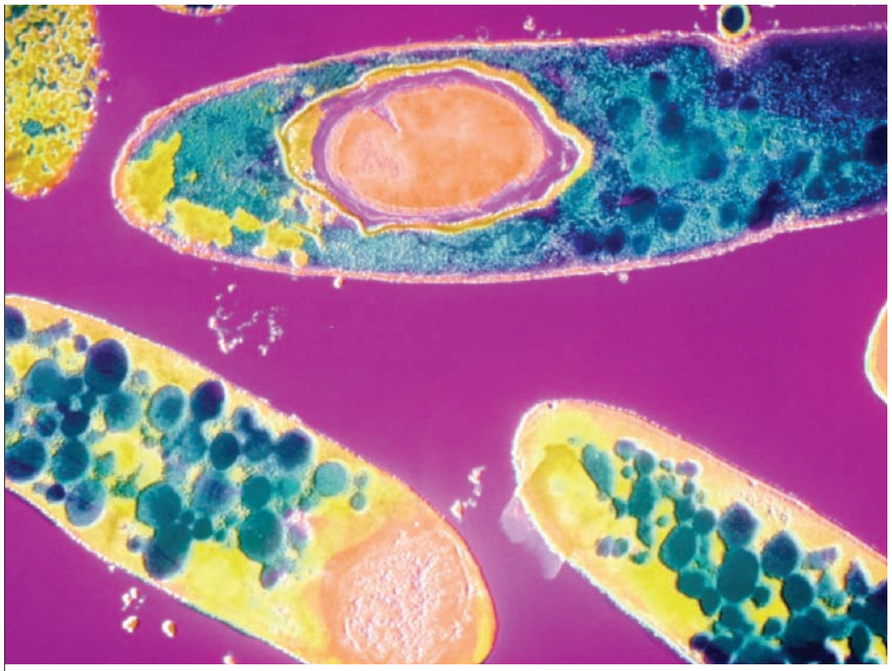


The bacterium *Clostridium butyricum*, one of the *Clostridium* species that produces the toxin botulin (colorized TEM).

Study Plan

25 Prokaryotes and Viruses

Why It Matters

You wait in line with anticipation at a fast-food restaurant, biding your time until you reach the counter and get your hamburger. Somewhere in the back of your mind may be the worry that the hamburger will contain bacteria that could make you sick or even cost you your life. The hamburger you receive will be well done, almost to the crispy stage, because of that fear. Not too many years ago, people were sickened, and a few even died, because their fast-food hamburgers were contaminated by a pathogenic strain of the bacterium *Escherichia coli,* the normally harmless bacteria that inhabit our intestinal tract. Since then, fast-food restaurants have cooked their hamburgers well beyond the point required to kill any lurking *E. coli* or other pathogenic bacteria.

The bacterium *E. coli* is a prokaryote, an organism lacking a true nucleus. Prokaryotes, the main topic of this chapter, are the smallest organisms of the world **(Figure 25.1).** Few species are more than 1 to 2 μm long; from 500 to 1000 of them would fit side by side across the dot above this letter "i."

Prokaryotes are small, but their total collective mass (their *biomass*) on Earth may be greater than that of all plant life. They colonize

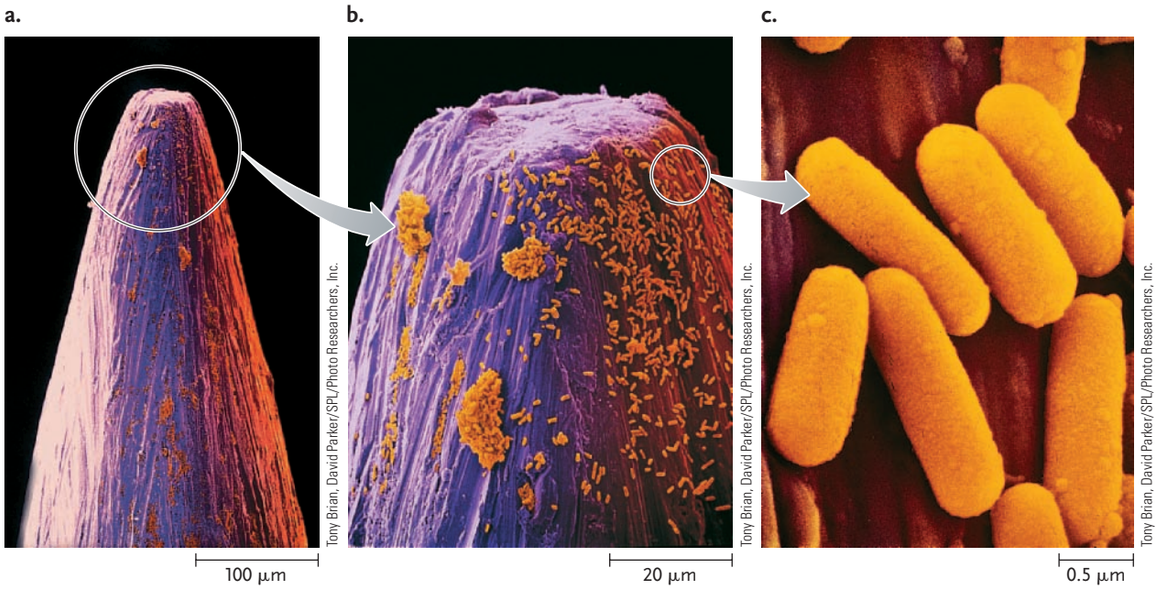


Figure 25.1
Bacillus bacteria on the point of a pin. Cells magnified **(a)** 70 times, **(b)** 350 times, and **(c)** 14,000 times.

every niche on Earth that supports life, meaning that they are found essentially everywhere. Huge numbers of bacteria inhabit surfaces and cavities of the human body, including the skin, the mouth and nasal passages, the large intestine, and the vagina. Collectively, the bacteria in and on the human body outnumber all the cells in the body.

Biologists classify prokaryotes into two of the three domains of life, the **Archaea** and the **Bacteria** (the third domain, the **Eukarya**, includes all eukaryotes). Bacteria are the prokaryotic organisms most familiar to us, including many types responsible for diseases of humans and other animals and many other types found in a wide variety of ecosystems. Many of the Archaea (*archaios* = ancient) live under conditions so extreme, including high salinity, acidity, or temperature, that their environments cannot be tolerated by other organisms, including bacteria.

As a group, prokaryotes have a wide range of metabolic capabilities. Their metabolic activities are crucial for maintenance of the biosphere. In particular, prokaryotes are the key players in the life-sustaining recycling of the elements carbon, nitrogen, and oxygen, and this recycling is necessary to sustain life. For example, prokaryotes are involved in breaking down organic material in dead plants and animals, releasing carbon dioxide that is used for plant growth. Prokaryotes are also the only living source of nitrogen, an element essential for all life. And a significant amount of the oxygen in the atmosphere originates from bacterial photosynthesis. An illustration of prokaryotes' importance is Biosphere 2, an attempt by scientists to build a completely closed ecosystem in Arizona. The attempt failed, in part because the researchers did not have a complete enough understanding of the activities of the microorganisms in the soil. Through respiration by soil microorganisms, the oxygen level in the Biosphere structure decreased to lower-than-expected levels and the ecosystem ceased to be self-sustaining. This small-scale example illustrates the essential role of prokaryotes in enabling life of all forms to exist.

Prokaryotes also have a great impact on the lives of humans. Among other things, they are important for the production of certain foods, they carry out chemical reactions that are of importance in industry, they are used for the production of pharmaceutical products, they cause diseases, and they are used for bioremediation of polluted sites.

Viruses, the other subject of this chapter, are also extremely important in the biosphere. Smaller still than prokaryotes, viruses are present in the environment in even greater numbers than bacteria. In some aquatic habitats, viruses that infect bacteria alone exist at concentrations approaching 100 million per milliliter! Viruses are classified separately from the three domains of life because they are considered to be nonliving. However, viruses of one kind or another can infect the cells of just about every kind of living organism.

25.1 Prokaryotic Structure and Function

Prokaryotes show great diversity in their ability to colonize areas that can sustain life. Their cells are small, but relatively complex in organization. For instance, although they do not have a membrane-bound nucleus or organelles, their DNA and some proteins are localized in particular places. They vary in how their cell membrane is protected, and some species have specialized surface structures that protect them from their environment or that enable them to move actively. Prokaryotes also show great diversity in the

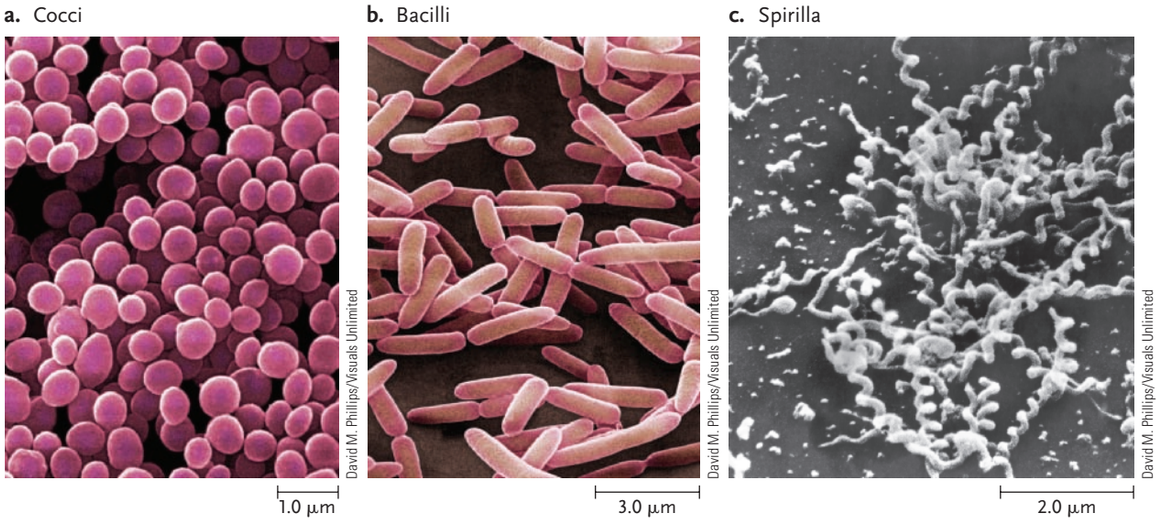


Figure 25.2
Common shapes among prokaryotes. **(a)** Scanning electron microscope (SEM) image of *Micrococcus*, a coccus bacterium; **(b)** SEM of *Salmonella*, a bacillus bacterium; **(c)** SEM of *Spiroplasma*, a spiral prokaryote of the spirillum type.

ways they obtain energy and in their metabolic activities.

The diversity of prokaryotes has arisen through rapid adaptation to their environments as a result of evolution by natural selection. Genetic variability in prokaryotic populations, the basis for this rapid adaptation, derives largely from mutation, and to a lesser degree from transfer of genes between organisms by transformation, transduction, and conjugation (see Chapter 17). Since prokaryotes have much shorter generation times than eukaryotes, and small genomes (roughly 1000 times smaller than an average eukaryote), prokaryotes have roughly 1000 times more mutations per gene, per unit time, per individual than is the case for eukaryotes. Further, prokaryotes typically have much larger population sizes than eukaryotes, contributing to their greater genetic variability. In short, prokaryotes have an enormous capacity to adapt and this has been key to their evolutionary success.

