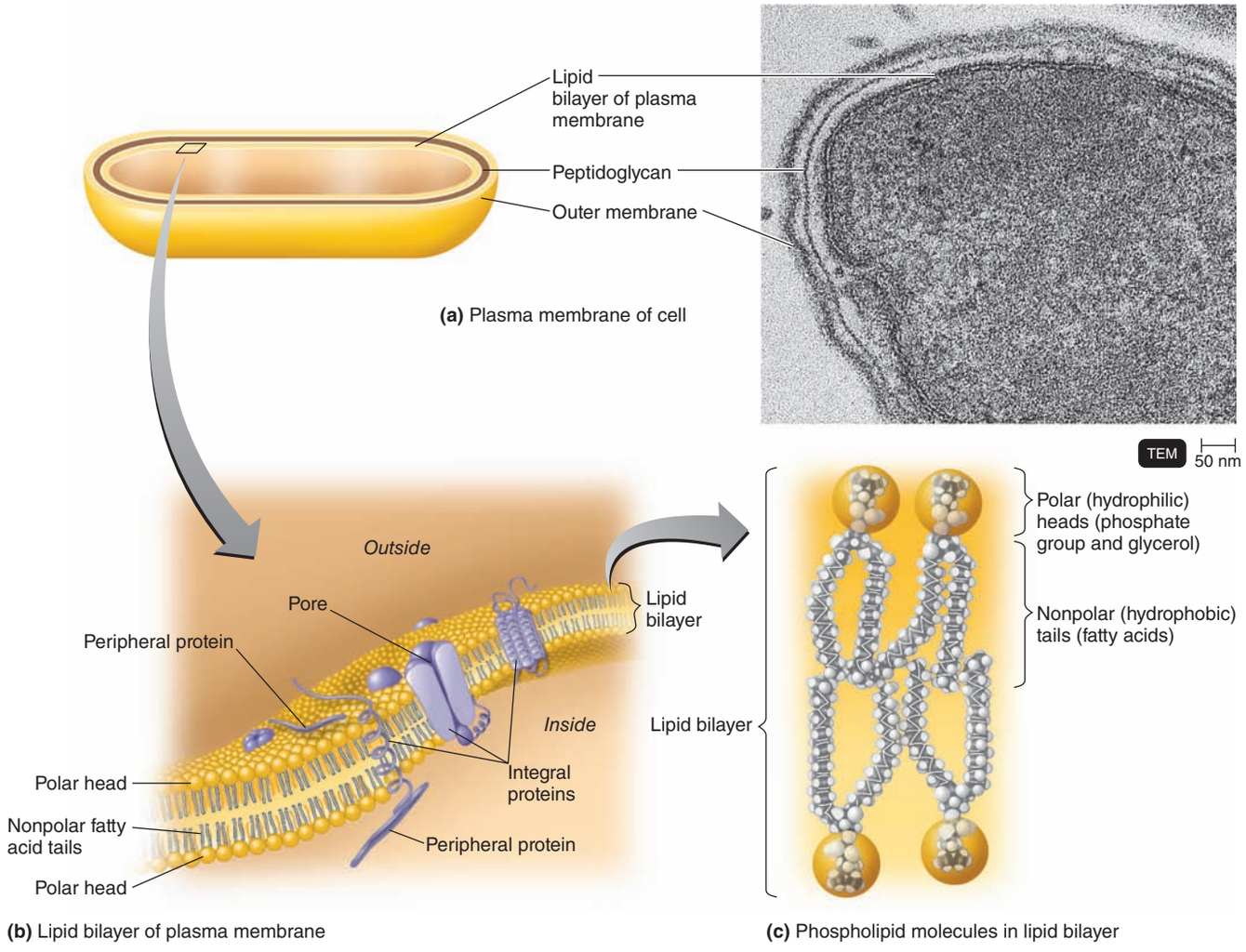



**Figure 4.14 Plasma membrane.** (**a**) A diagram and micrograph showing the lipid bilayer forming the inner plasma membrane of the gram-negative bacterium *Aquaspirillum serpens*. Layers of the cell wall, including the outer membrane, can be seen outside the inner membrane. (**b**) A portion of the inner membrane showing the lipid bilayer and proteins. The outer membrane of gram-negative bacteria is also a lipid bilayer. (**c**) Space-filling models of several phospholipid molecules as they are arranged in the lipid bilayer.

Q What is the difference between a peripheral and an integral protein?

Thus far, we have discussed the prokaryotic cell wall and structures external to it. We will now look inside the prokaryotic cell and discuss the structures and functions of the plasma membrane and components within the cytoplasm of the cell.

## The Plasma (Cytoplasmic) Membrane

The **plasma (cytoplasmic) membrane** (or *inner membrane*) is a thin structure lying inside the cell wall and enclosing the cytoplasm of the cell (see Figure 4.6). The plasma membrane of prokaryotes consists primarily of phospholipids (see Figure 2.10, page 40), which are the most abundant chemicals in the membrane, and proteins. Eukaryotic plasma membranes also contain carbohydrates and sterols, such as cholesterol. Because they lack sterols, prokaryotic plasma membranes are less rigid than eukaryotic membranes. One exception is the wall-less prokaryote *Mycoplasma*, which contains membrane sterols.

### Structure

In electron micrographs, prokaryotic and eukaryotic plasma membranes (and the outer membranes of gram-negative bacteria) look like two-layered structures; there are two dark lines with a light space between the lines (Figure 4.14a). The phospholipid molecules are arranged in two parallel rows, called a *lipid bilayer* (Figure 4.14b). As introduced in Chapter 2, each phospholipid molecule contains a polar head, composed of a phosphate group and glycerol that is hydrophilic (water-loving) and soluble in water, and nonpolar tails, composed of fatty acids that are hydrophobic (water-fearing) and insoluble in water (Figure 4.14c). The polar heads are on the two surfaces of the lipid bilayer, and the nonpolar tails are in the interior of the bilayer.

The protein molecules in the membrane can be arranged in a variety of ways. Some, called *peripheral proteins*, are easily removed from the membrane by mild treatments and lie at


**Figure 4.15 Chromatophores.** In this micrograph of *Rhodospirillum rubrum,* a purple (nonsulfur) bacterium, the chromatophores are clearly visible.

Q What is the function of chromatophores?

the inner or outer surface of the membrane. They may function as enzymes that catalyze chemical reactions, as a "scaffold" for support, and as mediators of changes in membrane shape during movement. Other proteins, called *integral proteins,* can be removed from the membrane only after disrupting the lipid bilayer (by using detergents, for example). Most integral proteins penetrate the membrane completely and are called *transmembrane proteins.* Some integral proteins are channels that have a pore, or hole, through which substances enter and exit the cell.

Many of the proteins and some of the lipids on the outer surface of the plasma membrane have carbohydrates attached to them. Proteins attached to carbohydrates are called **glycoproteins;** lipids attached to carbohydrates are called **glycolipids.** Both glycoproteins and glycolipids help protect and lubricate the cell and are involved in cell-to-cell interactions. For example, glycoproteins play a role in certain infectious diseases. The influenza virus and the toxins that cause cholera and botulism enter their target cells by first binding to glycoproteins on their plasma membranes.

Studies have demonstrated that the phospholipid and protein molecules in membranes are not static but move quite freely within the membrane surface. This movement is most probably associated with the many functions performed by the plasma membrane. Because the fatty acid tails cling together, phospholipids in the presence of water form a self-sealing bilayer; as a result, breaks and tears in the membrane heal themselves. The membrane must be about as viscous as olive oil, which allows membrane proteins to move freely enough to perform their functions without destroying the structure of the membrane. This dynamic arrangement of phospholipids and proteins is referred to as the **fluid mosaic model.**

## Functions

The most important function of the plasma membrane is to serve as a selective barrier through which materials enter and exit the cell. In this function, plasma membranes have **selective permeability** (sometimes called *semipermeability*). This term indicates that certain molecules and ions pass through the membrane, but that others are prevented from passing through it. The permeability of the membrane depends on several factors. Large molecules (such as proteins) cannot pass through the plasma membrane, possibly because these molecules are larger than the pores in integral proteins that function as channels. But smaller molecules (such as water, oxygen, carbon dioxide, and some simple sugars) usually pass through easily. Ions penetrate the membrane very slowly. Substances that dissolve easily in lipids (such as oxygen, carbon dioxide, and nonpolar organic molecules) enter and exit more easily than other substances because the membrane consists mostly of phospholipids. The movement of materials across plasma membranes also depends on transporter molecules, which will be described shortly.

Plasma membranes are also important to the breakdown of nutrients and the production of energy. The plasma membranes of bacteria contain enzymes capable of catalyzing the chemical reactions that break down nutrients and produce ATP. In some bacteria, pigments and enzymes involved in photosynthesis are found in infoldings of the plasma membrane that extend into the cytoplasm. These membranous structures are called **chromatophores** or **thylakoids** (Figure 4.15).

When viewed with an electron microscope, bacterial plasma membranes often appear to contain one or more large, irregular folds called **mesosomes.** Many functions have been proposed for mesosomes. However, it is now known that they are artifacts, not true cell structures. Mesosomes are believed to be folds in the plasma membrane that develop by the process used for preparing specimens for electron microscopy. **Animations** Membrane Structure; Membrane Permeability

## Destruction of the Plasma Membrane by Antimicrobial Agents

Because the plasma membrane is vital to the bacterial cell, it is not surprising that several antimicrobial agents exert their effects at this site. In addition to the chemicals that damage the cell wall and thereby indirectly expose the membrane to injury, many compounds specifically damage plasma membranes. These compounds include certain alcohols and quaternary ammonium compounds, which are used as disinfectants. By disrupting the membrane's phospholipids, a group of antibiotics known as the *polymyxins* cause leakage of intracellular contents and subsequent cell death. This mechanism will be discussed in Chapter 20.

## The Movement of Materials across Membranes

Materials move across plasma membranes of both prokaryotic and eukaryotic cells by two kinds of processes: passive and active. In *passive processes,* substances cross the membrane from an area of high concentration to an area of low concentration (move with the concentration gradient, or difference), without any expenditure of energy (ATP) by the cell. In *active processes,* the cell must use energy (ATP) to move substances from areas of low concentration to areas of high concentration (against the concentration gradient).

### Passive Processes

Passive processes include simple diffusion, facilitated diffusion, and osmosis.

**Simple diffusion** is the net (overall) movement of molecules or ions from an area of high concentration to an area of low concentration (Figure 4.16 and Figure 4.17a). The movement continues until the molecules or ions are evenly distributed. The point of even distribution is called *equilibrium.* Cells rely on simple diffusion to transport certain small molecules, such as oxygen and carbon dioxide, across their cell membranes.

In **facilitated diffusion,** integral membrane proteins function as channels or carriers that facilitate the movement of ions or large molecules across the plasma membrane. Such integral proteins are called *transporters* or *permeases.* Facilitated diffusion is similar to simple diffusion in that the cell *does not* expend energy, because the substance moves from a high to a low concentration. The process differs from simple diffusion in its use of transporters. Some transporters permit the passage of mostly small, inorganic ions that are too hydrophilic to penetrate the nonpolar interior of the lipid bilayer (Figure 4.17b). These transporters, which are common in prokaryotes, are nonspecific and allow the passage of a wide variety of ions (or even small molecules). Other transporters, which are common in eukaryotes, are specific and transport only specific, usually larger, molecules, such as simple sugars (glucose, fructose, and galactose) and vitamins. In this process, the transported substance binds to a specific transporter on the outer surface of the plasma membrane, which undergoes a change of shape; then the transporter releases the substance on the other side of the membrane (Figure 4.17c).


**Figure 4.16 The principle of simple diffusion.** (**a**) After a dye pellet is put into a beaker of water, the molecules of dye in the pellet diffuse into the water from an area of high dye concentration to areas of low dye concentration. (**b**) The dye potassium permanganate in the process of diffusing.

Q Why are passive processes important to a cell?

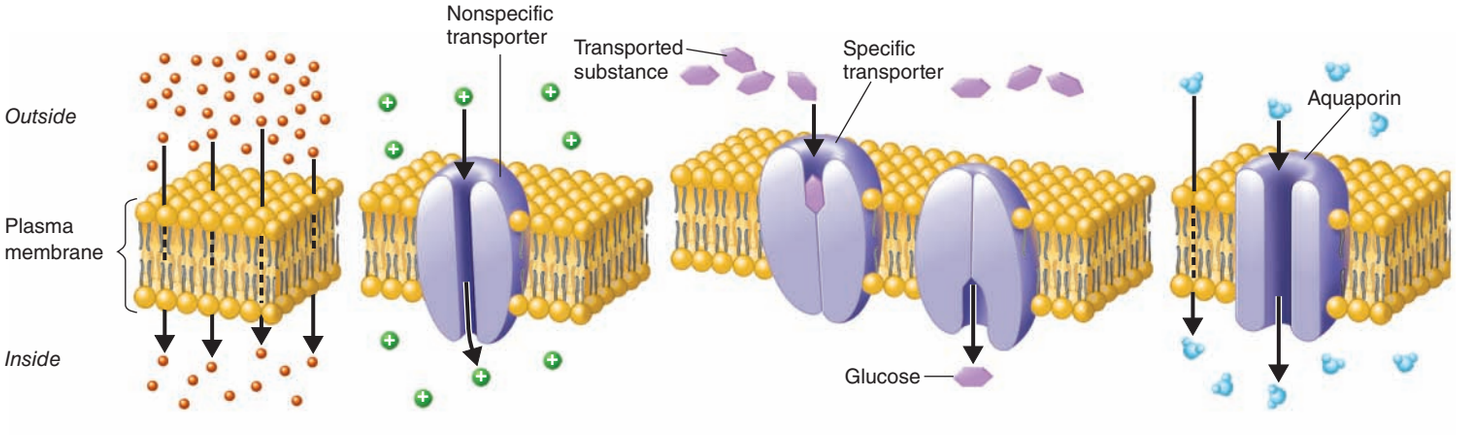



**Figure 4.17 Passive processes.**

Q How does simple diffusion differ from facilitated diffusion?