Prokaryotes Are Simple in Structure Compared with Eukaryotic Cells

Prokaryote cells examined under an electron microscope typically reveal little more than a cell wall and plasma membrane surrounding a cytoplasm with DNA concentrated in one region and ribosomes scattered throughout. They have no cytoplasmic organelles equivalent to the mitochondria, chloroplasts, endoplasmic reticulum, or Golgi complex of eukaryotic cells. With few exceptions, the reactions carried out by these organelles in eukaryotes are distributed between the cytoplasmic solution and the plasma membrane in prokaryotes.

Three shapes are common among prokaryotes: spherical, rodlike, and spiral **(Figure 25.2).** The spherical prokaryotes are **cocci** (singular, *coccus* = berry). Cylindrical or rod-shaped prokaryotes are **bacilli** (singular, *bacillus* = small staff or rod). The spiral prokaryotes are the **vibrios** (*vibrare* = to vibrate), which are curved and commalike, and the **spirilla** (singular, spirillum), which are twisted helically like a corkscrew. Among the prokaryotes of all structural types are some that live singly and others that link into chains or aggregates of cells.

Internal Structures. The genome of most prokaryotes consists of a single, circular DNA molecule called the *prokaryotic chromosome.* There are exceptions: a few bacterial species, for example the causative agent of Lyme disease *(Borrelia borgdorfri),* have a linear chromosome. Genome sequencing projects have shown that the range of genome sizes among bacteria and archaeans is about 20-fold, with the smallest genome, that of *Mycoplasma genitalium,* being about 580,000 bp. In all prokaryotes, the chromosome is packed into an area of the cell called the **nucleoid.** There is no nucleolus in the nucleoid, and it has no boundary membranes equivalent to the nuclear envelope of eukaryotes **(Figure 25.3).**

Besides the DNA of the nucleoid, many prokaryotes also contain small circles of DNA called **plasmids,** distributed in the cytoplasm. The plasmids, which often contain genes with functions that supplement those in the nucleoid, contain a replication origin that allows them to replicate along with the nucleoid DNA and be passed on during cell division (see Section 14.5).

Prokaryotic ribosomes are smaller than eukaryotic ribosomes and contain fewer proteins and RNA molecules. Archaeal ribosomes resemble those of bacteria

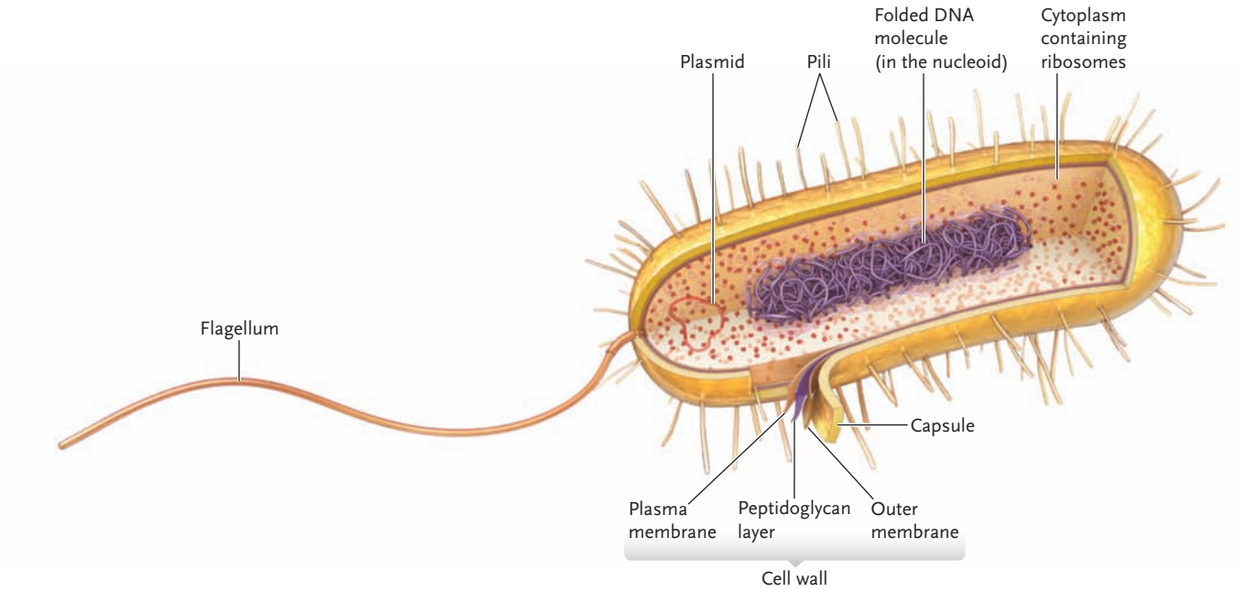


Figure 25.3
The structures of a bacterial cell.

in size, but differ in structure. Scientists have demonstrated that, with some differences in detail, bacterial ribosomes carry out protein synthesis by the same mechanisms as those of eukaryotes (see Section 15.4). Interestingly, protein synthesis in archaeans is a combination of bacterial and eukaryotic processes, with some unique archaeal features. As a result, antibiotics that stop bacterial infections by targeting ribosome activity do not stop protein synthesis of archaeans.

Some prokaryotes are capable of photosynthesis. These microorganisms have membranous structures corresponding to those that carry out photosynthesis in plants, but they are organized differently.

The cytoplasm of many prokaryotes also contains storage granules holding glycogen, lipids, phosphates, or other materials. The stored material is used as an energy reserve or a source of building blocks for synthetic reactions.

Prokaryotic Cell Walls. All prokaryotic cells are bounded by a plasma membrane. This membrane must withstand both high intracellular osmotic pressures and the action of natural chemicals in the environment that have detergent properties. Most prokaryotes have one or more layers of materials coating the plasma membrane that provide the necessary protection.

Bacteria typically are surrounded by a cell wall that lies outside the plasma membrane. The primary structural molecules of bacterial cell walls are **peptidoglycans**, polymeric substances formed from a polysaccharide backbone tied together by short polypeptides. The peptidoglycans vary in chemical structure among different bacterial species.

Differences in bacterial cell wall composition are important clinically. In 1882, Hans Christian Gram, a Danish physician, developed a staining method to distinguish in bodily fluids two types of bacteria, each of which could cause pneumonia. In this **Gram stain technique**, an investigator treats bacteria with the dye crystal violet and then with iodine, which fixes the dye to the cell wall. Next the bacteria are washed with alcohol, and then treated with a second strain, either fuchsin or safranin. Bacteria that appear purple after these steps have retained the crystal violet stain; they are **Gram-positive.** Bacteria that appear pink after these steps have lost the crystal violet stain in the alcohol wash and are stained pink with the second dye; they are **Gram-negative.** (Gram-positive cells also react with the second dye, but the stain does not affect the color imparted by the crystal violet.)

The staining difference reflects differences in the cell walls of the bacteria **(Figure 25.4).** The cell wall of Gram-positive bacteria consists of a thick peptidoglycan layer (see Figure 25.4a). In contrast, the cell wall of Gram-negative bacteria consists of a thin layer of peptidoglycans (see Figure 25.4b). Outside of the thin cell wall is an additional boundary membrane, called the **outer membrane**, which covers the peptidoglycan layer. The outer membrane contains **lipopolysaccharides**, assembled from lipid and polysaccharide subunits found nowhere else in nature. The outer membrane protects Gram-negative bacteria from potentially damaging substances in their environment. For example, the outer membrane of *E. coli* protects it from the detergent effects of bile released into the intestinal tract, which otherwise would lyse (break open) the bacterium and kill it.

Rapidly distinguishing between Gram-positive and Gram-negative bacteria is important for determining the first line of treatment for bacterial-caused human diseases. Most pathogenic bacteria are Gram-negative species; their outer membrane protects them against the body's defense systems and blocks the en-

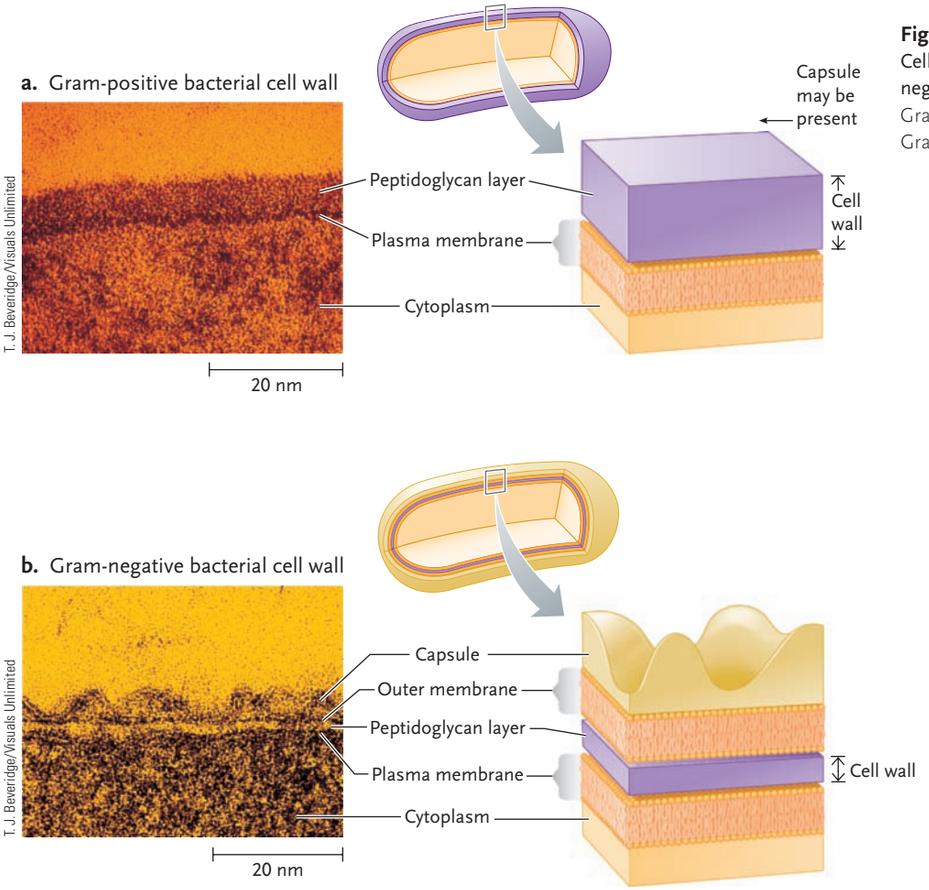


Figure 25.4
Cell wall structure in Gram-positive and Gram-negative bacteria. **(a)** The thick cell wall in Gram-positive bacteria. **(b)** The thin cell wall of Gram-negative bacteria.

try of drugs such as antibiotics. For example, the antibiotic penicillin blocks new bacterial cell wall formation by inhibiting peptidoglycan crosslinking. The weakened cell wall soon leads to the death of the bacterium. Penicillin is effective against Gram-positive pathogens, but it is less effective against Gram-negative pathogens because their outer membrane inhibits entry of the antibiotic.