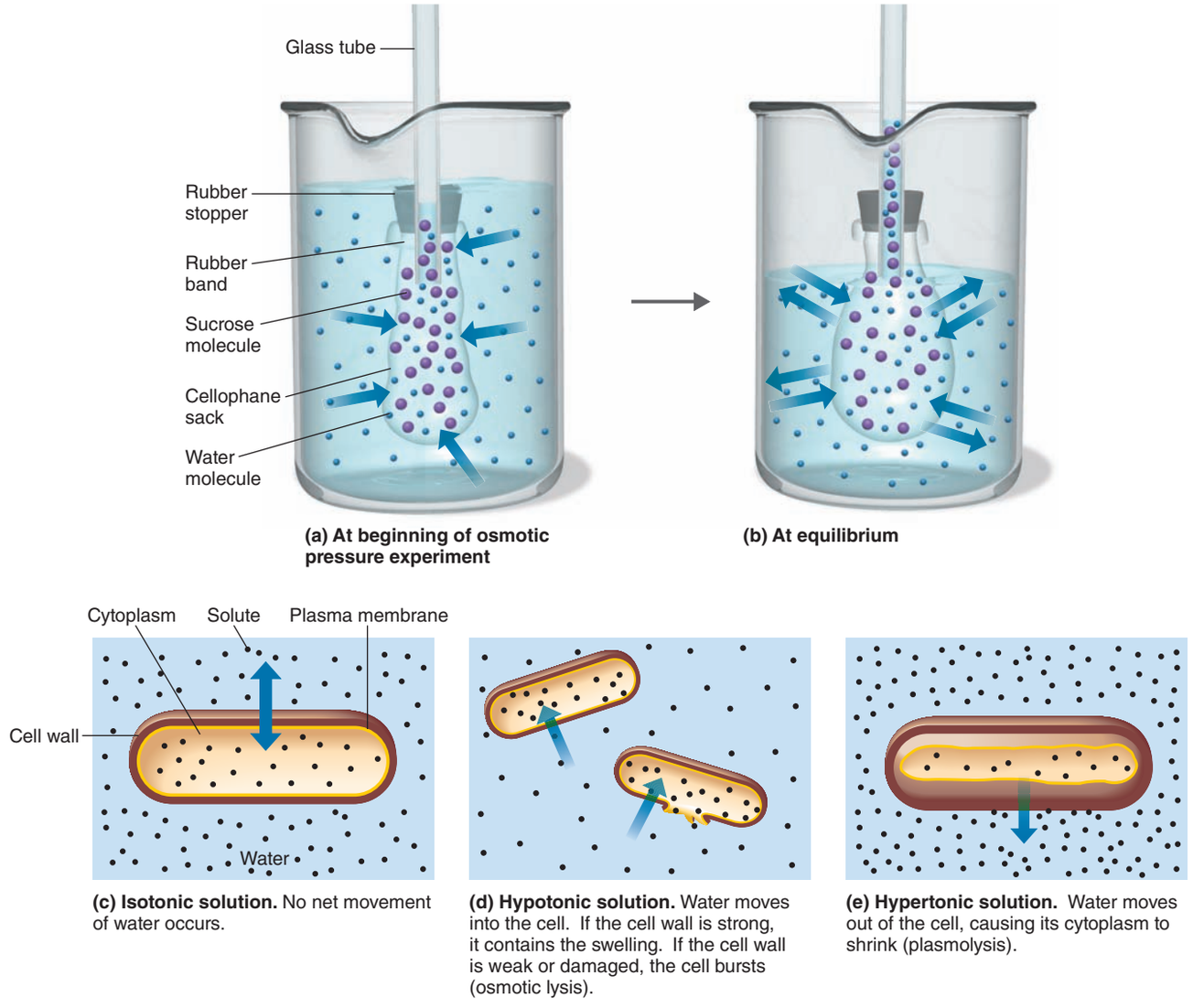



**Figure 4.18 The principle of osmosis.** (**a**) Setup at the beginning of an osmotic pressure experiment. Water molecules start to move from the beaker into the sack along the concentration gradient. (**b**) Setup at equilibrium. The osmotic pressure exerted by the solution in the sack pushes water molecules from the sack back into the beaker to balance the rate of water entry into the sack. The height of the solution in the glass tube at equilibrium is a measure of the osmotic pressure. (**c**)–(**e**) The effects of various solutions on bacterial cells.

Q Why is osmosis important?

In some cases, molecules that bacteria need are too large to be transported into the cells by these methods. Most bacteria, however, produce enzymes that can break down large molecules into simpler ones (such as proteins into amino acids, or polysaccharides into simple sugars). Such enzymes, which are released by the bacteria into the surrounding medium, are appropriately called *extracellular enzymes*. Once the enzymes degrade the large molecules, the subunits move into the cell with the help of transporters. For example, specific carriers retrieve DNA bases, such as the purine guanine, from extracellular media and bring them into the cell's cytoplasm.

**Osmosis** is the net movement of solvent molecules across a selectively permeable membrane from an area with a high concentration of solvent molecules (low concentration of solute molecules) to an area of low concentration of solvent molecules (high concentration of solute molecules). In living systems, the chief solvent is water. Water molecules may pass through plasma membranes by moving through the lipid bilayer by simple diffusion or through integral membrane proteins, called *aquaporins*, that function as water channels (Figure 4.17d).

Osmosis may be demonstrated with the apparatus shown in Figure 4.18a. A sack constructed from cellophane, which is a selectively permeable membrane, is filled with a solution of 20% sucrose (table sugar). The cellophane sack is placed into a beaker containing distilled water. Initially, the concentrations of water on either side of the membrane are different. Because of the

sucrose molecules, the concentration of water is lower inside the cellophane sack. Therefore, water moves from the beaker (where its concentration is higher) into the cellophane sack (where its concentration is lower).

There is no movement of sugar out of the cellophane sack into the beaker, however, because the cellophane is impermeable to molecules of sugar—the sugar molecules are too large to go through the pores of the membrane. As water moves into the cellophane sack, the sugar solution becomes increasingly dilute, and, because the cellophane sack has expanded to its limit as a result of an increased volume of water, water begins to move up the glass tube. In time, the water that has accumulated in the cellophane sack and the glass tube exerts a downward pressure that forces water molecules out of the cellophane sack and back into the beaker. This movement of water through a selectively permeable membrane produces osmotic pressure. **Osmotic pressure** is the pressure required to prevent the movement of pure water (water with no solutes) into a solution containing some solutes. In other words, osmotic pressure is the pressure needed to stop the flow of water across the selectively permeable membrane (cellophane). When water molecules leave and enter the cellophane sack at the same rate, equilibrium is reached (**Figure 4.18b**).

A bacterial cell may be subjected to any of three kinds of osmotic solutions: isotonic, hypotonic, or hypertonic. An **isotonic solution** is a medium in which the overall concentration of solutes equals that found inside a cell (*iso* means equal). Water leaves and enters the cell at the same rate (no net change); the cell's contents are in equilibrium with the solution outside the cell wall (**Figure 4.18c**).

Earlier we mentioned that lysozyme and certain antibiotics (such as penicillin) damage bacterial cell walls, causing the cells to rupture, or lyse. Such rupturing occurs because bacterial cytoplasm usually contains such a high concentration of solutes that, when the wall is weakened or removed, additional water enters the cell by osmosis. The damaged (or removed) cell wall cannot constrain the swelling of the cytoplasmic membrane, and the membrane bursts. This is an example of osmotic lysis caused by immersion in a hypotonic solution. A **hypotonic solution** outside the cell is a medium whose concentration of solutes is lower than that inside the cell (*hypo* means under or less). Most bacteria live in hypotonic solutions, and the cell wall resists further osmosis and protects cells from lysis. Cells with weak cell walls, such as gram-negative bacteria, may burst or undergo osmotic lysis as a result of excessive water intake (**Figure 4.18d**).

A **hypertonic solution** is a medium having a higher concentration of solutes than inside the cell has (*hyper* means above or more). Most bacterial cells placed in a hypertonic solution shrink and collapse or *plasmolyze* because water leaves the cells by osmosis (**Figure 4.18e**). Keep in mind that the terms *isotonic, hypotonic,* and *hypertonic* describe the concentration of solutions outside the cell *relative to* the concentration inside the cell. **Animations** Passive Transport: Principles of Diffusion, Special Types of Diffusion

## Active Processes

Simple diffusion and facilitated diffusion are useful mechanisms for transporting substances into cells when the concentrations of the substances are greater outside the cell. However, when a bacterial cell is in an environment in which nutrients are in low concentration, the cell must use active processes, such as active transport and group translocation, to accumulate the needed substances.

In performing **active transport,** the cell *uses energy* in the form of ATP to move substances across the plasma membrane. Among the substances actively transported are ions (for example $Na^+$, $K^+$, $H^+$, $Ca^{2+}$, and $Cl^-$), amino acids, and simple sugars. Although these substances can also be moved into cells by passive processes, their movement by active processes can go against the concentration gradient, allowing a cell to accumulate needed materials. The movement of a substance in active transport is usually from outside to inside, even though the concentration might be much higher inside the cell. Like facilitated diffusion, active transport depends on transporter proteins in the plasma membrane (see Figure 4.17b, c). There appears to be a different transporter for each transported substance or group of closely related transported substances. Active transport enables microbes to move substances across the plasma membrane at a constant rate, even if they are in short supply.

In active transport, the substance that crosses the membrane is not altered by transport across the membrane. In **group translocation,** a special form of active transport that occurs exclusively in prokaryotes, the substance is chemically altered during transport across the membrane. Once the substance is altered and inside the cell, the plasma membrane is impermeable to it, so it remains inside the cell. This important mechanism enables a cell to accumulate various substances even though they may be in low concentrations outside the cell. Group translocation requires energy supplied by high-energy phosphate compounds, such as phosphoenolpyruvic acid (PEP).

One example of group translocation is the transport of the sugar glucose, which is often used in growth media for bacteria. While a specific carrier protein is transporting the glucose molecule across the membrane, a phosphate group is added to the sugar. This phosphorylated form of glucose, which cannot be transported out, can then be used in the cell's metabolic pathways.

Some eukaryotic cells (those without cell walls) can use two additional active transport processes called phagocytosis and pinocytosis. These processes, which do not occur in bacteria, are explained on page 100. **Animations** Active Transport: Types, Overview

### CHECK YOUR UNDERSTANDING

- Which agents can cause injury to the bacterial plasma membrane? **4-8**
- How are simple diffusion and facilitated diffusion similar? How are they different? **4-9**

## Cytoplasm

For a prokaryotic cell, the term **cytoplasm** refers to the substance of the cell inside the plasma membrane (see Figure 4.6). Cytoplasm is about 80% water and contains primarily proteins (enzymes), carbohydrates, lipids, inorganic ions, and many low-molecular-weight compounds. Inorganic ions are present in much higher concentrations in cytoplasm than in most media. Cytoplasm is thick, aqueous, semitransparent, and elastic. The major structures in the cytoplasm of prokaryotes are a nucleoid (containing DNA), particles called ribosomes, and reserve deposits called inclusions. Protein filaments in the cytoplasm are most likely responsible for the rod and helical cell shapes of bacteria.

Prokaryotic cytoplasm lacks certain features of eukaryotic cytoplasm, such as a cytoskeleton and cytoplasmic streaming. These features will be described later.

## The Nucleoid

The **nucleoid** of a bacterial cell (see Figure 4.6) usually contains a single long, continuous, and frequently circularly arranged thread of double-stranded DNA called the **bacterial chromosome.** This is the cell's genetic information, which carries all the information required for the cell's structures and functions. Unlike the chromosomes of eukaryotic cells, bacterial chromosomes are not surrounded by a nuclear envelope (membrane) and do not include histones. The nucleoid can be spherical, elongated, or dumbbell-shaped. In actively growing bacteria, as much as 20% of the cell volume is occupied by DNA because such cells presynthesize nuclear material for future cells. The chromosome is attached to the plasma membrane. Proteins in the plasma membrane are believed to be responsible for replication of the DNA and segregation of the new chromosomes to daughter cells during cell division.

In addition to the bacterial chromosome, bacteria often contain small usually circular, double-stranded DNA molecules called **plasmids** (see the F factor in Figure 8.26a, page 234). These molecules are extrachromosomal genetic elements; that is, they are not connected to the main bacterial chromosome, and they replicate independently of chromosomal DNA. Research indicates that plasmids are associated with plasma membrane proteins. Plasmids usually contain from 5 to 100 genes that are generally not crucial for the survival of the bacterium under normal environmental conditions; plasmids may be gained or lost without harming the cell. Under certain conditions, however, plasmids are an advantage to cells. Plasmids may carry genes for such activities as antibiotic resistance, tolerance to toxic metals, the production of toxins, and the synthesis of enzymes. Plasmids can be transferred from one bacterium to another. In fact, plasmid DNA is used for gene manipulation in biotechnology.

## Ribosomes

All eukaryotic and prokaryotic cells contain **ribosomes,** which function as the sites of protein synthesis. Cells that have high rates of protein synthesis, such as those that are actively growing, have a large number of ribosomes. The cytoplasm of a prokaryotic cell contains tens of thousands of these very small structures, which give the cytoplasm a granular appearance (see Figure 4.6).

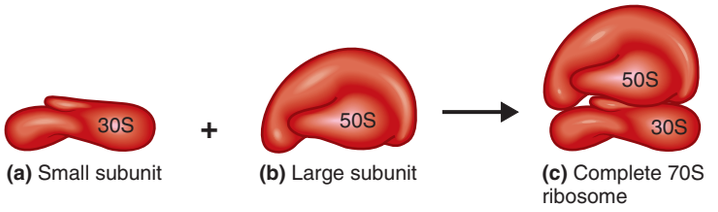



**Figure 4.19 The prokaryotic ribosome.** (**a**) A small 30S subunit and (**b**) a large 50S subunit make up (**c**) the complete 70S prokaryotic ribosome.

Q What is the importance of the differences between prokaryotic and eukaryotic ribosomes with regard to antibiotic therapy?