Many Gram-positive and Gram-negative bacteria are surrounded by a slime coat typically composed of polysaccharides. When the slime is attached to the cells, it is a **capsule (Figure 25.5),** and when it is loosely associated with the cells, it is a **slime layer,** although there is no sharp distinction between the two. Depending on the species, the capsule ranges from a layer that is thinner than the cell wall to many times thicker than the entire cell. Slime typically is essential for survival of the bacteria in natural environments. For example, the slime helps protect the cells from desiccation and antibiotics.

In many bacteria, the capsule prevents bacterial viruses and molecules such as enzymes, antibiotics, and antibodies from reaching the cell surface. In many pathogenic bacteria, the presence or absence of the protective capsule differentiates infective from noninfective forms. For example, normal *Streptococcus pneumoniae* bacteria are capsulated and are virulent, causing severe pneumonia in humans and other mammals. Mutant *S. pneumoniae* without capsules are nonvirulent and can easily be eliminated by the body's immune system if they are injected into mice or other animals (see Section 14.1).

Flagella and Pili. Many bacteria and archaeans can move actively through liquids and across wet surfaces. The most common mechanism for movement involves

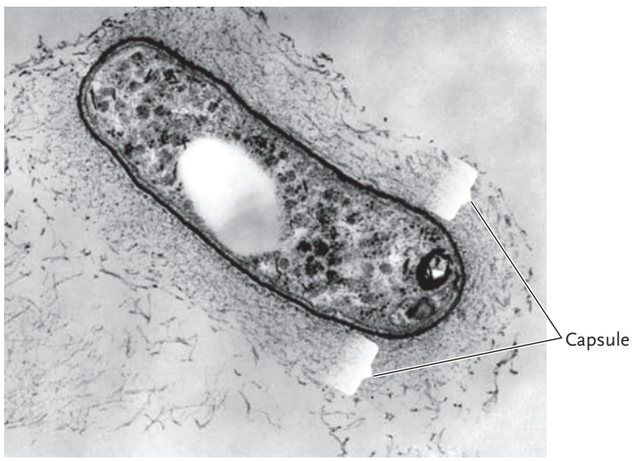


Figure 25.5
The capsule surrounding the cell wall of *Rhizobium*, a Gram-negative soil bacterium.

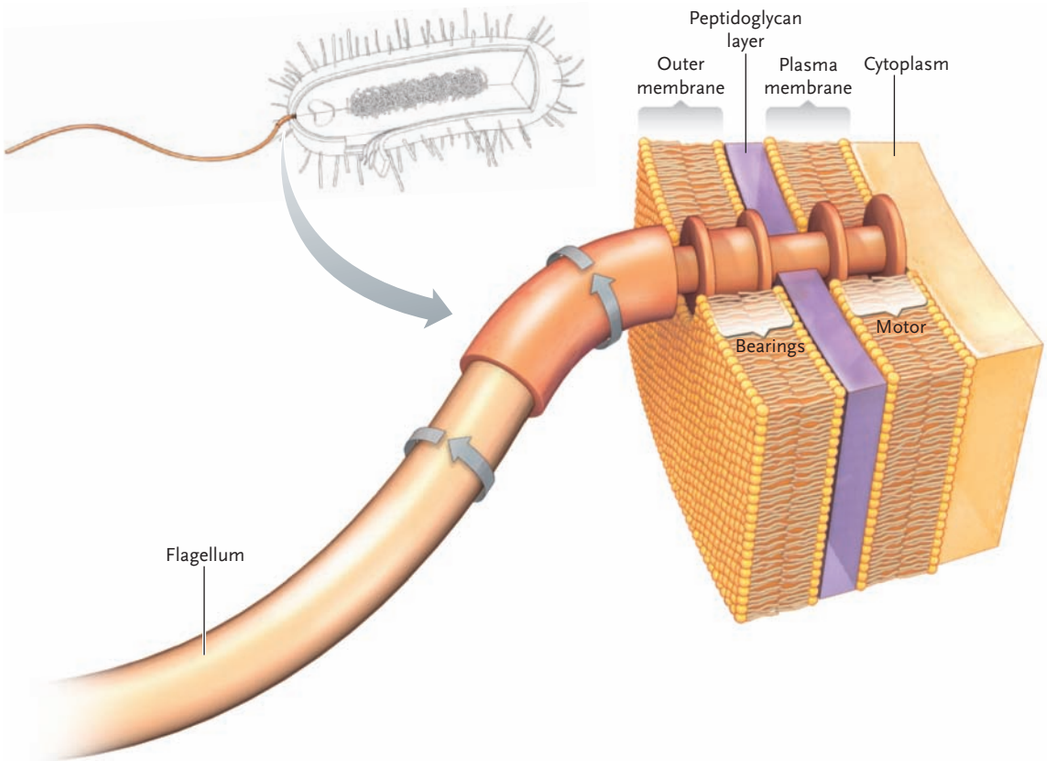


Figure 25.6
A flagellum of a Gram-negative bacterium. A proton (H^+) gradient drives the motor, which rotates the flagellum in a counterclockwise direction.

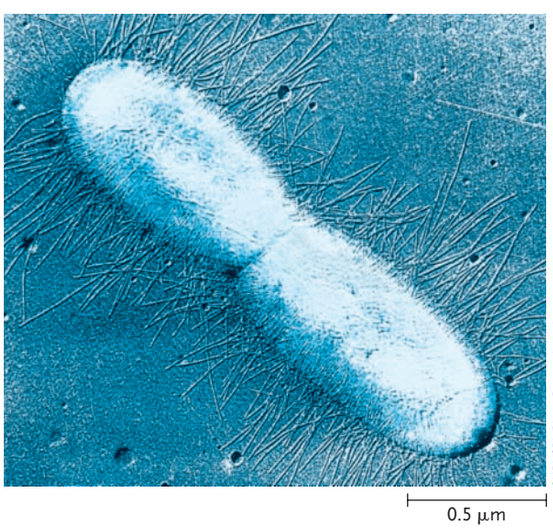
the action of **flagella** (singular, flagellum, meaning whip) extending from the cell wall **(Figure 25.6).** These flagella are much smaller and simpler than the flagella of eukaryotic cells and contain no microtubules (eukaryotic flagella are discussed in Section 5.3).

Bacterial flagella consist of a helical fiber of protein that rotates in a socket in the cell wall and plasma membrane, much like the propeller of a boat. The rotation, produced by what is essentially a tiny electric motor, pushes the cell through liquid. The motor is powered by a gradient of hydrogen or sodium ions, which flow through it as positive charges, creating an electrical repulsion that makes the flagellum rotate.

Archaeal flagella are analogous, not homologous, to bacterial flagella. That is, they carry out the same function, but the genes for the two types of flagellar systems are different.

Some bacteria and archaeans have rigid shafts of protein called **pili** (singular, pilus) extending from their cell walls **(Figure 25.7).** Among bacteria, pili are characteristic primarily of Gram-negative bacteria; relatively few Gram-positive bacteria produce these structures. A recognition protein at the tip of a pilus allows bacterial cells to adhere to other cells. One type, called *sex pili,* allows bacterial cells to adhere to each other as a prelude to conjugation, a primitive form of sexual reproduction (see Section 17.1). Other types help bacteria to bind to animal cells. For example, *Neisseria gonorrhoeae,* the Gram-negative bacterium that causes gonorrhea, has pili that allow it to attach to cells of the throat, eye, urogenital tract, or rectum in humans.

In sum, prokaryotes are simpler and less structurally diverse than eukaryotic cells. However, bacteria are much more diverse metabolically, as we will now explore.



CNRI/SPL/Photo Researchers, Inc.

Figure 25.7
Pili extending from the surface of a dividing *E. coli* bacterium.

Prokaryotes Have the Greatest Metabolic Diversity of All Living Organisms

All organisms take in carbon and energy in some form, but prokaryotes show the greatest diversity in their modes of securing these resources **(Figure 25.8).** Some prokaryotes are **autotrophs** (*auto* = self; *troph* = nourishment), meaning that they, like plants, obtain carbon from an inorganic molecule, CO_2. (Note that, while CO_2 contains a carbon atom, oxides containing carbon are considered inorganic molecules.) Others are **heterotrophs**, meaning that they, like humans and other animals, obtain carbon from organic molecules. Bacterial heterotrophs obtain carbon from the organic molecules of living hosts, or from organic molecules in the products, wastes, or remains of dead organisms.

Prokaryotes are also divided according to the source of the energy they use to drive biological activities. **Chemotrophs** (*chemo* = chemical; *troph* = nourishment) obtain energy by oxidizing inorganic or organic substances, while **phototrophs** obtain energy from light. Combining carbon source and energy gives us the following four types (see Figure 25.8):

		Energy source	
		Oxidation of molecules*	Light
Carbon source	CO_2	**CHEMOAUTOTROPH** Found in some bacteria and archaeans; not found in eukaryotes	**PHOTOAUTOTROPH** Found in some photosynthetic bacteria, in some protists, and in plants
	Organic molecules	**CHEMOHETEROTROPH** Include some bacteria and archaeans, and also in protists, fungi, animals, and plants	**PHOTOHETEROTROPH** Found in some photosynthetic bacteria

*Inorganic molecules for chemoautotrophs and organic molecules for chemoheterotrophs.

Figure 25.8
Modes of nutrition among Bacteria and Archaea. All four modes of nutrition occur in the Bacteria with chemoheterotrophs as the most common type; among the Archaea, chemoautotrophs are most common, while others are chemoheterotrophs.

1. **Chemoautotrophs:** Prokaryotic chemoautotrophs obtain energy by oxidizing inorganic substances such as hydrogen, iron, sulfur, ammonia, nitrites, and nitrates and use CO_2 as their carbon source. They use the electrons they remove in the oxidations to make organic molecules by reducing CO_2 or to provide energy for ATP synthesis (using an electron transfer system embedded in the plasma membrane). Chemoautotrophs occur widely among the prokaryotes, including many bacteria and most archaeans, but are not found among eukaryotes.
2. **Chemoheterotrophs:** Prokaryotic chemoheterotrophs oxidize organic molecules as their energy source and obtain carbon in organic form. They include most of the bacteria that cause disease in humans, domestic animals, and plants and many bacteria responsible for decomposing matter. They are the largest prokaryotic group in terms of numbers of species.
3. **Photoautotrophs:** Photoautotrophs are photosynthetic organisms that use light as their energy source and CO_2 as their carbon source. They include several groups of bacteria, for example, the *cyanobacteria,* the *green sulfur bacteria,* and the *purple sulfur bacteria,* as well as plants and many protists. The cyanobacteria use water as their source of electrons for reducing CO_2, while the two types of sulfur bacteria use sulfur or sulfur compounds.
4. **Photoheterotrophs:** Photoheterotrophs use light as their ultimate energy source but obtain carbon in organic form rather than as CO_2. Photoheterotrophs are limited to two groups of bacteria, the *green* and *purple nonsulfur bacteria*. "Nonsulfur" indicates they are unable to oxidize sulfur or other inorganic substances as an ultimate source of electrons for reductions; instead, they use a variety of substrates, including H_2, alcohols, or organic acids.

Prokaryotes Differ in Whether Oxygen Can Be Used in Their Metabolism

Prokaryotes also differ in how their metabolic systems function with respect to oxygen (see Chapter 8). **Aerobes** require oxygen for cellular respiration (in other words, oxygen is the final electron acceptor for that process); **obligate aerobes** cannot grow without oxygen. **Anaerobes** do not require oxygen to live. **Obligate anaerobes** are poisoned by oxygen, and survive either by fermentation, in which organic molecules are the final electron acceptors (see Section 8.5), or by a form of respiration in which inorganic molecules such as nitrate ions (NO_3^-) or sulfate ions (SO_4^{2-}) are used as final electron acceptors. **Facultative anaerobes** use O_2 when it is present, but under anaerobic conditions, they live by fermentation.

Prokaryotes Fix and Metabolize Nitrogen

Nitrogen is a component of amino acids and nucleotides and, hence, is of vital importance for the cell. Prokaryotes are able to metabolize nitrogen in many forms. For example, a number of bacteria and archaeans are able to reduce atmospheric nitrogen (N_2, the major component of Earth's atmosphere) to ammonia (NH_3), a process called **nitrogen fixation.** The

ammonia is quickly ionized to ammonium (NH_4^+), which the cell then uses in biosynthetic pathways to produce nitrogen-containing molecules such as amino acids and nucleic acids. Nitrogen fixation is an exclusively prokaryotic process and is the only means of replenishing the nitrogen sources used by most microorganisms and by all plants and animals. In other words, all organisms use nitrogen fixed by bacteria. Examples of nitrogen-fixing bacteria are some of the cyanobacteria and *Azotobacter* among free-living bacteria and *Rhizobium* among bacteria that are symbiotic with plants (see Chapter 33).

Not all bacteria convert fixed nitrogen directly into organic molecules. Some bacteria carry out **nitrification**, the conversion of ammonium (NH_4^+) to nitrate (NO_3^-). This is carried out in two steps by two types of *nitrifying bacteria*. One type of nitrifying bacteria converts ammonium to nitrite (NO_2^-) (for example, *Nitrosomonas*), while the other converts nitrite to nitrate (for example, *Nitrobacter*). Because of this specialization, both types of nitrifying bacteria are usually present in soils and water, with some converting ammonium to nitrite and others using that nitrite to produce nitrate. The nitrate can be used by plants and fungi to incorporate nitrogen into organic molecules. Animals obtain nitrogen in organic form by eating other organisms.

In sum, nitrification makes nitrogen available to many other organisms, including plants and animals and bacteria that cannot metabolize ammonia. You will learn more about nitrogen metabolism in connection with the nitrogen cycle (see Chapter 51). The metabolic versatility of the prokaryotes is one factor that accounts for their abundance and persistence on the planet; another factor is their impressive reproductive capacity.

Prokaryotes Reproduce Asexually or, Rarely, by a Form of Sexual Reproduction

In prokaryotes, asexual reproduction is the normal mode of reproduction. In this process, a parent cell divides by binary fission into two daughter cells that are exact genetic copies of the parent (see Figure 10.18).

Conjugation, in which two parent cells join or "mate," occurs in some bacterial and archaeal species. Conjugation depends upon genes carried by a plasmid that replicates separately from the prokaryotic chromosome. Usually only the plasmid is passed on during conjugation, but in some bacteria, the plasmid integrates into the chromosome of the host so that host genes transfer from one parent (donor) to the other (recipient). Genetic recombination then occurs, thereby achieving a prokaryotic form of sexual reproduction. The recombinant cell divides to produce daughter cells that differ in genetic information from either parent. (Conjugation and the transfer of host genes between bacterial cells is described in Section 17.1.)

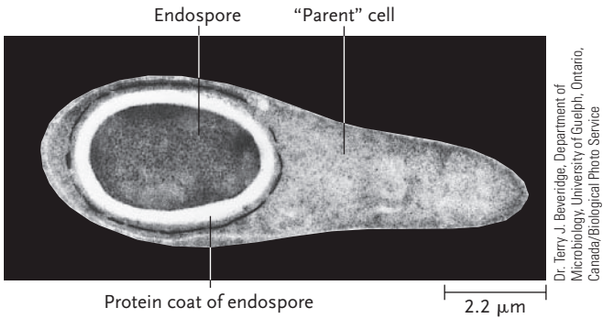


Figure 25.9
A developing endospore of the bacterium *Clostridium tetani*, a dangerous pathogen that causes tetanus.

A small number of bacteria can produce an **endospore**, so-called because it develops *within* the cell **(Figure 25.9).** The endospore, which typically develops when environmental conditions become unfavorable, is metabolically inactive and highly resistant to heat, desiccation, and attack by enzymes or other chemical agents. When an endospore forms, binary fission cuts the parent cell into parts of unequal size. The larger cell then envelops the smaller one and surrounds it with a tough, chemically resistant protein coat; the smaller cell develops into the endospore. Rupture of the larger cell releases the endospore to the environment. If environmental conditions become favorable for growth, the spore germinates: it becomes permeable, water enters the cell, its surface coat breaks, and the cell is released in a metabolically active form.

No one is certain how long endospores can survive. There are claims that endospores survive for thousands or millions of years, but the data are controversial.

In Nature, Bacteria May Live in Communities Attached to a Surface

Researchers grow prokaryotes as individuals in liquid cultures or as isolated colonies on solid media. The results from studies using pure cultures have been crucial in developing an understanding of, among many other things, the nature of the genetic material, DNA replication, gene expression, and gene regulation. But, since pure cultures are extremely rare in nature, some of the information learned from them may not apply to populations of prokaryotes in nature.

Researchers have discovered that, in nature, prokaryotes may live in communities where they interact in a variety of ways. The communities may consist of one or more species of bacteria, or archaeans, or both bacteria and archaeans. Eukaryotic microorganisms may also be in the communities. One important type of prokaryotic community is known as a **biofilm**, which consists of a complex aggregation of microorganisms

attached to a surface. Benefits of biofilm formation to prokaryotes include adherence of the organisms to hospitable surfaces, the transfer of genes between species, and living off the products of other organisms in the biofilm. Biofilms form on any surface with sufficient water and nutrients for prokaryotes to grow. For instance, they may be found on lake surfaces, on rocks in freshwater or marine environments (making them slippery), surrounding plant roots and root hairs, and on animal tissues such as intestinal mucosa and teeth (human dental plaque is a biofilm).

Biofilms have practical consequences for humans, both beneficial and detrimental. On the beneficial side, for example, biofilms on solid supports are used in sewage treatment plants for processing organic matter before the water is discharged, and they can be effective in bioremediation (biological clean-up) of toxic organic molecules contaminating the groundwater. On the detrimental side, however, biofilms can be harmful to human health. For example, biofilms adhere to many kinds of surgical equipment and supplies, including catheters and synthetic implants such as pacemakers and artificial joints. When pathogenic bacteria are involved, infections occur. Those infections are difficult to treat, because pathogenic bacteria in a biofilm are up to 1000 times more resistant to antibiotics than are the same bacteria in liquid cultures. Other examples of medical conditions resulting from activities of biofilms include middle-ear infections, bacterial endocarditis (an infection of the heart's inner lining or the heart valves), and Legionnaire's disease (an acute respiratory infection caused by breathing in pieces of biofilms containing the pathogenic bacterium *Legionnella*).

How does a biofilm form? Imagine a surface, living or environmental, over which water containing nutrients is flowing **(Figure 25.10).** The surface rapidly becomes coated with polymeric organic molecules from the liquid, such as polysaccharides or glycoproteins. Once the surface is conditioned with organic molecules, free bacteria attach in a reversible manner in a matter of seconds (see Figure 25.10, step 1). If the bacteria remain attached, the association may become irreversible (step 2), at which point the bacteria grow and divide on the surface (step 3). Next, the physiology of the bacteria changes and the cells begin to secrete *extracellular polymer substances* (EPS), a slimy, gluelike substance similar to the molecules found in bacterial slime layers. EPS extends between cells in the mixture, forming a matrix that binds cells to each other and anchors the complex to the surface, thereby establishing the biofilm (step 4). The slime layer entraps a variety of materials, such as dead cells and insoluble minerals. Over time, other organisms are attracted to and join the biofilm; depending on the environment, these may include other bacterial species, algae, fungi, or protozoa, producing diverse microbial communities (step 5).

Genomic and proteomic studies have shown that the changes in prokaryote physiology accompanying the formation of a biofilm result from marked changes in the prokaryote's gene expression pattern. In effect, the prokaryote becomes a significantly different organism. This change has large implications when pathogenic bacteria are involved, for example, because most research on the control of those bacteria is done with liquid cultures. The challenge now is to devise new treatment strategies for biofilm-caused diseases. If we can gain a better understanding of the genetic changes involved in the transition from free-floating to biofilm state, then perhaps we can devise treatments that will switch the bacteria back to the free-living state, where they are more susceptible to antibiotics.

In sum, we must recognize that rather than living as individuals as once was thought, prokaryotes typically live in communities in nature. Much remains to be learned about how bacteria form a biofilm, how the change in gene expression during the transition is regulated, and how they interact.

In the next two sections, we describe the major groups of prokaryotes.

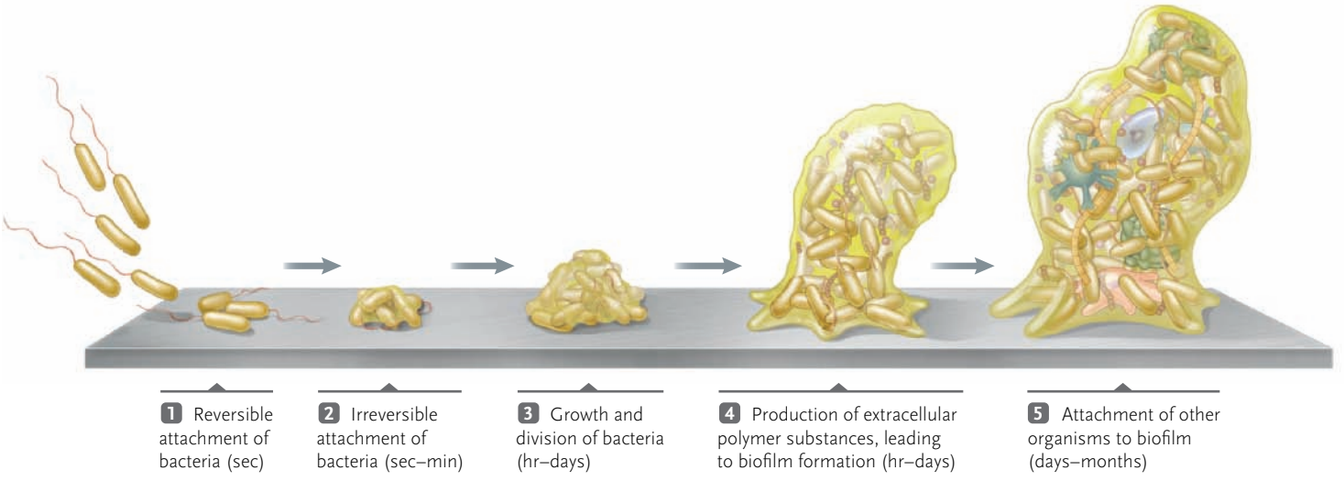


Figure 25.10 Steps in the formation of a biofilm.