Ribosomes are composed of two subunits, each of which consists of protein and a type of RNA called *ribosomal RNA (rRNA).* Prokaryotic ribosomes differ from eukaryotic ribosomes in the number of proteins and rRNA molecules they contain; they are also somewhat smaller and less dense than ribosomes of eukaryotic cells. Accordingly, prokaryotic ribosomes are called 70S ribosomes (Figure 4.19), and those of eukaryotic cells are known as 80S ribosomes. The letter S refers to Svedberg units, which indicate the relative rate of sedimentation during ultra-high-speed centrifugation. Sedimentation rate is a function of the size, weight, and shape of a particle. The subunits of a 70S ribosome are a small 30S subunit containing one molecule of rRNA and a larger 50S subunit containing two molecules of rRNA.

Several antibiotics work by inhibiting protein synthesis on prokaryotic ribosomes. Antibiotics such as streptomycin and gentamicin attach to the 30S subunit and interfere with protein synthesis. Other antibiotics, such as erythromycin and chloramphenicol, interfere with protein synthesis by attaching to the 50S subunit. Because of differences in prokaryotic and eukaryotic ribosomes, the microbial cell can be killed by the antibiotic while the eukaryotic host cell remains unaffected.

## Inclusions

Within the cytoplasm of prokaryotic cells are several kinds of reserve deposits, known as **inclusions.** Cells may accumulate certain nutrients when they are plentiful and use them when the environment is deficient. Evidence suggests that macromolecules concentrated in inclusions avoid the increase in osmotic pressure that would result if the molecules were dispersed in the cytoplasm. Some inclusions are common to a wide variety of bacteria, whereas others are limited to a small number of species and therefore serve as a basis for identification.

## Clinical Case

The antibiotic killed the bacteria, but endotoxin is released when the cells die, causing Jessie's condition to worsen. Jessie's physician prescribes polymyxin, an antibiotic primarily used for imipenem-resistant gram-negative infections, to which Jessie responds favorably.

As Irene sits with Jessie, she notices another patient being fed ice chips by a relative. On a hunch, Irene hurries back to her office to find out whether the ice machines had been swabbed. They have not. She immediately orders the machines to be swabbed and cultured. Her hunch turns out to be correct: the samples are positive for *K. pneumoniae*. Bacteria growing in the hospital's water pipes entered the ice machine with incoming water.

**How can *K. pneumoniae* grow in water pipes?**

76 86 88 **95** 97

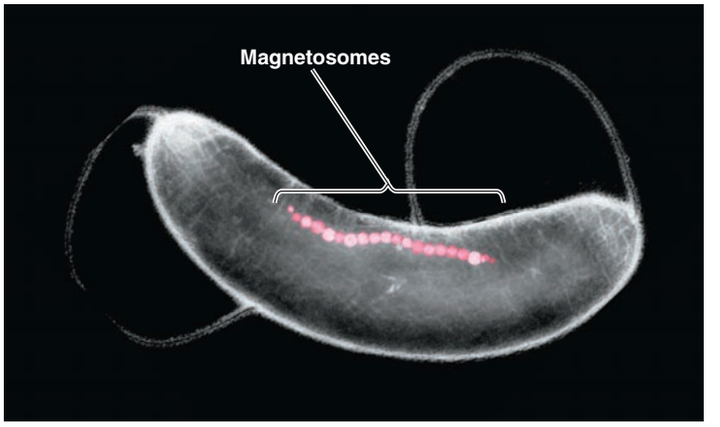



**Figure 4.20 Magnetosomes.** This micrograph of *Magnetospirillum magnetotacticum* shows a chain of magnetosomes. This bacterium is usually found in shallow freshwater mud.

How do magnetosomes behave like magnets?

### Metachromatic Granules

**Metachromatic granules** are large inclusions that take their name from the fact that they sometimes stain red with certain blue dyes such as methylene blue. Collectively they are known as **volutin.** Volutin represents a reserve of inorganic phosphate (polyphosphate) that can be used in the synthesis of ATP. It is generally formed by cells that grow in phosphate-rich environments. Metachromatic granules are found in algae, fungi, and protozoa, as well as in bacteria. These granules are characteristic of *Corynebacterium diphtheriae* (kô-rī-nē-bak-ti′ rē-um dif-thi′ rē-ī), the causative agent of diphtheria; thus, they have diagnostic significance.

### Polysaccharide Granules

Inclusions known as **polysaccharide granules** typically consist of glycogen and starch, and their presence can be demonstrated when iodine is applied to the cells. In the presence of iodine, glycogen granules appear reddish brown and starch granules appear blue.

### Lipid Inclusions

**Lipid inclusions** appear in various species of *Mycobacterium, Bacillus, Azotobacter* (ä-zō-tō-bak′ tér), *Spirillum* (spī-ril′ lum), and other genera. A common lipid-storage material, one unique to bacteria, is the polymer *poly-β-hydroxybutyric acid.* Lipid inclusions are revealed by staining cells with fat-soluble dyes, such as Sudan dyes.

### Sulfur Granules

Certain bacteria—for example, the "sulfur bacteria" that belong to the genus *Thiobacillus*—derive energy by oxidizing sulfur and sulfur-containing compounds. These bacteria may deposit **sulfur granules** in the cell, where they serve as an energy reserve.

### Carboxysomes

**Carboxysomes** are inclusions that contain the enzyme ribulose 1,5-diphosphate carboxylase. Photosynthetic bacteria use carbon dioxide as their sole source of carbon and require this enzyme for carbon dioxide fixation. Among the bacteria containing carboxysomes are nitrifying bacteria, cyanobacteria, and thiobacilli.

### Gas Vacuoles

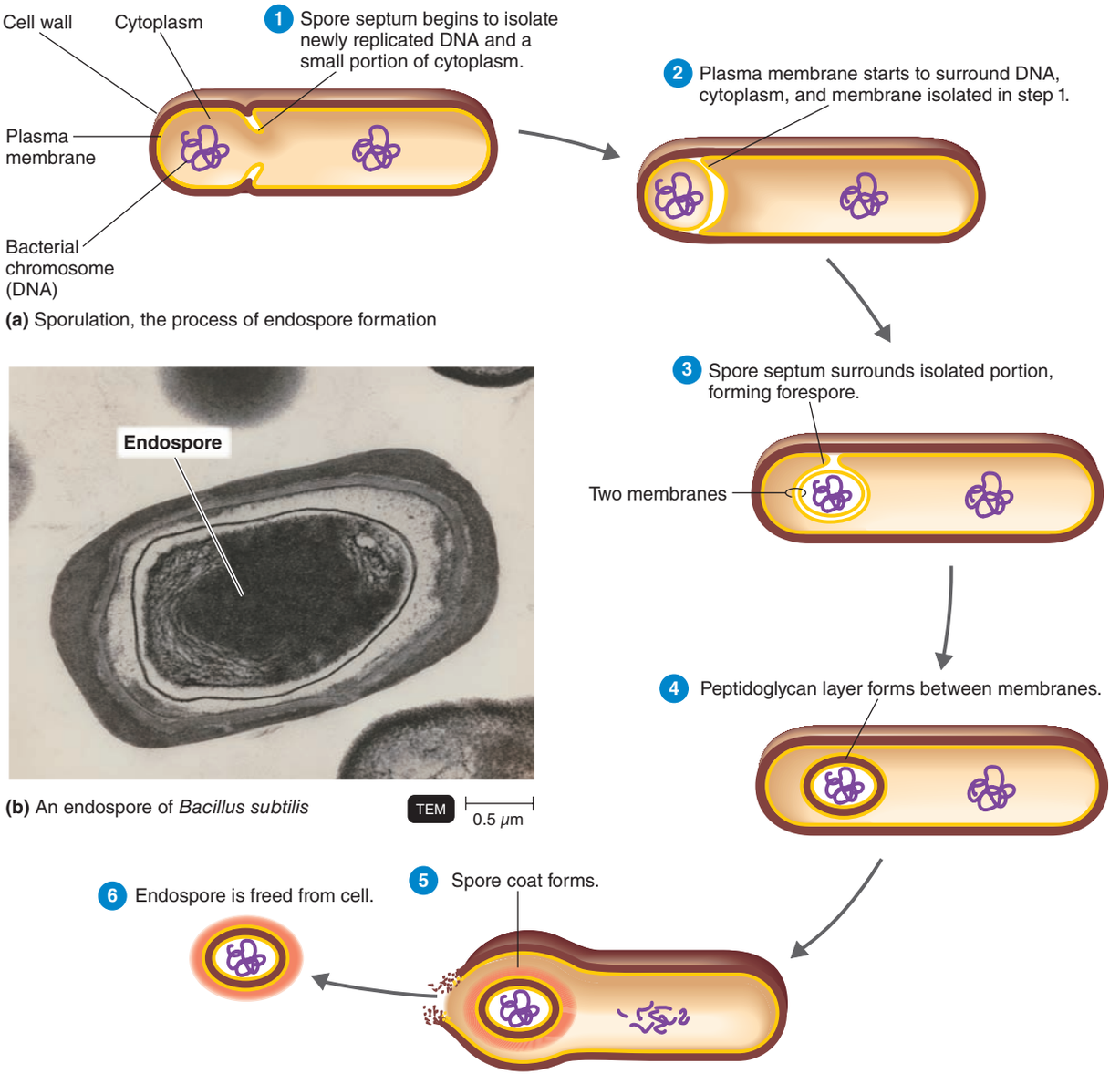
Hollow cavities found in many aquatic prokaryotes, including cyanobacteria, anoxygenic photosynthetic bacteria, and halobacteria are called **gas vacuoles.** Each vacuole consists of rows of several individual *gas vesicles,* which are hollow cylinders covered by protein. Gas vacuoles maintain buoyancy so that the cells can remain at the depth in the water appropriate for them to receive sufficient amounts of oxygen, light, and nutrients.

### Magnetosomes

**Magnetosomes** are inclusions of iron oxide ($Fe_3O_4$) surrounded by invaginations of the plasma membrane. Magnetosomes are formed by several gram-negative bacteria such as *Magnetospirillum magnetotacticum* and act like magnets (**Figure 4.20**). Bacteria may use magnetosomes to move downward until they reach a suitable attachment site. In vitro, magnetosomes can decompose hydrogen peroxide, which forms in cells in the presence of oxygen. Researchers speculate that magnetosomes may protect the cell against hydrogen peroxide accumulation.

## Endospores

When essential nutrients are depleted, certain gram-positive bacteria, such as those of the genera *Clostridium* and *Bacillus,* form specialized "resting" cells called **endospores** (**Figure 4.21**). As




**(a)** Sporulation, the process of endospore formation

**(b)** An endospore of *Bacillus subtilis*

**Figure 4.21** **Formation of endospores by sporulation.**

Q What properties make endospores resistant to processes that normally kill vegetative cells?

you will see later, some members of the genus *Clostridium* cause diseases such as gangrene, tetanus, botulism, and food poisoning. Some members of the genus *Bacillus* cause anthrax and food poisoning. Unique to bacteria, endospores are highly durable dehydrated cells with thick walls and additional layers. They are formed internal to the bacterial cell membrane.

When released into the environment, they can survive extreme heat, lack of water, and exposure to many toxic chemicals and radiation. For example, 7500-year-old endospores of *Thermoactinomyces vulgaris* (thėr-mō-ak-tin-ō-mī′sēs vul-ga′-ris) from the freezing muds of Elk Lake in Minnesota have germinated when rewarmed and placed in a nutrient medium, and 25- to 40-million-year-old endospores found in the gut of a stingless bee entombed in amber (hardened tree resin) in the Dominican Republic are reported to have germinated when placed in nutrient media. Although true endospores are found in gram-positive bacteria, one gram-negative species, *Coxiella burnetii* (käks-ē-el′lä bėr-ne′tē-ē), the cause of Q fever, forms endosporelike structures that resist heat and chemicals and can be stained with endospore stains (see Figure 24.14, page 696).

The process of endospore formation within a vegetative cell takes several hours and is known as **sporulation** or **sporogenesis** (Figure 4.21a). Vegetative cells of endospore-forming bacteria begin sporulation when a key nutrient, such as the carbon or

nitrogen source, becomes scarce or unavailable. In the first observable stage of sporulation, a newly replicated bacterial chromosome and a small portion of cytoplasm are isolated by an ingrowth of the plasma membrane called a *spore septum*. The spore septum becomes a double-layered membrane that surrounds the chromosome and cytoplasm. This structure, entirely enclosed within the original cell, is called a *forespore*. Thick layers of peptidoglycan are laid down between the two membrane layers. Then a thick *spore coat* of protein forms around the outside membrane; this coat is responsible for the resistance of endospores to many harsh chemicals. The original cell is degraded, and the endospore is released.

The diameter of the endospore may be the same as, smaller than, or larger than the diameter of the vegetative cell. Depending on the species, the endospore might be located *terminally* (at one end), *subterminally* (near one end; **Figure 4.21b**), or *centrally* inside the vegetative cell. When the endospore matures, the vegetative cell wall ruptures (lyses), killing the cell, and the endospore is freed.

Most of the water present in the forespore cytoplasm is eliminated by the time sporulation is complete, and endospores do not carry out metabolic reactions. The endospore contains a large amount of an organic acid called *dipicolinic acid* (DPA), which is accompanied by a large number of calcium ions. Evidence indicates that DPA protects the endospore DNA against damage. The highly dehydrated endospore core contains only DNA, small amounts of RNA, ribosomes, enzymes, and a few important small molecules. These cellular components are essential for resuming metabolism later.

Endospores can remain dormant for thousands of years. An endospore returns to its vegetative state by a process called **germination.** Germination is triggered by physical or chemical damage to the endospore's coat. The endospore's enzymes then break down the extra layers surrounding the endospore, water enters, and metabolism resumes. Because one vegetative cell forms a single endospore, which, after germination, remains one cell, sporulation in bacteria is *not* a means of reproduction. This process does not increase the number of cells. Bacterial endospores differ from spores formed by (prokaryotic) actinomycetes and the eukaryotic fungi and algae, which detach from the parent and develop into another organism and, therefore, represent reproduction.

Endospores are important from a clinical viewpoint and in the food industry because they are resistant to processes that normally kill vegetative cells. Such processes include heating, freezing, desiccation, use of chemicals, and radiation. Whereas most vegetative cells are killed by temperatures above 70°C, endospores can survive in boiling water for several hours or more. Endospores of thermophilic (heat-loving) bacteria can survive in boiling water for 19 hours. Endospore-forming bacteria are a problem in the food industry because they are likely to survive underprocessing, and, if conditions for growth occur, some species produce toxins and disease. Special methods for controlling organisms that produce endospores are discussed in Chapter 7.