Study Break

1. What distinguishes a prokaryotic cell from a eukaryotic cell?
2. What is the difference between a chemoheterotroph and a photoautotroph?
3. What is the difference between an obligate anaerobe and a facultative anaerobe?
4. What is the difference between nitrogen fixation and nitrification? Why are nitrogen-fixing prokaryotes important?
5. What is a biofilm? Give an example of a biofilm that is beneficial to humans and one that is harmful.

25.2 The Domain Bacteria

Prokaryote classification has been revolutionized by molecular techniques that allow researchers to obtain and compare bacterial DNA, RNA, and protein sequences as tests of relatedness and evolutionary origin. Ribosomal RNA (rRNA) sequences, which are present in all organisms, have been most widely used in the evolutionary studies of prokaryotes. Under the assumption that mutations causing sequence changes occur at constant rates, researchers use the degree of sequence divergence to estimate how much time has passed since any two species shared the same ancestor (see Section 23.6). The sequencing studies thus provide a means to trace the evolutionary origins of prokaryotes and to place them in taxonomic groups. In this way, prokaryotes have been classified into the domains Bacteria and Archaea (the Eukarya is the third domain of life) **(Figure 25.11).** Researchers have identified several evolutionary branches within each prokaryote domain. In the future, full genomic sequences will likely be compared to refine this taxonomic classification. We discuss the major groups of the domain Bacteria in this section and of the domain Archaea in the next section.

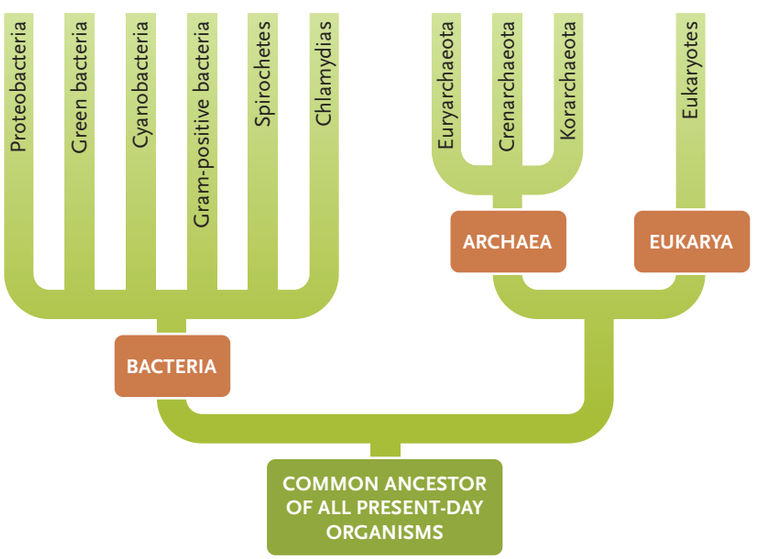
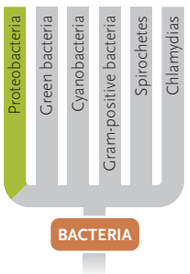


Figure 25.11
An abbreviated phylogenetic tree of prokaryotes.

Molecular Studies Reveal More Than a Dozen Evolutionary Branches in the Bacteria

Sequencing studies reveal that bacteria have more than 12 distinct and separate evolutionary branches, variously called kingdoms, subkingdoms, phyla, or divisions. Although all these groups are of significance to science, medicine, and the human economy, we restrict our discussion to six that are particularly important—the proteobacteria, the green bacteria, the cyanobacteria, the Gram-positive bacteria, the spirochetes, and the chlamydias (see Figure 25.11).



Proteobacteria: The Purple Bacteria and Their Relatives. The proteobacteria are a highly diverse group of Gram-negative bacteria that scientists hypothesize derive from a purple, photosynthesizing evolutionary ancestor. Many present-day species retain those characteristics, carrying out photosynthesis as either photoautotrophs (the purple sulfur bacteria) or photoheterotrophs (the purple nonsulfur bacteria). "Purple" refers to the color given to the cells by their photosynthetic pigment, a type of chlorophyll distinct from that of plants. Proteobacteria carry out a type of photosynthesis that does not use water as an electron donor and does not release oxygen as a by-product of photosynthesis.

Other present-day proteobacteria are chemoheterotrophs that are thought to have evolved as an evolutionary branch following the loss of photosynthetic capabilities in an early proteobacterium. The evolutionary ancestors of mitochondria are considered likely to have been ancient nonphotosynthetic proteobacteria.

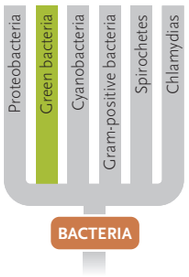
Among the chemoheterotrophs classified with the proteobacteria are bacteria that cause human diseases such as bubonic plague, Legionnaire's disease, gonorrhea, and various forms of gastroenteritis and dysentery; bacterial plant pathogens that cause rots, scabs, and wilts; and the colon-inhabiting *E. coli* (shown dividing in Figure 25.7). The proteobacteria also include both free-living and symbiotic nitrogen-fixing bacteria.

Among the more unusual nonphotosynthetic proteobacteria are the myxobacteria, which form colonies held together by the slime they produce. Enzymes secreted by the colonies digest "prey"—other bacteria, primarily—that become stuck in the slime. When environmental conditions become unfavorable, as when soil nutrients or water are depleted, myxobacteria form a *fruiting body* **(Figure 25.12),** which contains clusters of

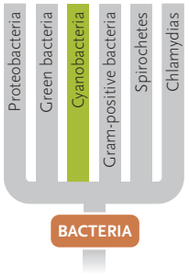
Hans Reichenbach, Gesellschaft for Biotechnologische Forschung, Braunsweig, Germany

Figure 25.12
The fruiting body of *Chondromyces crocatus*, a myxobacterium. Cells of this species collect together to form the fruiting body.

spores. When the fruiting body bursts, the spores disperse and form new colonies.

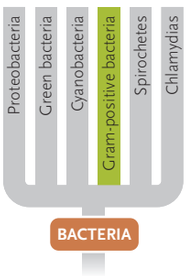


Green Bacteria. The green bacteria are a diverse group of Gram-negative photosynthesizers with photosynthetic pigments that give the cells a green color. The pigments are a form of chlorophyll distinct from the chlorophyll of plants. Like the purple bacteria, they do not release oxygen as a by-product of photosynthesis. Green bacteria occur in two subgroups: green sulfur bacteria, which are photoautotrophs, and green nonsulfur bacteria, which are photoheterotrophs. The green sulfur bacteria are fairly closely related to the Archaea and are usually found in hot springs. The green nonsulfur bacteria are found typically in marine and high-salt environments.



Cyanobacteria. The cyanobacteria **(Figure 25.13)** are Gram-negative photoautotrophs that have a blue-green color and carry out photosynthesis by the same pathways as eukaryotic algae and plants, using the same chlorophyll as in plants as their primary photosynthetic pigment. They release oxygen as a by-product of photosynthesis. The first appearance of oxygen in quantity in Earth's atmosphere depended on the activities of ancient cyanobacteria.

The direct ancestors of present-day cyanobacteria were the first organisms to use the water-splitting reactions of photosynthesis. As such, they were critical to the appearance of oxygen in the atmosphere, which allowed the evolutionary development of aerobic organisms. Chloroplasts probably evolved from early cyanobacteria that were incorporated into the cytoplasm of primitive eukaryotes, which eventually gave rise to the algae and higher plants (see Section 24.3). Besides releasing oxygen, present-day cyanobacteria help fix nitrogen into organic compounds in aquatic habitats and in lichens, which are symbiotic organisms consisting of a cyanobacterium with a filamentous fungus (see Chapter 28).



Gram-Positive Bacteria. The large group of Gram-positive bacteria contains many species that live primarily as chemoheterotrophs. One species, *Bacillus subtilis,* is studied by biochemists and geneticists almost as extensively as is *E. coli*. A number of Gram-positive bacteria cause human diseases, including *Bacillus an-*

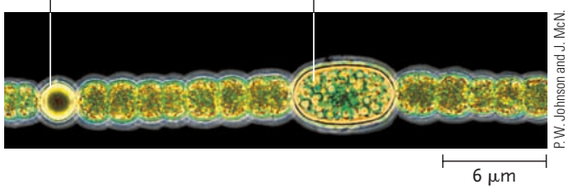
a.

Dr. Jeremy Burgess/SPL/Photo Researchers, Inc.

b.

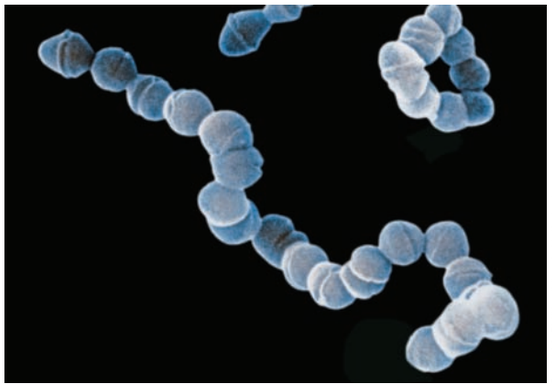
Tony Brian/SPL/Photo Researchers, Inc.

c.



P. W. Johnson and J. McN. Sieburth, University of Rhode Island/Biological Photo Service

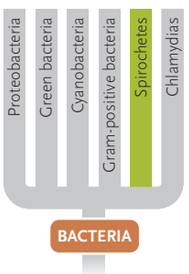
Figure 25.13
Cyanobacteria. **(a)** A population of cyanobacteria covering the surface of a pond. **(b)** and **(c)** Chains of cyanobacterial cells. Some cells in the chains form spores. The heterocyst is a specialized cell that fixes nitrogen.



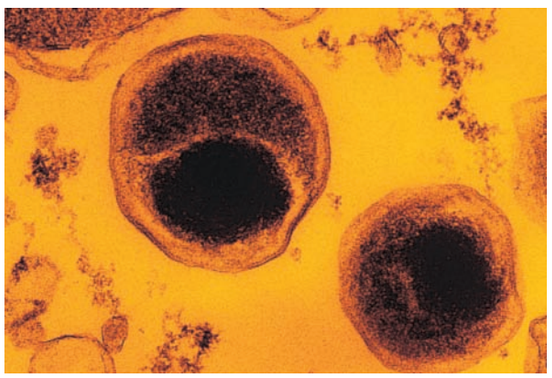
David M. Phillips/Visuals Unlimited

Figure 25.14
Streptococcus bacteria forming the long chains of cells typical of many species in this genus.

thracis, which causes anthrax and has been much in the news as a possible terrorist weapon; *Staphylococcus,* which causes some forms of food poisoning, skin infections such as pimples and boils, toxic shock syndrome, pneumonia, and meningitis; and *Streptococcus* **(Figure 25.14),** which causes strep throat, some forms of pneumonia, scarlet fever, and kidney infections. Nevertheless, some Gram-positive bacteria are beneficial; *Lactobacillus,* for example, carries out the lactic acid fermentation used in the production of pickles, sauerkraut, and yogurt. One unusual group of bacteria, the mycoplasmas, is placed among the Gram-positive bacteria by molecular studies even though they are Gram-negative. Their staining reaction reflects that they are naked cells that secondarily lost their cell walls in evolution. Some mycoplasmas, with diameters from 0.1 to 0.2 μm, are the smallest known cells.