### Clinical Case Resolved

It is the glycocalyx that enables bacteria in water to stick inside a pipe. The bacteria grow slowly in the nutrient-poor tap water but do not get washed away by the flowing water. A slimy layer of bacteria can accumulate in a pipe. Irene discovers that the disinfectant in the hospital's water supply was inadequate to prevent bacterial growth. Some bacteria can get dislodged by flowing water, and even normally harmless bacteria can infect a surgical incision or weakened host.

76 86 88 95 **97**

### CHECK YOUR UNDERSTANDING

- Where is the DNA located in a prokaryotic cell? **4-10**
- What is the general function of inclusions? **4-11**
- Under what conditions do endospores form? **4-12**

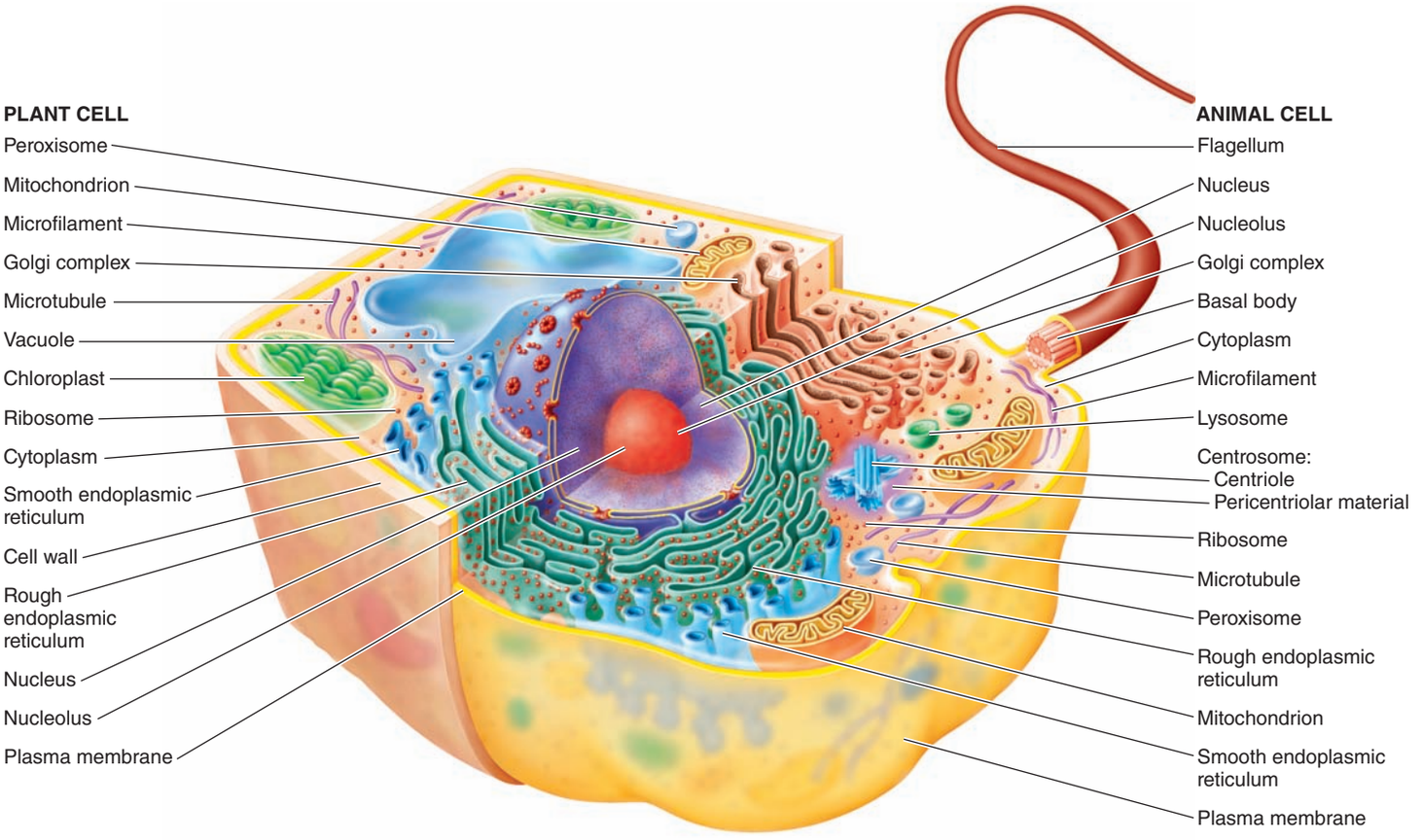
* * *

Having examined the functional anatomy of the prokaryotic cell, we will now look at the functional anatomy of the eukaryotic cell.

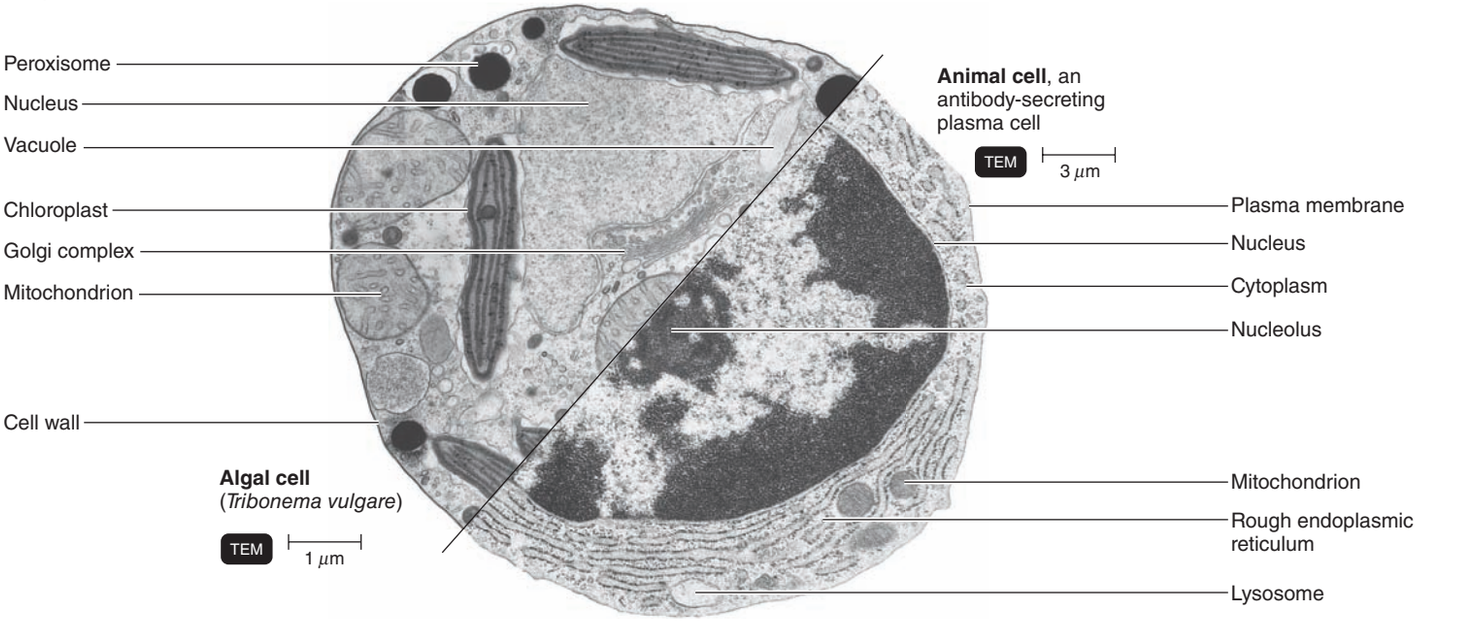
## The Eukaryotic Cell

As mentioned earlier, eukaryotic organisms include algae, protozoa, fungi, plants, and animals. The eukaryotic cell is typically larger and structurally more complex than the prokaryotic cell (**Figure 4.22**). When the structure of the prokaryotic cell in Figure 4.6 is compared with that of the eukaryotic cell, the differences between the two types of cells become apparent. The principal differences between prokaryotic and eukaryotic cells are summarized in **Table 4.2** page 100.

The following discussion of eukaryotic cells will parallel our discussion of prokaryotic cells by starting with structures that extend to the outside of the cell.




**(a)** Highly schematic diagram of a composite eukaryotic cell, half plant and half animal




**(b)** Transmission electron micrographs of plant and animal cells.

**Figure 4.22** **Eukaryotic cells showing typical structures.**

Q What kingdoms contain eukaryotic organisms?

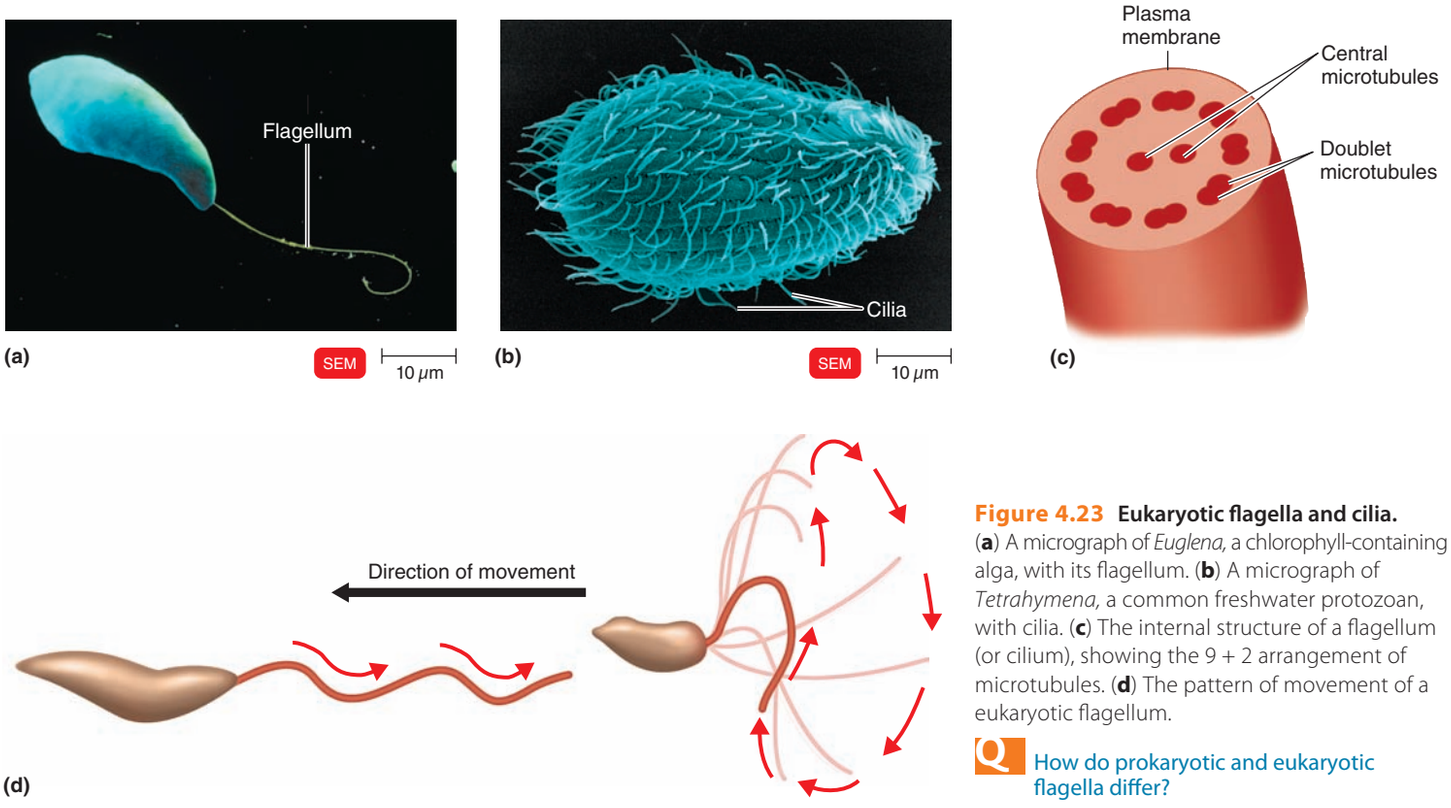



**Figure 4.23 Eukaryotic flagella and cilia.** (**a**) A micrograph of *Euglena,* a chlorophyll-containing alga, with its flagellum. (**b**) A micrograph of *Tetrahymena,* a common freshwater protozoan, with cilia. (**c**) The internal structure of a flagellum (or cilium), showing the 9 + 2 arrangement of microtubules. (**d**) The pattern of movement of a eukaryotic flagellum.

Q How do prokaryotic and eukaryotic flagella differ?

## Flagella and Cilia

### LEARNING OBJECTIVE

**4-13** Differentiate prokaryotic and eukaryotic flagella.

Many types of eukaryotic cells have projections that are used for cellular locomotion or for moving substances along the surface of the cell. These projections contain cytoplasm and are enclosed by the plasma membrane. If the projections are few and are long in relation to the size of the cell, they are called **flagella.** If the projections are numerous and short, they are called **cilia** (singular: **cilium**).

Algae of the genus *Euglena* (ū-glē′na) use a flagellum for locomotion, whereas protozoa, such as *Tetrahymena* (tet-rä-hī′me-nä), use cilia for locomotion (Figure 4.23a and Figure 4.23b). Both flagella and cilia are anchored to the plasma membrane by a basal body, and both consist of nine pairs of microtubules (doublets) arranged in a ring, plus another two microtubules in the center of the ring, an arrangement called a *9 + 2 array* (Figure 4.23c). **Microtubules** are long, hollow tubes made up of a protein called *tubulin.* A prokaryotic flagellum rotates, but a eukaryotic flagellum moves in a wavelike manner (Figure 4.23d). To help keep foreign material out of the lungs, ciliated cells of the human respiratory system move the material along the surface of the cells in the bronchial tubes and trachea toward the throat and mouth (see Figure 16.4, page 454).