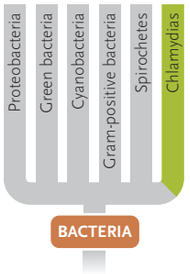


Spirochetes. The spirochetes are Gram-negative bacteria with helically spiraled bodies and an unusual form of movement in which bacterial flagella, embedded in the cytoplasm, cause the entire cell to twist in a corkscrew pattern. Their corkscrew movements enable them to move in viscous environments such as mud and sewage, where they are common. Two spirochetes, *Treponema denticola* and *Treponema vincentii,* are more or less harmless inhabitants of the human mouth; another species, *Treponema pallidum,* is the cause of syphilis. Other pathogenic spirochetes cause relapsing fever and Lyme disease. Beneficial spirochetes in termite intestines aid in the digestion of plant fiber.



David M. Phillips/Visuals Unlimited

Figure 25.15
Cells of *Chlamydia trachomatis* inside a human cell. This bacterium is a major infectious cause of human eye and genital disease.



Chlamydias. The chlamydias are structurally unusual among bacteria because, although they are Gram-negative and have cell walls with a membrane outside of them, they lack peptidoglycans. All the known chlamydias are intracellular parasites that cause various diseases in animals. One bacterium of this group, *Chlamydia trachomatis* **(Figure 25.15),** is responsible for one of the most common sexually transmitted infections of the urinary and reproductive tracts of humans. The same bacterium causes trachoma, an infection of the cornea that is the leading cause of preventable blindness in humans.

Bacteria Cause Diseases by Several Mechanisms

As you have just learned, some bacteria cause diseases while others are beneficial. Here we focus on pathogenic bacteria.

Bacteria vary in the pathways by which they cause diseases. A number of bacterial lineages produce **exotoxins,** toxic proteins that leak from or are secreted from the bacterium and interfere with the biochemical processes of body cells in various ways. For example, the exotoxin of the Gram-positive bacterium *Clostridium botulinum* is found as a contaminant of poorly preserved foods, and causes botulism. The botulism exotoxin is one of the most poisonous substances known: a few nanograms can cause illness, and a few hundred grams could kill every human on Earth. It acts by interfering with the transmission of nerve impulses. The muscle paralysis produced by the exotoxin can be fatal if the muscles that control breathing are affected. Interestingly, the botulism exotoxin, with the brand name Botox, is used in low doses for the cosmetic removal of wrinkles, and in the treatment of migraine headaches, involuntary contraction of the eye muscles, and some other medical conditions.

Some other bacteria cause disease through **endotoxins.** Endotoxins are not released by living cells as exotoxins are; instead, they are lipopolysaccharides released from the outer membrane that surrounds cell walls when bacteria die and lyse. Endotoxins are natural components of the outer membrane of all Gram-negative bacteria, which include *E. coli, Salmonella,* and *Shigella.* These lipopolysaccharides cause disease by overstimulating the host's immune system, often triggering inflammation. Endotoxin release has different effects, depending on the bacterial species and the site

of infection, that include typhoid or other fevers, diarrhea, and, in severe cases, organ failure and death. For example, *Salmonella typhi,* the cause of typhoid, enter the human intestines and penetrate the intestinal wall, eventually ending up in the lymph nodes. There they multiply, and some of the cells die and lyse, releasing endotoxins into the bloodstream. This both triggers the host's immune response and causes blood poisoning, a serious medical condition in which the circulatory system becomes dysfunctional. If the infection is not successfully treated, the condition can progress to multiple organ system failure and, eventually, death.

Some bacteria release **exoenzymes**, enzymatic proteins that digest plasma membranes and cause cells of the infected host to rupture and die. Exoenzymes may also digest extracellular materials such as collagen, causing connective tissue diseases. Some exoenzymes attack red or white blood cells, leading to anemias, impairment of the immune response, or interference with blood clotting. Among the bacteria that release exoenzymes are *Streptococcus, Staphylococcus,* and *Clostridium.* Necrotizing fasciitis (flesh-eating disease), the spectacularly destructive and rapid degeneration of subcutaneous tissues in the skin, is caused by an exoenzyme released by *Streptococcus* and some other bacteria.

Some of the ill effects of bacteria have little to do with exotoxins, endotoxins, or exoenzymes, but are caused purely by the body's responses to infection. The severe pneumonia caused by *Streptococcus pneumoniae,* for example, results from massive accumulation of fluid and white blood cells in the lungs in response to the infection. The white blood cells have little effect on the bacteria, however, because of the bacterial cell's protective capsule. As the fluid, white blood cells, and bacteria continue to accumulate, they block air passages in the lungs and severely impair breathing.

Pathogenic Bacteria Commonly Develop Resistance to Antibiotics

Antibiotics are routinely used to treat bacterial infections. These substances, produced as defensive molecules by some bacteria and fungi, or by chemical synthesis, kill or inhibit the growth of other microbial species. For example, streptomycins, produced by soil bacteria, block protein synthesis in their targets. Penicillins, produced by fungi, prevent formation of covalent bonds that hold bacterial cell walls together, weakening the wall and causing the cells to rupture.

Many pathogenic bacteria develop resistance to antibiotics through mutations that allow them to break down the drugs or otherwise counteract their effects (see *Why It Matters,* Chapter 20). Resistance is also acquired through genes carried on plasmids, picked up by conjugation or on DNA brought into pathogens by other pathways such as transformation and transduction (see Section 17.1). Taking antibiotics routinely in mild doses, or failing to complete a prescribed dosage, contribute to the development of resistance by selecting strains that can survive in the presence of the drug. Overprescription of antibiotics for colds and other virus-caused diseases can also promote bacterial resistance. That is, viruses are unaffected by antibiotics, but the presence of antibiotics in the system can lead to resistance as just described. Antibacterial agents that may promote resistance are also commonly included in such commercial products as soaps, detergents, and deodorants. Resistance is a form of evolutionary adaptation; antibiotics alter the bacterium's environment, conferring a reproductive advantage on those strains best adapted to the altered conditions.

The development of resistant strains has made tuberculosis, cholera, typhoid fever, gonorrhea, "staph," and other diseases caused by bacteria difficult to treat with antibiotics. For example, as recently as 1988, drug-resistant strains of *Streptococcus pneumoniae,* which causes pneumonia, meningitis, and middle-ear infections, were practically unheard of in the United States. Now, resistant strains of *S. pneumoniae* are common and increasingly difficult to treat.

In this section, you have seen that bacteria thrive in nearly every habitat on Earth, including the human body. However, some members of the second prokaryotic domain, the Archaea, the subject of the next section, live in habitats that are too forbidding even for the bacteria.

Study Break

1. What methodologies have been used to classify prokaryotes?
2. What were the likely characteristics of the evolutionary ancestor of present-day proteobacteria?
3. What are the differences between the way photosynthesis is carried out by photosynthetic Proteobacteria and by cyanobacteria?
4. What is an exotoxin, an endotoxin, and an exoenzyme, and how do they differ with respect to how they cause disease?

25.3 The Domain Archaea

Archaea were first discovered in 1977, and scientists believed they were bacteria. However, research showed that they have some eukaryotic features, some bacterial features, and some features that are unique to the group (also discussed in Section 24.3; **Table 25.1** compares the characteristics of Bacteria, Archaea, and Eukarya). Based on research by Carl Woese and his colleagues that compared their DNA and rRNA sequences with those of other organisms, Archaea were

Table 25.1 Characteristics of the Bacteria, Archaea, and Eukarya

Characteristic	Bacteria	Archaea	Eukarya
DNA arrangement	Single, circular in most, but some linear and/or multiple	Single, circular	Multiple linear molecules
Chromosomal proteins	Prokaryotic histone-like proteins	Five eukaryotic histones	Five eukaryotic histones
Genes arranged in operons	Yes	Yes	No
Nuclear envelope	No	No	Yes
Mitochondria	No	No	Yes
Chloroplasts	No	No	Yes
Peptidoglycans in cell wall	Present	Present but modified, or absent	Absent
Membrane lipids	Unbranched; linked by ester linkages	Branched; linked by ether linkages	Unbranched; linked by ester linkages
RNA polymerase	One type	Multiple types	Multiple types
Ribosomal proteins	Prokaryotic	Some prokaryotic, some eukaryotic	Eukaryotic
First amino acid placed in proteins	Formylmethionine	Methionine	Methionine
Aminoacyl-tRNA synthetases	Prokaryotic	Eukaryotic	Eukaryotic
Cell division proteins	Prokaryotic	Prokaryotic	Eukaryotic
Proteins of energy metabolism	Prokaryotic	Prokaryotic	Eukaryotic
Sensitivity to chloramphenicol and streptomycin	Yes	No	No

subsequently classified as a separate domain of life. (*Insights from the Molecular Revolution* describes the research that first revealed the complete DNA sequence of an archaean.) Scientists use sequencing studies and the archeans' unique characteristics to identify the organisms in this group.

Archaea Have Some Unique Characteristics

The first-studied Archaea were found in extreme environments, such as hot springs, hydrothermal vents on the ocean floor, and salt lakes **(Figure 25.16).** For that reason, these prokaryotes were called *extremophiles* ("extreme lovers"). Subsequently archaeans have also been found living in normal environments; like bacteria, these are *mesophiles.*

Many Archaea are chemoautotrophs that obtain energy by oxidizing inorganic substances, while others are chemoheterotrophs that oxidize organic molecules. No known member of the Archaea has been shown to be pathogenic.

The cell structure of archaeans is basically prokaryotic. Among their unique characteristics are certain features of the plasma membrane and cell wall. The lipid molecules in archaean plasma membranes have a chemical bond between the hydrocarbon chains and

Figure 25.16
Typically extreme archaean habitats. **(a)** Highly saline water in Great Salt Lake, Utah, colored red-purple by Archaea. **(b)** Hot, sulfur-rich water in Emerald Pool, Yellowstone National Park, colored brightly by the oxidative activity of archaeans, which converts H_2S to elemental sulfur.

a.

Barry Rokeach

b.