## The Cell Wall and Glycocalyx

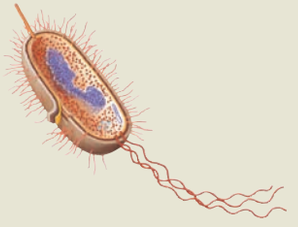
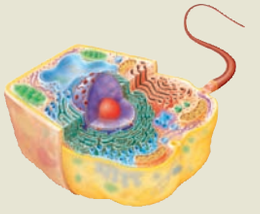
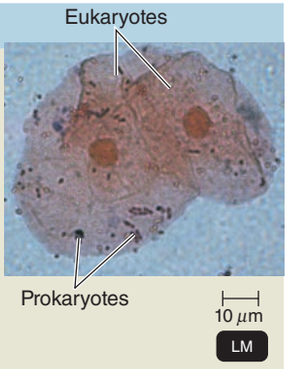
### LEARNING OBJECTIVE

**4-14** Compare and contrast prokaryotic and eukaryotic cell walls and glycocalyxes.

Most eukaryotic cells have cell walls, although they are generally much simpler than those of prokaryotic cells. Many algae have cell walls consisting of the polysaccharide *cellulose* (as do all plants); other chemicals may be present as well. Cell walls of some fungi also contain cellulose, but in most fungi the principal structural component of the cell wall is the polysaccharide *chitin,* a polymer of N-acetylglucosamine (NAG) units. (Chitin is also the main structural component of the exoskeleton of crustaceans and insects.) The cell walls of yeasts contain the polysaccharides *glucan* and *mannan.* In eukaryotes that lack a cell wall, the plasma membrane may be the outer covering; however, cells that have direct contact with the environment may have coatings outside the plasma membrane. Protozoa do not have a typical cell wall; instead, they have a flexible outer protein covering called a *pellicle.*

In other eukaryotic cells, including animal cells, the plasma membrane is covered by a **glycocalyx,** a layer of material containing substantial amounts of sticky carbohydrates. Some of these carbohydrates are covalently bonded to proteins and lipids in the plasma membrane, forming glycoproteins and glycolipids that anchor the glycocalyx to the cell. The glycocalyx strengthens the cell surface, helps attach cells together, and may contribute to cell–cell recognition.

**TABLE 4.2 Principal Differences between Prokaryotic and Eukaryotic Cells**

| Characteristic | Prokaryotic | Eukaryotic |
|---|---|---|
| |  |    |
| **Size of Cell** | Typically 0.2–2.0 μm in diameter | Typically 10–100 μm in diameter |
| **Nucleus** | No nuclear membrane or nucleoli | True nucleus, consisting of nuclear membrane and nucleoli |
| **Membrane-Enclosed Organelles** | Absent | Present; examples include lysosomes, Golgi complex, endoplasmic reticulum, mitochondria, and chloroplasts |
| **Flagella** | Consist of two protein building blocks | Complex; consist of multiple microtubules |
| **Glycocalyx** | Present as a capsule or slime layer | Present in some cells that lack a cell wall |
| **Cell Wall** | Usually present; chemically complex (typical bacterial cell wall includes peptidoglycan) | When present, chemically simple (includes cellulose and chitin) |
| **Plasma Membrane** | No carbohydrates and generally lacks sterols | Sterols and carbohydrates that serve as receptors |
| **Cytoplasm** | No cytoskeleton or cytoplasmic streaming | Cytoskeleton; cytoplasmic streaming |
| **Ribosomes** | Smaller size (70S) | Larger size (80S); smaller size (70S) in organelles |
| **Chromosome (DNA)** | Usually single circular chromosome; typically lacks histones | Multiple linear chromosomes with histones |
| **Cell Division** | Binary fission | Involves mitosis |
| **Sexual Recombination** | None; transfer of DNA only | Involves meiosis |

Eukaryotic cells do not contain peptidoglycan, the framework of the prokaryotic cell wall. This is significant medically because antibiotics, such as penicillins and cephalosporins, act against peptidoglycan and therefore do not affect human eukaryotic cells.

## The Plasma (Cytoplasmic) Membrane

### LEARNING OBJECTIVE

**4-15** Compare and contrast prokaryotic and eukaryotic plasma membranes.

The **plasma (cytoplasmic) membrane** of eukaryotic and prokaryotic cells is very similar in function and basic structure. There are, however, differences in the types of proteins found in the membranes. Eukaryotic membranes also contain carbohydrates, which serve as attachment sites for bacteria and as receptor sites that assume a role in such functions as cell–cell recognition. Eukaryotic plasma membranes also contain *sterols,* complex lipids not found in prokaryotic plasma membranes (with the exception of *Mycoplasma* cells). Sterols seem to be associated with the ability of the membranes to resist lysis resulting from increased osmotic pressure.

Substances can cross eukaryotic and prokaryotic plasma membranes by simple diffusion, facilitated diffusion, osmosis, or active transport. Group translocation does not occur in eukaryotic cells. However, eukaryotic cells can use a mechanism called **endocytosis.** This occurs when a segment of the plasma membrane surrounds a particle or large molecule, encloses it, and brings it into the cell.

The three types of endocytosis are phagocytosis, pinocytosis, and receptor-mediated endocytosis. During *phagocytosis,* cellular projections called pseudopods engulf particles and bring them into the cell. Phagocytosis is used by white blood cells to destroy bacteria and foreign substances (see Figure 16.8, page 464, and further discussion in Chapter 16). In *pinocytosis,* the plasma membrane folds inward, bringing extracellular fluid into the cell, along with whatever substances are dissolved in the fluid. In *receptor-mediated endocytosis*, substances (ligands)

bind to receptors in the membrane. When binding occurs, the membrane folds inward. Receptor-mediated endocytosis is one of the ways viruses can enter animal cells (see Figure 13.14a, page 386).

# Cytoplasm

### LEARNING OBJECTIVE

**4-16** Compare and contrast prokaryotic and eukaryotic cytoplasms.

The **cytoplasm** of eukaryotic cells encompasses the substance inside the plasma membrane and outside the nucleus (see Figure 4.22). The cytoplasm is the substance in which various cellular components are found. (The term **cytosol** refers to the fluid portion of cytoplasm.) A major difference between eukaryotic and prokaryotic cytoplasm is that eukaryotic cytoplasm has a complex internal structure, consisting of exceedingly small rods (*microfilaments* and *intermediate filaments*) and cylinders (*microtubules*). Together, they form the **cytoskeleton.** The cytoskeleton provides support and shape and assists in transporting substances through the cell (and even in moving the entire cell, as in phagocytosis). The movement of eukaryotic cytoplasm from one part of the cell to another, which helps distribute nutrients and move the cell over a surface, is called **cytoplasmic streaming.** Another difference between prokaryotic and eukaryotic cytoplasm is that many of the important enzymes found in the cytoplasmic fluid of prokaryotes are sequestered in the organelles of eukaryotes.

# Ribosomes

### LEARNING OBJECTIVE

**4-17** Compare the structure and function of eukaryotic and prokaryotic ribosomes.

Attached to the outer surface of rough endoplasmic reticulum (discussed on page 102) are **ribosomes** (see Figure 4.25), which are also found free in the cytoplasm. As in prokaryotes, ribosomes are the sites of protein synthesis in the cell.

The ribosomes of eukaryotic endoplasmic reticulum and cytoplasm are somewhat larger and denser than those of prokaryotic cells. These eukaryotic ribosomes are 80S ribosomes, each of which consists of a large 60S subunit containing three molecules of rRNA and a smaller 40S subunit with one molecule of rRNA. The subunits are made separately in the nucleolus and, once produced, exit the nucleus and join together in the cytosol. Chloroplasts and mitochondria contain 70S ribosomes, which may indicate their evolution from prokaryotes. (This theory is discussed on page 105.) The role of ribosomes in protein synthesis will be discussed in more detail in Chapter 8.

Some ribosomes, called *free ribosomes,* are unattached to any structure in the cytoplasm. Primarily, free ribosomes synthesize proteins used *inside* the cell. Other ribosomes, called *membrane-bound ribosomes,* attach to the nuclear membrane and the endoplasmic reticulum. These ribosomes synthesize proteins destined for insertion in the plasma membrane or for export from the cell. Ribosomes located within mitochondria synthesize mitochondrial proteins. Sometimes 10 to 20 ribosomes join together in a stringlike arrangement called a *polyribosome.*

### CHECK YOUR UNDERSTANDING

- Identify at least one significant difference between eukaryotic and prokaryotic flagella and cilia, cell walls, plasma membranes, and cytoplasm. **4-13–4-16**
- The antibiotic erythromycin binds with the 50S portion of a ribosome. What effect does this have on a prokaryotic cell? On a eukaryotic cell? **4–17**

# Organelles

### LEARNING OBJECTIVES

**4-18** Define *organelle.*

**4-19** Describe the functions of the nucleus, endoplasmic reticulum, Golgi complex, lysosomes, vacuoles, mitochondria, chloroplasts, peroxisomes, and centrosomes.

**Organelles** are structures with specific shapes and specialized functions and are characteristic of eukaryotic cells. They include the nucleus, endoplasmic reticulum, Golgi complex, lysosomes, vacuoles, mitochondria, chloroplasts, peroxisomes, and centrosomes. Not all of the organelles described are found in all cells. Certain cells have their own type and distribution of organelles based on specialization, age, and level of activity.

## The Nucleus

The most characteristic eukaryotic organelle is the nucleus (see Figure 4.22). The **nucleus** (Figure 4.24) is usually spherical or oval, is frequently the largest structure in the cell, and contains almost all of the cell's hereditary information (DNA). Some DNA is also found in mitochondria and in the chloroplasts of photosynthetic organisms.

The nucleus is surrounded by a double membrane called the **nuclear envelope.** Both membranes resemble the plasma membrane in structure. Tiny channels in the membrane called **nuclear pores** allow the nucleus to communicate with the cytoplasm (Figure 4.24b). Nuclear pores control the movement of substances between the nucleus and cytoplasm. Within the nuclear envelope are one or more spherical bodies called **nucleoli** (singular: **nucleolus**). Nucleoli are actually condensed regions of chromosomes where ribosomal RNA is being synthesized. Ribosomal RNA is an essential component of ribosomes.

The nucleus also contains most of the cell's DNA, which is combined with several proteins, including some basic proteins called **histones** and nonhistones. The combination of about 165 base pairs of DNA and 9 molecules of histones is referred to as a *nucleosome.* When the cell is not reproducing, the DNA

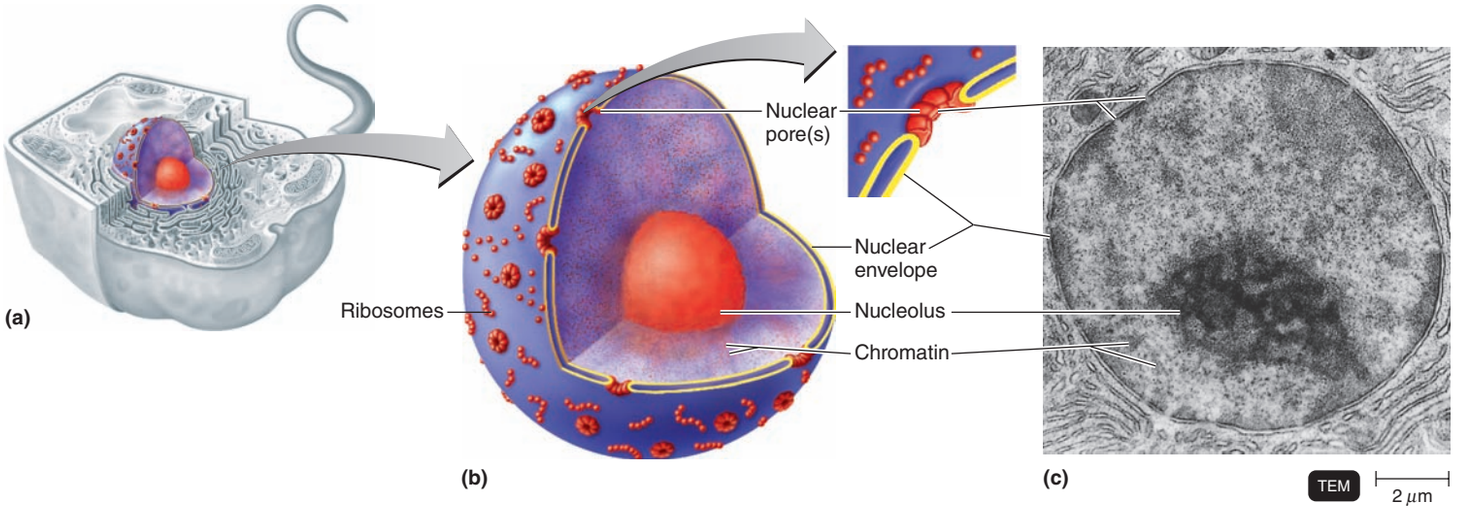



**Figure 4.24 The eukaryotic nucleus.** (**a, b**) Drawings of details of a nucleus. (**c**) A micrograph of a nucleus.

Q What keeps the nucleus suspended in the cell?

and its associated proteins appear as a threadlike mass called **chromatin.** During nuclear division, the chromatin coils into shorter and thicker rodlike bodies called **chromosomes.** Prokaryotic chromosomes do not undergo this process, do not have histones, and are not enclosed in a nuclear envelope.

Eukaryotic cells require two elaborate mechanisms: mitosis and meiosis to segregate chromosomes prior to cell division. Neither process occurs in prokaryotic cells.

## Endoplasmic Reticulum

Within the cytoplasm of eukaryotic cells is the **endoplasmic reticulum,** or **ER,** an extensive network of flattened membranous sacs or tubules called **cisternae** (Figure 4.25). The ER network is continuous with the nuclear envelope (see Figure 4.22a).

Most eukaryotic cells contain two distinct, but interrelated, forms of ER that differ in structure and function. The membrane of **rough ER** is continuous with the nuclear membrane and usually unfolds into a series of flattened sacs. The outer surface of rough ER is studded with ribosomes, the sites of protein synthesis. Proteins synthesized by ribosomes that are attached to rough ER enter cisternae within the ER for processing and sorting. In some cases, enzymes within the cisternae attach the proteins to carbohydrates to form glycoproteins. In other cases, enzymes attach the proteins to phospholipids, also synthesized by rough ER. These molecules may be incorporated into organelle membranes or the plasma membrane. Thus, rough ER is a factory for synthesizing secretory proteins and membrane molecules.

**Smooth ER** extends from the rough ER to form a network of membrane tubules (see Figure 4.25). Unlike rough ER, smooth ER does not have ribosomes on the outer surface of its membrane. However, smooth ER contains unique enzymes that make it functionally more diverse than rough ER. Although it does not synthesize proteins, smooth ER does synthesize phospholipids, as does rough ER. Smooth ER also synthesizes fats and steroids, such as estrogens and testosterone. In liver cells, enzymes of the smooth ER help release glucose into the bloodstream and inactivate or detoxify drugs and other potentially harmful substances (for example, alcohol). In muscle cells, calcium ions released from the sarcoplasmic reticulum, a form of smooth ER, trigger the contraction process.

## Golgi Complex

Most of the proteins synthesized by ribosomes attached to rough ER are ultimately transported to other regions of the cell. The first step in the transport pathway is through an organelle called the **Golgi complex.** It consists of 3 to 20 cisternae that resemble a stack of pita bread (Figure 4.26). The cisternae are often curved, giving the Golgi complex a cuplike shape.

Proteins synthesized by ribosomes on the rough ER are surrounded by a portion of the ER membrane, which eventually buds from the membrane surface to form a **transport vesicle.** The transport vesicle fuses with a cistern of the Golgi complex, releasing proteins into the cistern. The proteins are modified and move from one cistern to another via **transfer vesicles** that bud from the edges of the cisternae. Enzymes in the cisternae modify the proteins to form glycoproteins, glycolipids, and lipoproteins. Some of the processed proteins leave the cisternae in **secretory vesicles,** which detach from the cistern and deliver the proteins to the plasma membrane, where they are discharged by exocytosis. Other processed proteins leave the cisternae in vesicles that deliver their contents to the plasma membrane for incorporation into the membrane. Finally, some processed proteins leave the cisternae in vesicles that are called

**storage vesicles.** The major storage vesicle is a lysosome, whose structure and functions are discussed next.

## Lysosomes

**Lysosomes** are formed from Golgi complexes and look like membrane-enclosed spheres. Unlike mitochondria, lysosomes have only a single membrane and lack internal structure (see Figure 4.22). But they contain as many as 40 different kinds of powerful digestive enzymes capable of breaking down various molecules. Moreover, these enzymes can also digest bacteria that enter the cell. Human white blood cells, which use phagocytosis to ingest bacteria, contain large numbers of lysosomes.

## Vacuoles

A **vacuole** (see Figure 4.22) is a space or cavity in the cytoplasm of a cell that is enclosed by a membrane called a *tonoplast*. In plant cells, vacuoles may occupy 5–90% of the cell volume, depending on the type of cell. Vacuoles are derived from the Golgi complex and have several diverse functions. Some vacuoles serve as temporary storage organelles for substances such as proteins, sugars, organic acids, and inorganic ions. Other vacuoles form during endocytosis to help bring food into the cell. Many plant cells also store metabolic wastes and poisons that would otherwise be injurious if they accumulated in the cytoplasm. Finally, vacuoles may take up water, enabling plant cells to increase in size and also providing rigidity to leaves and stems.

## Mitochondria

Spherical or rod-shaped organelles called **mitochondria** (singular: **mitochondrion**) appear throughout the cytoplasm of most eukaryotic cells (see Figure 4.22). The number of mitochondria per cell varies greatly among different types of cells. For example, the protozoan *Giardia* has no mitochondria, whereas liver cells contain 1000 to 2000 per cell. A mitochondrion consists of a double membrane similar in structure to the plasma membrane (Figure 4.27). The outer mitochondrial membrane is smooth, but the inner mitochondrial membrane is arranged in a series of folds called **cristae** (singular: **crista**). The center of the mitochondrion is a semifluid substance called the **matrix.** Because of the nature and arrangement of the cristae, the inner membrane provides an enormous surface area on which chemical reactions can occur. Some proteins that function in cellular respiration, including the enzyme that makes ATP, are located on the cristae of the inner mitochondrial membrane, and many of the metabolic steps involved in cellular respiration are concentrated in the matrix (see Chapter 5). Mitochondria are often called the "powerhouses of the cell" because of their central role in ATP production.

Mitochondria contain 70S ribosomes and some DNA of their own, as well as the machinery necessary to replicate, transcribe, and translate the information encoded by their DNA. In addition, mitochondria can reproduce more or less on their own by growing and dividing in two.

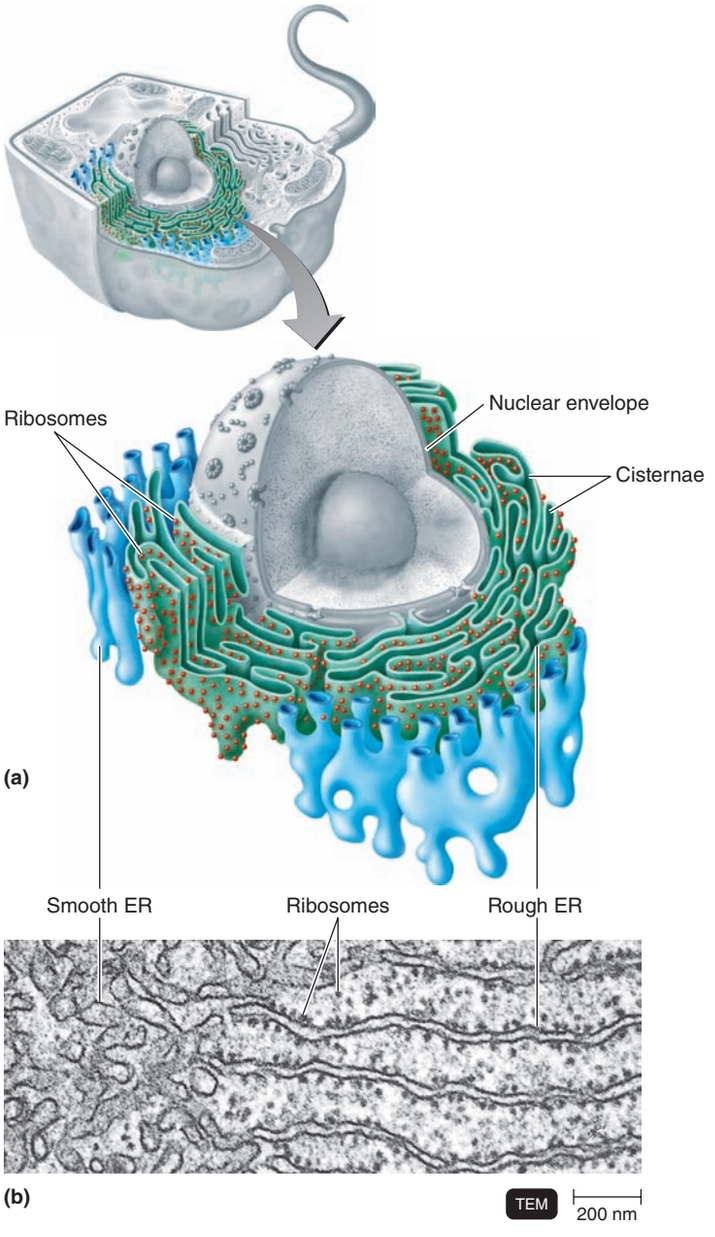



**Figure 4.25 Rough endoplasmic reticulum and ribosomes.** (**a**) A drawing of details of the endoplasmic reticulum. (**b**) A micrograph of the endoplasmic reticulum and ribosomes.

Q What functions of the smooth ER and rough ER are similar?

## Chloroplasts

Algae and green plants contain a unique organelle called a **chloroplast** (Figure 4.28), a membrane-enclosed structure that contains both the pigment chlorophyll and the enzymes required for the light-gathering phases of photosynthesis (see Chapter 5). The chlorophyll is contained in flattened membrane sacs called **thylakoids;** stacks of thylakoids are called *grana* (singular: **granum**) (see Figure 4.28).

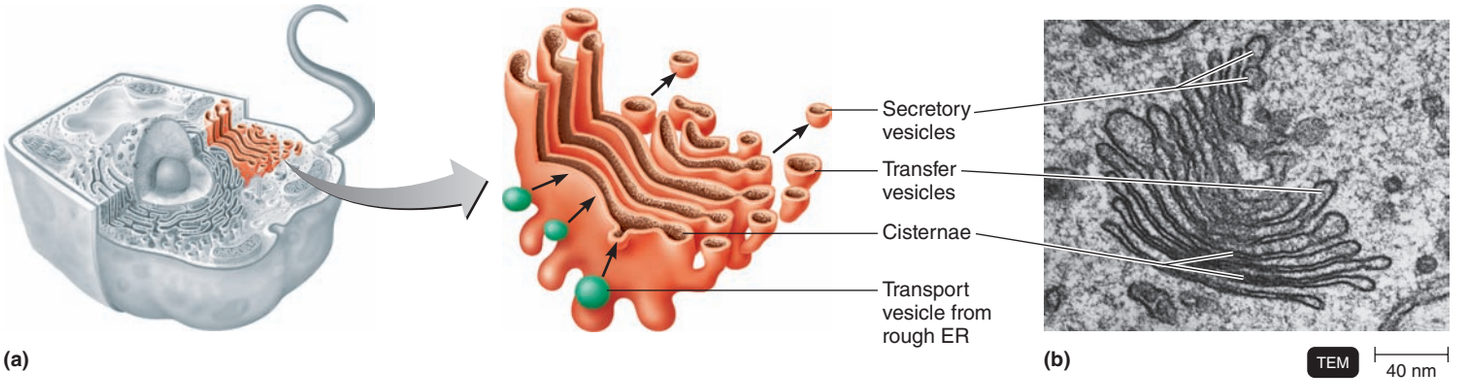



**Figure 4.26 Golgi complex.** (**a**) A drawing of details of a Golgi complex. (**b**) A micrograph of a Golgi complex.

Q What is the function of the Golgi complex?

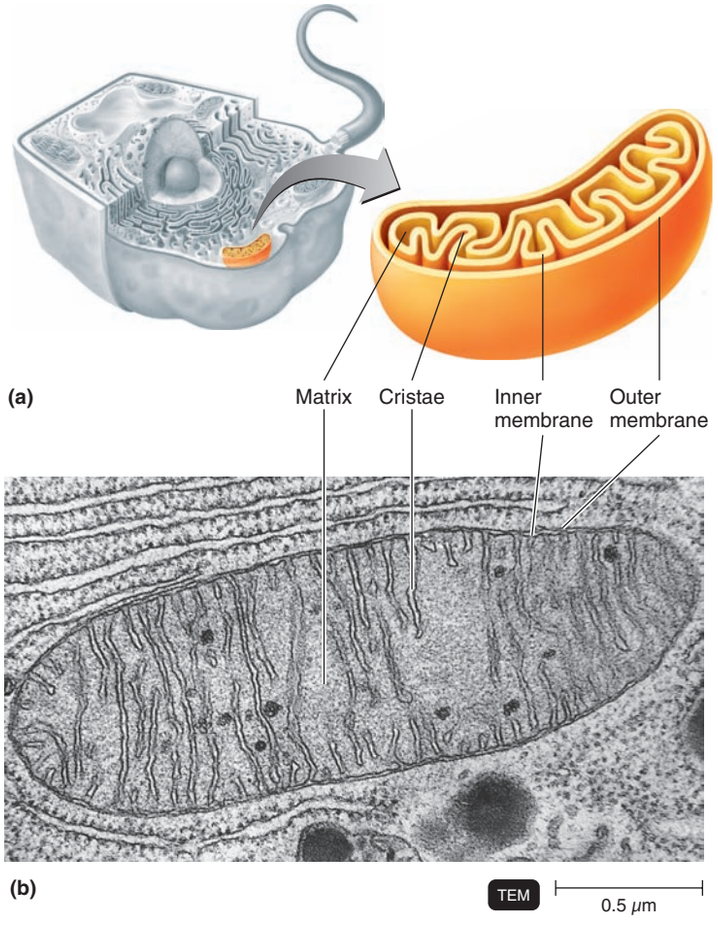



**Figure 4.27 Mitochondria.** (**a**) A drawing of details of a mitochondrion. (**b**) A micrograph of a mitochondrion from a rat pancreas cell.

Q How are mitochondria similar to prokaryotic cells?

Like mitochondria, chloroplasts contain 70S ribosomes, DNA, and enzymes involved in protein synthesis. They are capable of multiplying on their own within the cell. The way both chloroplasts and mitochondria multiply—by increasing in size and then dividing in two—is strikingly reminiscent of bacterial multiplication.

## Peroxisomes

Organelles similar in structure to lysosomes, but smaller, are called **peroxisomes** (see Figure 4.22). Although peroxisomes were once thought to form by budding off the ER, it is now generally agreed that they form by the division of preexisting peroxisomes.

Peroxisomes contain one or more enzymes that can oxidize various organic substances. For example, substances such as amino acids and fatty acids are oxidized in peroxisomes as part of normal metabolism. In addition, enzymes in peroxisomes oxidize toxic substances, such as alcohol. A by-product of the oxidation reactions is hydrogen peroxide ($H_2O_2$), a potentially toxic compound. However, peroxisomes also contain the enzyme *catalase,* which decomposes $H_2O_2$ (see Chapter 6, page 160). Because the generation and degradation of $H_2O_2$ occurs within the same organelle, peroxisomes protect other parts of the cell from the toxic effects of $H_2O_2$.