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Insights from the Molecular Revolution

Extreme but Still in Between

In 1996 Carol J. Bult, Carl R. Woese, J. Craig Venter, and 37 other scientists at the Institute for Genomic Research obtained the complete DNA sequence of the archaean *Methanococcus jannaschii*. It was the first archaean genome to be sequenced. The results were obtained by sequencing randomly chosen overlapping DNA fragments from a DNA library until the entire genome was completed (the whole-genome shotgun approach, described in Section 18.3). Comparisons of the *Methanococcus* sequence with bacterial sequences and that of a eukaryote, the brewer's yeast *Saccharomyces cerevisiae,* give strong support to the proposal that the Archaea are a separate domain of living organisms.

Many archaeans have a lifestyle clearly different from those of the bacteria and eukaryotes, and *Methanococcus* is no exception. It was first discovered by the deep-sea submarine *Alvin* in a hot-water vent at a depth of more than 2600 m. It can live at temperatures as high as 94°C, only a few degrees less than the temperature of boiling water, and can tolerate pressure as high as 200 times the pressure of air at sea level.

The *Methanococcus* main genome, which includes 1,664,976 base pairs, was found to contain 1682 protein-encoding sequences. Two plasmids also contain protein-encoding genes, one plasmid with 44 genes and the other with 12. Of the total of 1738 protein-encoding sequences, only 38%—less than half—could be given probable identities based on sequence similarities with those of genes coding for known proteins in other organisms. Some of the sequences were similar to proteins of bacteria, and some to those of eukaryotes. Among the eukaryote-like genes are those encoding all five of the histone chromosomal proteins typical of eukaryotes and eukaryotic forms of the enzymes carrying out DNA replication and RNA transcription.

Other identified genes encode proteins unique to the Archaea, such as those encoding some enzymes and other proteins of the pathway reducing CO_2 to methane. Many other proteins with no known counterparts in the Bacteria or Eukarya are among the unidentified 62%, demonstrating the unique character of the Archaea and providing a rich lode of new proteins for mining by molecular biologists and other scientists.

glycerol unlike that in the plasma membranes of all other organisms. The difference is significant because the exceptional linkage is more resistant to disruption, making the plasma membranes of the Archaea more tolerant of the extreme environmental conditions under which many of these organisms live.

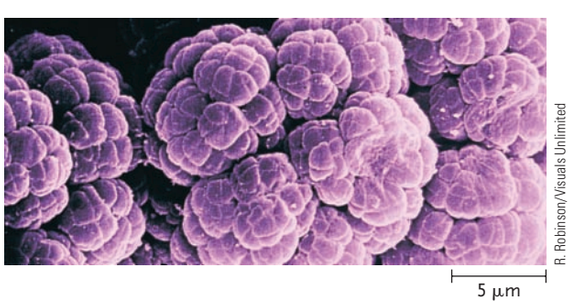
The cell walls of some archaeans are assembled from molecules related to the peptidoglycans, but with different molecular components and bonding structure. Others have walls assembled from proteins or polysaccharides instead of peptidoglycans. The cell walls of archaeans are as resistant to physical disruption as the plasma membrane is; some archaeans can be boiled in strong detergents without disruption. Different archaeans stain as either Gram-positive or Gram-negative.

Molecular Studies Reveal Three Evolutionary Branches in the Archaea

Based on differences between the rRNA coding sequences in their genomes, the domain Archaea is divided into three groups (see Figure 25.11). Two major groups, the **Euryarchaeota** and the **Crenarchaeota**, contain archaeans that have been cultured and examined in the laboratory. The third group, the **Korarchaeota**, has been recognized solely on the basis of rRNA coding sequences in DNA taken from environmental samples. A fourth group, the **Nanoarchaeota**, was proposed based on rRNA sequence analysis of a thermophilic archaean found in a symbiotic relationship with another thermophilic archaean. Genome sequence comparisons have now shown that the Nanoarchaeota are most probably a subgroup of the Euryarchaeota.

Euryarchaeota. The Euryarchaeota are found in different extreme environments. They include methogens, which produce methane; extreme halophiles, which live in high concentrations of salt; and some extreme thermophiles, which live under high-temperature conditions.

Methanogens (methane generators) live in reducing environments **(Figure 25.17),** and represent about one half of all known species of archaeans. All known methanogens belong to the Euryarchaeota. Examples are *Methanococcus* and *Methanobacterium*. Methanogens are obligate anaerobes,



R. Robinson/Visuals Unlimited

Figure 25.17
A colony of the methanogenic archaean *Methanosarcina,* which lives in the sulfurous, waterlogged soils of marshes and swamps.

meaning they are killed by oxygen. They are found in the anoxic (oxygen-lacking) sediments of swamps, lakes, marshes, and sewage works, as well as in more moderate environments, such as the rumen of cattle, sheep, and camels; the large intestine of dogs and humans; and the hindguts of insects such as termites and cockroaches. Methanogens generate energy by converting at least ten different substrates such as carbon dioxide and hydrogen gas, methanol, or acetate into methane gas (CH_4), which is released into the atmosphere. A single species may use two or three substrates, for example converting carbon dioxide and hydrogen into methane and water.

Halophiles are salt-loving organisms. Extreme halophilic Archaea live in highly saline (salty) environments such as the Great Salt Lake or the Dead Sea, and on foods preserved by salting. Moreover, they require a high concentration of salt to live: they need a minimum NaCl concentration of about 1.5 M (about 9% solution), and can live in a fully saturated solution (5.5 M, or 32%). All known extreme halophilic Archaea belong to the Euryarchaeota. Most are aerobic chemoheterotrophs; they obtain energy from sugars, alcohols, and amino acids using pathways similar to those of bacteria. Examples are *Halobacterium* and *Natrosobacterium*. *Halobacterium,* like a number of extreme halophiles, uses light as a secondary energy source supplementing the oxidations that are its primary source of energy.

Extreme thermophiles live in extremely hot environments. Extreme thermophilic Archaea live in thermal areas such as ocean floor hydrothermal vents and hot springs such as those in Yellowstone National Park. Their optimal temperature range for growth is 70° to 95°C, approaching the boiling point of water. By comparison, no eukaryotic organism is known to live at a temperature higher than 60°C. Some extreme thermophiles are members of the Euryarchaeota. Some of them, such as *Pyrophilus,* are obligate anaerobes, while others, such as *Thermoplasma,* are facultative anaerobes that grow on a variety of organic compounds.

Crenarchaeota. The group Crenarchaeota contains most of the extreme thermophiles. Their optimal temperature range of 75° to 105°C is higher than that of the Euryarchaeota. Most are unable to grow at temperatures below 70°C. The most thermophilic member of the group, *Pyrobolus,* grows optimally at 106°C, but dies below 90°C. It can also grow at 113°C and survive an hour of autoclaving at 121°C! *Pyrobolus* lives in ocean floor hydrothermal vents where the pressure makes it possible to have temperatures above 100°C, the boiling point of water on Earth's surface.

Also within this group are **psychrophiles** ("cold loving"), organisms that grow optimally in cold temperatures in the range −10 to 20°C. These organisms are found mostly in the Antarctic and Arctic oceans, which are frozen most of the year, and in the intense cold at ocean depths.

Mesophilic members of the Crenarchaeota comprise a large part of plankton in cool, marine waters where they are food sources for other marine organisms. As yet, no individual species of these archaeans has been isolated and characterized.

Crenarchaeota archaeans exhibit a wide range of metabolism with regard to oxygen, including obligate anaerobes, facultative anaerobes, and aerobes.

Korarchaeota. The group Korarchaeota has been recognized solely on the basis of analyzing rRNA sequences in DNA obtained from marine and terrestrial hydrothermal environments, such as the Obsidian Pool at Yellowstone National Park. To date, no members of this group have been isolated and cultivated in the lab, and nothing is known about their physiology. They are the oldest lineage in the domain Archaea according to molecular data.

Thermophilic archaeans are important commercially. For example, enzymes from some species are used in basic and applied research, such as the thermostable DNA polymerase used in the polymerase chain reaction (PCR; see Chapter 18). Other enzymes from thermophilic archaeans are being tested for addition to detergents, where it is hoped that they will be active under high temperatures and acidic pH.

From the highly varied prokaryotes, we now turn to the viruses, which occur in most environments in even greater numbers than bacteria and archaeans. The next section also discusses prions and viroids, infective agents that are even simpler and smaller than viruses.

Study Break

1. What distinguishes members of the Archaea from members of the Bacteria and Eukarya?
2. How does a methanogen obtain its energy? In which group or groups of Archaea are methanogens found?
3. Where do extreme halophilic archaeans live? How do they obtain energy? In which group or groups of Archaea are the extreme halophiles found?
4. What are extreme thermophiles and psychrophiles?

25.4 Viruses, Viroids, and Prions

A **virus** (Latin for poison) is a biological particle that can infect the cells of a living organism. Viral infections usually have detrimental effects on their hosts.

The study of viruses is called *virology,* and researchers studying viruses are known as *virologists.*

All viruses contain a nucleic acid molecule (the genome), surrounded by a layer of protein called the **coat** or **capsid.** The complete virus particle is also called a **virion.** Viruses are considered nonliving primarily because they have no metabolic system of their own to provide energy for their life cycles; instead, they are dependent upon the host cells they infect for that function. That is, expression of virus genes in an infected host cell directs that cell to use its own machinery to duplicate the virus. However, their genome contains all the information required to convert host cells to the duplication of viruses of the same type. Although they are considered to be nonliving material, viruses are classified by the International Committee on Taxonomy of Viruses into orders, families, genera, and species using several criteria, including size and structure, type and number of nucleic acid molecules, method of replication of the nucleic acid molecules inside host cells, host range, and infective cycle. More than 4000 species of viruses have been classified into more than 80 families according to these criteria.

One or more kinds of viruses probably infect all living organisms. Usually a virus infects only a single species or a few closely related species. (A virus may even infect only one organ system, or a single tissue or cell type in its host.) However, some viruses are able to infect unrelated species, either naturally or after mutating. For example, some humans have contracted bird flu from being infected with the natural bird flu virus as a result of contact with virus-infected birds. At least 65 deaths of people in Asia have been attributed to bird flu. The bird flu virus has the potential to mutate to give efficient human-to-human transmission, raising significant concern about the possibility of a worldwide epidemic of bird flu virus infections of humans, with the possibility of millions of deaths. Of the viral families, 21 include viruses that cause human diseases. Viruses also cause diseases of wild and domestic animals; plant viruses cause annual losses of millions of tons of crops, especially cereals, potatoes, sugar beets, and sugar cane. (**Table 25.2** lists some important families that infect animals.)

The effects of viruses on the organisms they infect range from undetectable, through merely bothersome, to seriously debilitating or lethal. For instance, some viral infections of humans, such as those causing cold sores, chicken pox, and the common cold, are usually little more than a nuisance to healthy adults. Others, including AIDS, encephalitis, yellow fever, and smallpox, are among the most severe and deadly human diseases. While most viruses have detrimental effects, some may be considered beneficial. One of the primary reasons why bacteria do not completely overrun the planet is that they are destroyed in incredibly huge numbers by viruses known as **bacteriophages**, or **phages** for short (*phagein* = to eat; see Chapters 14 and 17 for the use of phages in important discoveries in molecular biology and bacterial genetics). Viruses also provide a natural means to control some insect pests.