## Centrosome

The **centrosome,** located near the nucleus, consists of two components: the pericentriolar area and centrioles (see Figure 4.22). The *pericentriolar material* is a region of the cytosol composed of a dense network of small protein fibers. This area is the organizing center for the mitotic spindle, which plays a critical role in cell division, and for microtubule formation in nondividing cells. Within the pericentriolar material is a pair of cylindrical structures called *centrioles,* each of which is composed of nine clusters of three microtubules (triplets) arranged in a circular

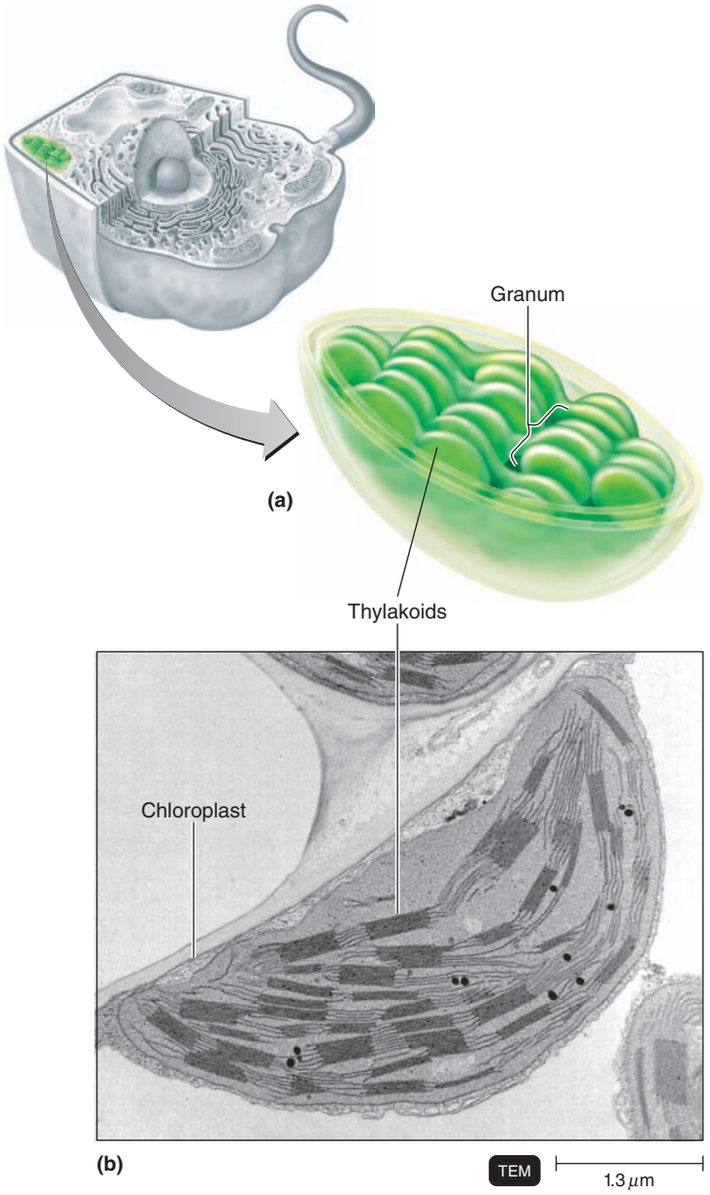



**Figure 4.28 Chloroplasts.** Photosynthesis occurs in chloroplasts; the light-trapping pigments are located on the thylakoids. (**a**) A drawing of details of a chloroplast, showing grana. (**b**) A micrograph of chloroplasts in a plant cell.

Q What are the similarities between chloroplasts and prokaryotic cells?

pattern, an arrangement called a *9 + 0 array*. The 9 refers to the nine clusters of microtubules, and the 0 refers to the absence of microtubules in the center. The long axis of one centriole is at a right angle to the long axis of the other.

### CHECK YOUR UNDERSTANDING

- Compare the structure of the nucleus of a eukaryote and the nucleoid of a prokaryote. **4-18**
- How do rough and smooth ER compare structurally and functionally? **4-19**

## The Evolution of Eukaryotes

### LEARNING OBJECTIVE

**4-20** Discuss evidence that supports the endosymbiotic theory of eukaryotic evolution.

Biologists generally believe that life arose on Earth in the form of very simple organisms, similar to prokaryotic cells, about 3.5 to 4 billion years ago. About 2.5 billion years ago, the first eukaryotic cells evolved from prokaryotic cells. Recall that prokaryotes and eukaryotes differ mainly in that eukaryotes contain highly specialized organelles. The theory explaining the origin of eukaryotes from prokaryotes, pioneered by Lynn Margulis, is the **endosymbiotic theory.** According to this theory, larger bacterial cells lost their cell walls and engulfed smaller bacterial cells. This relationship, in which one organism lives within another, is called *endosymbiosis* (*symbiosis* = living together).

According to the endosymbiotic theory, the ancestral eukaryote developed a rudimentary nucleus when the plasma membrane folded around the chromosome (see Figure 10.2, page 275). This cell, called a nucleoplasm, may have ingested aerobic bacteria. Some ingested bacteria lived inside the host nucleoplasm. This arrangement evolved into a symbiotic relationship in which the host nucleoplasm supplied nutrients and the endosymbiotic bacterium produced energy that could be used by the nucleoplasm. Similarly, chloroplasts may be descendants of photosynthetic prokaryotes ingested by this early nucleoplasm. Eukaryotic flagella and cilia are believed to have originated from symbiotic associations between the plasma membrane of early eukaryotes and motile spiral bacteria called spirochetes. A living example that suggests how flagella developed is described in the box on the next page.

Studies comparing prokaryotic and eukaryotic cells provide evidence for the endosymbiotic theory. For example, both mitochondria and chloroplasts resemble bacteria in size and shape. Further, these organelles contain circular DNA, which is typical of prokaryotes, and the organelles can reproduce independently of their host cell. Moreover, mitochondrial and chloroplast ribosomes resemble those of prokaryotes, and their mechanism of protein synthesis is more similar to that found in bacteria than eukaryotes. Also, the same antibiotics that inhibit protein synthesis on ribosomes in bacteria also inhibit protein synthesis on ribosomes in mitochondria and chloroplasts.

### CHECK YOUR UNDERSTANDING

- Which three organelles are not associated with the Golgi complex? What does this suggest about their origin? **4-20**

* * *

Our next concern is to examine microbial metabolism. In Chapter 5, you will learn about the importance of enzymes to microorganisms and the ways microbes produce and use energy.

# Why Microbiologists Study Termites

**Although termites are famous for their ability to eat wood,** causing damage to wooden structures and recycling cellulose in the soil, they are unable to digest the wood that they eat. To break down the cellulose, termites enlist the help of a variety of microorganisms. Some termites, for example, dig tunnels in the wood, then inoculate the tunnels with fungi that grow on the wood. These termites then eat the fungi, not the wood itself.

What microbiologists find more interesting are the termites that contain, within their digestive tracts, symbiotic microorganisms that digest the cellulose that the termites chew and swallow. In fact, these symbiotic microorganisms can survive only because of even smaller symbionts that live on and within them, without which they would not even be able to move. By studying how a single termite survives, microbiologists have begun to gain an entirely new understanding of symbiosis.

The termite's dependence on nitrogen-fixing bacteria to supply its nitrogen and on protozoans such as *Trichonympha sphaerica* to digest cellulose are examples of endosymbiosis, a symbiotic relationship with an organism that lives inside the body of the host organism (in this case, within the hindgut of the termite).

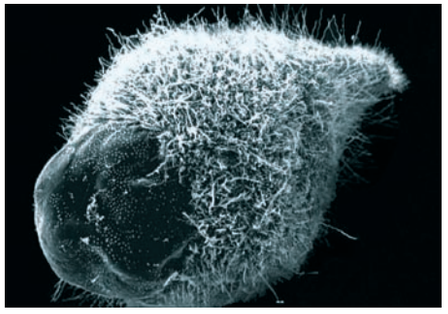
The picture is more complicated than this, however, for *T. sphaerica* is unable to digest cellulose without the aid of bacteria that live within its body: in other words, the protozoan has its own endosymbionts.

Certain hindgut flagellates such as *T. sphaerica* also demonstrate another form of symbiosis—ectosymbiosis, a symbiotic relationship with organisms that live outside its body. Advances in microscopy have shown that these flagellates are covered by precise rows consisting of thousands of bacteria, either rods or spirochetes. If these bacteria are killed, the protozoan is unable to move. Instead of using its own flagella, the protozoan relies on the rows of bacteria to row it about like oarsmen in a boat.

The protozoan *Mixotricha,* for example, has rows of spirochetes on its surface (see photo, upper right). The end of each spirochete abuts against a swelling known as a bracket; see part a of the figure. The spirochetes undulate in unison, thereby creating waves of motion along *Mixotricha's* surface.

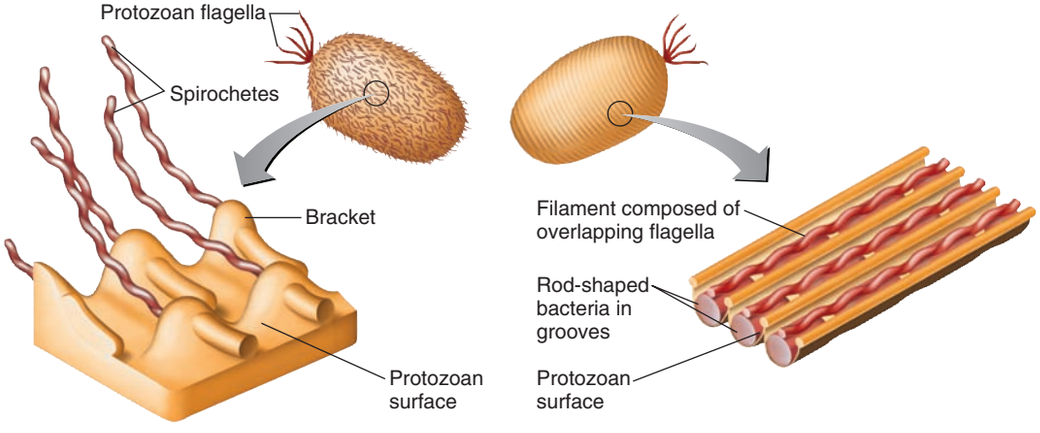
Rod-shaped bacteria align in grooves that cover the surface of devescovinids, another group of termite-hindgut protozoans. Each rod has 12 flagella that overlap the flagella of the adjacent bacteria to form a continuous filament along the groove (see part b). The bacteria rotate their flagella, thus creating coordinated waves along all these rows of filaments, which propel the protozoan.

Sid Tamm and his colleagues at Boston University have found that the protozoa cannot control motility of the ectosymbiotics. *Mixotricha* uses its flagella to steer, and the bacteria push the protozoa forward—shoving and being shoved by its neighbors, much like bumper cars.




***Mixotricha,* a protozoan that lives in the termite gut.**

**Arrangements of bacteria on the surfaces of two protozoans.**




**(a)** Spirochetes attached to brackets over the surface of a *Mixotricha* protozoan align themselves and move in unison.

**(b)** On this devescovinid protozoan, the flagella from one rod-shaped bacterium overlap the next to form a continuous filament.

## Study Outline

MasteringMICROBIOLOGY™

Test your understanding with quizzes, microbe review, and a chapter post-test at www.masteringmicrobiology.com.

### Comparing Prokaryotic and Eukaryotic Cells: An Overview (p. 76)

1. Prokaryotic and eukaryotic cells are similar in their chemical composition and chemical reactions.

2. Prokaryotic cells lack membrane-enclosed organelles (including a nucleus).
3. Peptidoglycan is found in prokaryotic cell walls but not in eukaryotic cell walls.
4. Eukaryotic cells have a membrane-bound nucleus and other or ganelles.

# The Prokaryotic Cell (pp. 76–97)

1. Bacteria are unicellular, and most of them multiply by binary fission.
2. Bacterial species are differentiated by morphology, chemical composition, nutritional requirements, biochemical activities, and source of energy.

## The Size, Shape, and Arrangement of Bacterial Cells (pp. 77–78)

1. Most bacteria are 0.2 to 2.0 μm in diameter and 2 to 8 μm in length.
2. The three basic bacterial shapes are coccus (spherical), bacillus (rod-shaped), and spiral (twisted).
3. Pleomorphic bacteria can assume several shapes.

## Structures External to the Cell Wall (pp. 78–84)

### Glycocalyx (p. 80)

1. The glycocalyx (capsule, slime layer, or extracellular polysaccharide) is a gelatinous polysaccharide and/or polypeptide covering.
2. Capsules may protect pathogens from phagocytosis.
3. Capsules enable adherence to surfaces, prevent desiccation, and may provide nutrients.

### Flagella (pp. 81–82)

4. Flagella are relatively long filamentous appendages consisting of a filament, hook, and basal body.
5. Prokaryotic flagella rotate to push the cell.
6. Motile bacteria exhibit taxis; positive taxis is movement toward an attractant, and negative taxis is movement away from a repellent.
7. Flagellar (H) protein is an antigen.

### Axial Filaments (p. 82)

8. Spiral cells that move by means of an axial filament (endoflagellum) are called spirochetes.
9. Axial filaments are similar to flagella, except that they wrap around the cell.

### Fimbriae and Pili (pp. 82–84)

10. Fimbriae help cells adhere to surfaces.
11. Pili are involved in twitching motility and DNA transfer.

## The Cell Wall (pp. 84–88)

### Composition and Characteristics (pp. 84–86)

1. The cell wall surrounds the plasma membrane and protects the cell from changes in water pressure.
2. The bacterial cell wall consists of peptidoglycan, a polymer consisting of NAG and NAM and short chains of amino acids.
3. Penicillin interferes with peptidoglycan synthesis.
4. Gram-positive cell walls consist of many layers of peptidoglycan and also contain teichoic acids.
5. Gram-negative bacteria have a lipopolysaccharide-lipoprotein-phospholipid outer membrane surrounding a thin peptidoglycan layer.
6. The outer membrane protects the cell from phagocytosis and from penicillin, lysozyme, and other chemicals.
7. Porins are proteins that permit small molecules to pass through the outer membrane; specific channel proteins allow other molecules to move through the outer membrane.
8. The lipopolysaccharide component of the outer membrane consists of sugars (O polysaccharides), which function as antigens, and lipid A, which is an endotoxin.

### Cell Walls and the Gram Stain Mechanism (pp. 86–87)

9. The crystal violet–iodine complex combines with peptidoglycan.
10. The decolorizer removes the lipid outer membrane of gram-negative bacteria and washes out the crystal violet.

### Atypical Cell Walls (pp. 87–88)

11. *Mycoplasma* is a bacterial genus that naturally lacks cell walls.
12. Archaea have pseudomurein; they lack peptidoglycan.
13. Acid-fast cell walls have a layer of mycolic acid outside a thin peptidoglycan layer.

### Damage to the Cell Wall (p. 88)

14. In the presence of lysozyme, gram-positive cell walls are destroyed, and the remaining cellular contents are referred to as a protoplast.
15. In the presence of lysozyme, gram-negative cell walls are not completely destroyed, and the remaining cellular contents are referred to as a spheroplast.
16. L forms are gram-positive or gram-negative bacteria that do not make a cell wall.
17. Antibiotics such as penicillin interfere with cell wall synthesis.

## Structures Internal to the Cell Wall (pp. 88–97)

### The Plasma (Cytoplasmic) Membrane (pp. 89–90)

1. The plasma membrane encloses the cytoplasm and is a lipid bilayer with peripheral and integral proteins (the fluid mosaic model).
2. The plasma membrane is selectively permeable.
3. Plasma membranes contain enzymes for metabolic reactions, such as nutrient breakdown, energy production, and photosynthesis.
4. Mesosomes, irregular infoldings of the plasma membrane, are artifacts, not true cell structures.
5. Plasma membranes can be destroyed by alcohols and polymyxins.

### The Movement of Materials across Membranes (pp. 91–93)

6. Movement across the membrane may be by passive processes, in which materials move from areas of higher to lower concentration and no energy is expended by the cell.
7. In simple diffusion, molecules and ions move until equilibrium is reached.
8. In facilitated diffusion, substances are transported by transporter proteins across membranes from areas of high to low concentration.
9. Osmosis is the movement of water from areas of high to low concentration across a selectively permeable membrane until equilibrium is reached.

10. In active transport, materials move from areas of low to high concentration by transporter proteins, and the cell must expend energy.
11. In group translocation, energy is expended to modify chemicals and transport them across the membrane.

### Cytoplasm (p. 94)

12. Cytoplasm is the fluid component inside the plasma membrane.
13. The cytoplasm is mostly water, with inorganic and organic molecules, DNA, ribosomes, and inclusions.

### The Nucleoid (p. 94)

14. The nucleoid contains the DNA of the bacterial chromosome.
15. Bacteria can also contain plasmids, which are circular, extrachromosomal DNA molecules.

### Ribosomes (p. 94)

16. The cytoplasm of a prokaryote contains numerous 70S ribosomes; ribosomes consist of rRNA and protein.
17. Protein synthesis occurs at ribosomes; it can be inhibited by certain antibiotics.

### Inclusions (pp. 94–95)

18. Inclusions are reserve deposits found in prokaryotic and eukaryotic cells.
19. Among the inclusions found in bacteria are metachromatic granules (inorganic phosphate), polysaccharide granules (usually glycogen or starch), lipid inclusions, sulfur granules, carboxysomes (ribulose 1,5-diphosphate carboxylase), magnetosomes ($Fe_3O_4$), and gas vacuoles.

### Endospores (pp. 95–97)

20. Endospores are resting structures formed by some bacteria; they allow survival during adverse environmental conditions.
21. The process of endospore formation is called sporulation; the return of an endospore to its vegetative state is called germination.

## The Eukaryotic Cell (pp. 97–106)

### Flagella and Cilia (pp. 97–99)

1. Flagella are few and long in relation to cell size; cilia are numerous and short.
2. Flagella and cilia are used for motility, and cilia also move substances along the surface of the cells.
3. Both flagella and cilia consist of an arrangement of nine pairs and two single microtubules.

### The Cell Wall and Glycocalyx (p. 99)

1. The cell walls of many algae and some fungi contain cellulose.
2. The main material of fungal cell walls is chitin.
3. Yeast cell walls consist of glucan and mannan.
4. Animal cells are surrounded by a glycocalyx, which strengthens the cell and provides a means of attachment to other cells.

### The Plasma (Cytoplasmic) Membrane (p. 100)

1. Like the prokaryotic plasma membrane, the eukaryotic plasma membrane is a phospholipid bilayer containing proteins.
2. Eukaryotic plasma membranes contain carbohydrates attached to the proteins and sterols not found in prokaryotic cells (except *Mycoplasma* bacteria).
3. Eukaryotic cells can move materials across the plasma membrane by the passive processes used by prokaryotes and by active transport and endocytosis (phagocytosis, pinocytosis, and receptor-mediated endocytosis).

### Cytoplasm (p. 101)

1. The cytoplasm of eukaryotic cells includes everything inside the plasma membrane and external to the nucleus.
2. The chemical characteristics of the cytoplasm of eukaryotic cells resemble those of the cytoplasm of prokaryotic cells.
3. Eukaryotic cytoplasm has a cytoskeleton and exhibits cytoplasmic streaming.

### Ribosomes (p. 101)

1. 80S ribosomes are found in the cytoplasm or attached to the rough endoplasmic reticulum.

### Organelles (pp. 101–105 )

1. Organelles are specialized membrane-enclosed structures in the cytoplasm of eukaryotic cells.
2. The nucleus, which contains DNA in the form of chromosomes, is the most characteristic eukaryotic organelle.
3. The nuclear envelope is connected to a system of membranes in the cytoplasm called the endoplasmic reticulum (ER).
4. The ER provides a surface for chemical reactions and serves as a transport network. Protein synthesis and transport occur on the rough ER; lipid synthesis occurs on the smooth ER.
5. The Golgi complex consists of flattened sacs called cisterns. It functions in membrane formation and protein secretion.
6. Lysosomes are formed from Golgi complexes. They store digestive enzymes.
7. Vacuoles are membrane-enclosed cavities derived from the Golgi complex or endocytosis. They are usually found in plant cells that store various substances and provide rigidity to leaves and stems.
8. Mitochondria are the primary sites of ATP production. They contain 70S ribosomes and DNA, and they multiply by binary fission.
9. Chloroplasts contain chlorophyll and enzymes for photosynthesis. Like mitochondria, they contain 70S ribosomes and DNA and multiply by binary fission.
10. A variety of organic compounds are oxidized in peroxisomes. Catalase in peroxisomes destroys $H_2O_2$.
11. The centrosome consists of the pericentriolar material and centrioles. Centrioles are 9 triplet microtubules involved in formation of the mitotic spindle and microtubules.

### The Evolution of Eukaryotes (p. 105)

1. According to the endosymbiotic theory, eukaryotic cells evolved from symbiotic prokaryotes living inside other prokaryotic cells.

# Study Questions

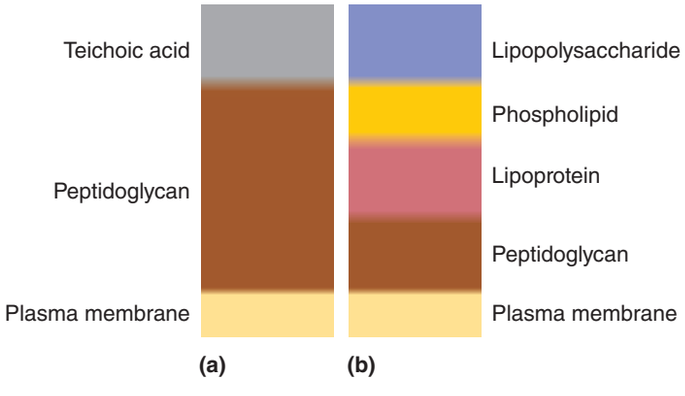
Answers to the Review and Multiple Choice questions can be found by turning to the Answers tab at the back of the textbook.

## Review

1. DRAW IT Diagram each of the following flagellar arrangements:
   **a.** lophotrichous **d.** amphitrichous
   **b.** monotrichous **e.** polar
   **c.** peritrichous
2. Endospore formation is called (a) _____. It is initiated by (b) _____. Formation of a new cell from an endospore is called (c) _____. This process is triggered by (d) _____.
3. DRAW IT Draw the bacterial shapes listed in (a), (b), and (c). Then draw the shapes in (d), (e), and (f), showing how they are special conditions of a, b, and c, respectively.
   **a.** spiral **d.** spirochetes
   **b.** bacillus **e.** streptobacilli
   **c.** coccus **f.** staphylococci
4. Match the structures in column A to their functions in column B.

| Column A | Column B |
|---|---|
| _____ **a.** Cell wall | **1.** Attachment to surfaces |
| _____ **b.** Endospore | **2.** Cell wall formation |
| _____ **c.** Fimbriae | **3.** Motility |
| _____ **d.** Flagella | **4.** Protection from osmotic lysis |
| _____ **e.** Glycocalyx | **5.** Protection from phagocytes |
| _____ **f.** Pili | **6.** Resting |
| _____ **g.** Plasma membrane | **7.** Protein synthesis |
| _____ **h.** Ribosomes | **8.** Selective permeability |
| | **9.** Transfer of genetic material |

5. Why is an endospore called a resting structure? Of what advantage is an endospore to a bacterial cell?
6. Compare and contrast the following:
   **a.** simple diffusion and facilitated diffusion
   **b.** active transport and facilitated diffusion
   **c.** active transport and group translocation
7. Answer the following questions using the diagrams provided, which represent cross sections of bacterial cell walls.
   **a.** Which diagram represents a gram-positive bacterium? How can you tell?




   **b.** Explain how the Gram stain works to distinguish these two types of cell walls.
   **c.** Why does penicillin have no effect on most gram-negative cells?
   **d.** How do essential molecules enter cells through each wall?
   **e.** Which cell wall is toxic to humans?
8. Starch is readily metabolized by many cells, but a starch molecule is too large to cross the plasma membrane. How does a cell obtain the glucose molecules from a starch polymer? How does the cell transport these glucose molecules across the plasma membrane?
9. Match the characteristics of eukaryotic cells in column A with their functions in column B.

| Column A | Column B |
|---|---|
| _____ **a.** Pericentriolar material | **1.** Digestive enzyme storage |
| _____ **b.** Chloroplasts | **2.** Oxidation of fatty acids |
| _____ **c.** Golgi complex | **3.** Microtubule formation |
| _____ **d.** Lysosomes | **4.** Photosynthesis |
| _____ **e.** Mitochondria | **5.** Protein synthesis |
| _____ **f.** Peroxisomes | **6.** Respiration |
| _____ **g.** Rough ER | **7.** Secretion |

10. NAME IT What group of microbes is characterized by cells that form filaments, reproduce by spores, and have peptidoglycan in their cell walls?

## Multiple Choice

1. Which of the following is *not* a distinguishing characteristic of prokaryotic cells?
   **a.** They usually have a single, circular chromosome.
   **b.** They lack membrane-enclosed organelles.
   **c.** They have cell walls containing peptidoglycan.
   **d.** Their DNA is not associated with histones.
   **e.** They lack a plasma membrane.

Use the following choices to answer questions 2–4.

   **a.** No change will result; the solution is isotonic.
   **b.** Water will move into the cell.
   **c.** Water will move out of the cell.
   **d.** The cell will undergo osmotic lysis.
   **e.** Sucrose will move into the cell from an area of higher concentration to one of lower concentration.

2. Which statement best describes what happens when a gram-positive bacterium is placed in distilled water and penicillin?
3. Which statement best describes what happens when a gram-negative bacterium is placed in distilled water and penicillin?
4. Which statement best describes what happens when a gram-positive bacterium is placed in an aqueous solution of lysozyme and 10% sucrose?
5. Which of the following statements best describes what happens to a cell exposed to polymyxins that destroy phospholipids?
   **a.** In an isotonic solution, nothing will happen.
   **b.** In a hypotonic solution, the cell will lyse.
   **c.** Water will move into the cell.
   **d.** Intracellular contents will leak from the cell.
   **e.** Any of the above might happen.

6. Which of the following is *false* about fimbriae?
   a. They are composed of protein.
   b. They may be used for attachment.
   c. They are found on gram-negative cells.
   d. They are composed of pilin.
   e. They may be used for motility.
7. Which of the following pairs is *mismatched*?
   a. glycocalyx—adherence
   b. pili—reproduction
   c. cell wall—toxin
   d. cell wall—protection
   e. plasma membrane—transport
8. Which of the following pairs is *mismatched*?
   a. metachromatic granules—stored phosphates
   b. polysaccharide granules—stored starch
   c. lipid inclusions—poly-β-hydroxybutyric acid
   d. sulfur granules—energy reserve
   e. ribosomes—protein storage
9. You have isolated a motile, gram-positive cell with no visible nucleus. You can assume this cell has
   a. ribosomes.
   b. mitochondria.
   c. an endoplasmic reticulum.
   d. a Golgi complex.
   e. all of the above
10. The antibiotic amphothericin B disrupts plasma membranes by combining with sterols; it will affect all of the following cells *except*
    a. animal cells.
    b. gram-negative bacterial cells.
    c. fungal cells.
    d. *Mycoplasma* cells.
    e. plant cells.

## Critical Thinking

1. How can prokaryotic cells be smaller than eukaryotic cells and still carry on all the functions of life?
2. The smallest eukaryotic cell is the motile alga *Micromonas.* What is the minimum number of organelles this alga must have?
3. Two types of prokaryotic cells have been distinguished: bacteria and archaea. How do these cells differ from each other? How are they similar?
4. In 1985, a 0.5-mm cell was discovered in surgeonfish and named *Epulopiscium fishelsoni* (see Figure 11.14 page 315). It was presumed to be a protozoan. In 1993, researchers determined that *Epulopiscium* was actually a gram-positive bacterium. Why do you suppose this organism was initially identified as a protozoan? What evidence would change the classification to bacterium?
5. When *E. coli* cells are exposed to a hypertonic solution, the bacteria produce a transporter protein that can move $K^+$ (potassium ions) into the cell. Of what value is the active transport of $K^+$, which requires ATP?

## Clinical Applications

1. *Clostridium botulinum* is a strict anaerobe; that is, it is killed by the molecular oxygen ($O_2$) present in air. Humans can die of botulism from eating foods in which *C. botulinum* is growing. How does this bacterium survive on plants picked for human consumption? Why are home-canned foods most often the source of botulism?
2. A South San Francisco child enjoyed bath time at his home because of the colorful orange and red water. The water did not have this rusty color at its source, and the water department could not culture the *Thiobacillus* bacteria responsible for the rusty color from the source. How were the bacteria getting into the household water? What bacterial structures make this possible?
3. Live cultures of *Bacillus thuringiensis* (Dipel) and *B. subtilis* (Kodiak) are sold as pesticides. What bacterial structures make it possible to package and sell these bacteria? For what purpose is each product used? (*Hint:* Refer to Chapter 11.)