Table 25.2 **Major Animal Viruses**

Viral Family	Envelope	Nucleic Acid	Diseases
Adenoviruses	No	ds DNA	Respiratory infections, tumors
Flaviviruses	Yes	ss RNA	Yellow fever, dengue, hepatitis C
Hepadnaviruses	Yes	ds DNA	Hepatitis B
Herpesviruses	Yes	ds DNA	
H. simplex I			Oral herpes, cold sores
H. simplex II			Genital herpes
Varicella-zoster			Chicken pox, shingles
Orthomyxovirus	Yes	ss RNA	Influenza
Papovaviruses	No	ds DNA	Benign and malignant warts
Paramyxoviruses	Yes	ss RNA	Measles, mumps, pneumonia
Picornaviruses	No	ss RNA	
Enteroviruses			Polio, hemorrhagic eye disease, gastroenteritis
Rhinoviruses			Common cold
Hepatitis A virus			Hepatitis A
Apthovirus			Foot-and-mouth disease in livestock
Poxviruses	Yes	ds DNA	Smallpox, cowpox
Retroviruses	Yes	ss RNA	
HTLV I, II			T-cell leukemia
HIV			AIDS
Rhabdoviruses	Yes	ss RNA	Rabies, other animal diseases

ss = single-stranded; ds = double-stranded.

Viral Structure Is Reduced to the Minimum Necessary to Transmit Nucleic Acid Molecules from One Host Cell to Another

The nucleic acid genome of a virus, depending on the viral type, may be either DNA or RNA, in either double- or single-stranded form. The nucleic acid molecule contains genes encoding proteins of the viral coat, and often also enzymes required to duplicate the genome. The simplest viral nucleic acid molecules contain only a few genes, but those of the most complex viruses may contain a hundred or more.

Some viruses have coats assembled from protein molecules of a single type; more complex viruses have coats made up of several different proteins—in some, 50 or more, including the recognition proteins that bind to host cells. The particles of some viruses also

contain the DNA or RNA polymerase enzymes required for viral nucleic acid replication and an enzyme that attacks cell walls or membranes.

Most viruses take one of two basic structural forms, helical or polyhedral. In **helical viruses** the protein subunits assemble in a rodlike spiral around the genome **(Figure 25.18a).** A number of viruses that infect plant cells are helical. In **polyhedral viruses** the coat proteins form triangular units that fit together like the parts of a geodesic sphere **(Figure 25.18b).** The polyhedral viruses include forms that infect animals, plants, and bacteria. In some polyhedral viruses, protein spikes that provide host cell recognition extend from the corners where the facets fit together. Some viruses, the **enveloped viruses**, are covered by a surface membrane derived from their host cells; both enveloped helical and enveloped polyhedral viruses are known **(Figure 25.18c).** For example, HIV (for *h*uman *i*mmunodeficiency *v*irus), the virus that causes AIDS, is an enveloped polyhedral virus. Protein spikes extend through the membrane, giving the particle its recognition and adhesion functions.

A number of bacteriophages with DNA genomes, such as T2 (see Section 14.1), have a **tail** attached at one side of a polyhedral **head**, forming what is known as a **complex virus (Figure 25.18d).** The genome is packed into the head; the tail is made up of proteins forming a collar, sheath, baseplate, and tail fibers. The tail has recognition proteins at its tip and, once attached to a host cell, functions as a sort of syringe that injects the DNA genome into the cell.

Viruses Infect Bacterial, Animal, and Plant Cells by Similar Pathways

Free viral particles move by random molecular motions until they contact the surface of a host cell. For infection to occur, the virus or the viral genome must then enter the cell. Inside the cell, typically the viral genes are expressed, leading to replication of the viral genome and assembly of progeny viruses. The viruses are then released from the host cell, a process that often ruptures the host cell, killing it.

Infection of Bacterial Cells. Bacteriophages vary as to whether they have a DNA or an RNA genome, and whether that nucleic acid is double-stranded or single-stranded. A DNA bacteriophage such as the virulent phage T2 (see Figure 25.18d) infects a bacterial cell and goes through the *lytic cycle,* in which the host cell is killed in each cycle of infection (described in Section 17.2 and Figure 17.9). In brief review, the lytic cycle of phage T2 is as follows: After the phage attaches to a host cell, an enzyme present in the baseplate of the viral coat, *lysozyme,* digests a hole in the cell wall through which the DNA of the phage enters the bacterium while the proteins of the viral coat remain outside. Once inside the bacterium, expression of phage genes directs the replication of the phage DNA, synthesis of phage proteins, and assembly of progeny phage particles. Next, the phage directs synthesis of a phage-encoded lysozyme enzyme that lyses the bacterial cell wall, causing the cell to rupture and releasing the progeny phages to the surroundings where they can infect other bacteria.

Some bacteriophages alternate between a lytic cycle and a *lysogenic cycle,* in which the viral DNA inserts into the host cell DNA and production of new viral particles is delayed (see Section 17.2). During the lysogenic cycle, the integrated viral DNA, known as the *prophage,* remains partially or completely inactive, but is replicated and passed on with the host DNA to all descendants of the infected cell. In response to certain environmental signals, the prophage loops out of the chromosome and the lytic cycle of the phage proceeds.

Infection of Animal Cells. Viruses infecting animal cells follow a similar pattern except that both the viral coat and genome, which is DNA or RNA depending

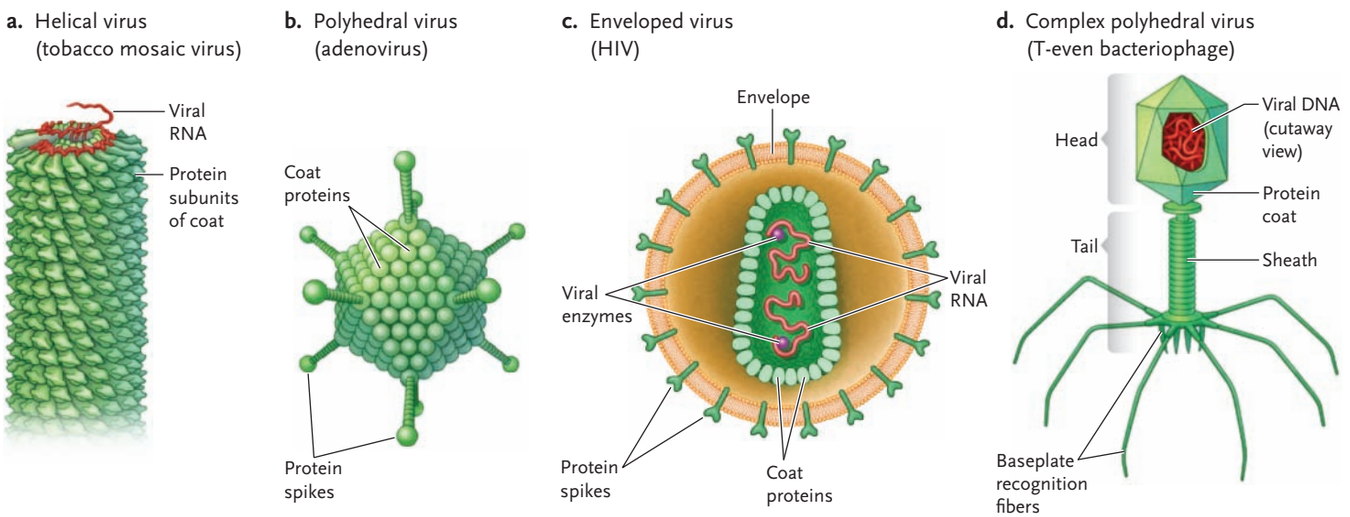


Figure 25.18
Viral structure. The tobacco mosaic virus in **(a)** assembles from more than 2000 identical protein subunits.

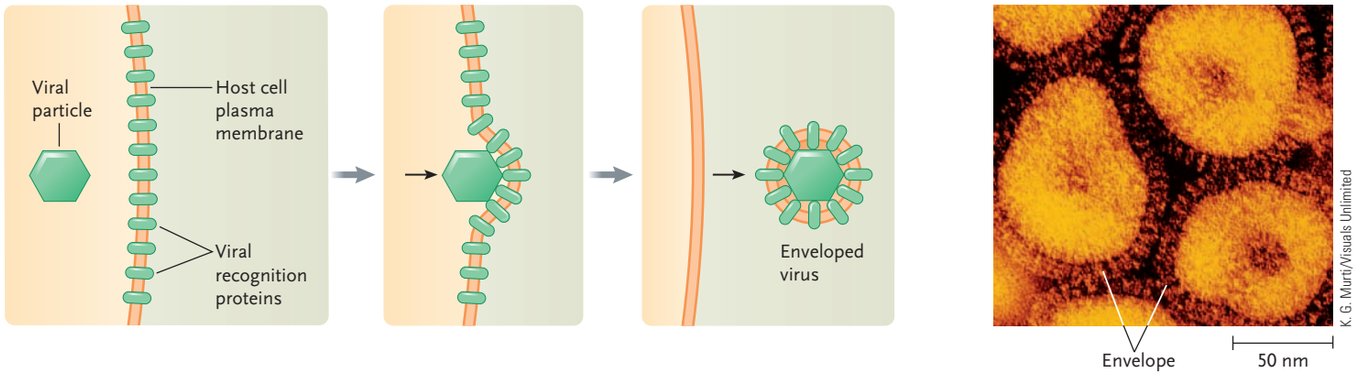


Figure 25.19 How enveloped viruses acquire their envelope. The micrograph shows the influenza virus with its envelope. Note the recognition proteins studding the envelope.

on the viral type, enter a host cell. Depending on the virus, removal of the coat to release the genome occurs during or after cell entry; the envelope does not enter the cell.

Viruses without an envelope, such as adenovirus (DNA genome) and poliovirus (RNA genome), bind by their recognition proteins to the plasma membrane and are then taken into the host cell by endocytosis. The virus coat and genome of enveloped viruses, such as herpesviruses and pox viruses (DNA genome), and HIV and influenza virus (RNA genome), enter the host cell by fusion of their envelope with the host cell plasma membrane.

Once inside the host cell, the genome directs the synthesis of additional viral particles by basically the same pathways as bacterial viruses. Newly completed viruses that do not acquire an envelope are released by rupture of the cell's plasma membrane, typically killing the cell. In contrast, most enveloped viruses receive their envelope as they pass through the plasma membrane, usually without breaking the membrane **(Figure 25.19).** This pattern of viral release typically does not injure the host cell.

The vast majority of animal virus infections are asymptomatic; pathogenesis—the causation of disease—is of no value to the virus. However, there are a number of pathogenic viruses, and they cause diseases in a variety of ways. Some viruses, for instance, cause cell death when progeny viruses are released from the cell. This can lead to massive cell death, destroying vital tissues such as nervous tissue or white or red blood cells, or causing lesions such as ulcers in skin and mucous membranes. Some other viruses release cellular molecules when infected cells break down, which can induce fever and inflammation. Yet other viruses alter gene function when they insert into the host cell DNA, leading to cancer and other abnormalities.

Some animal viruses enter a **latent phase** in which the virus remains in the cell in an inactive form: the viral nucleic acid is present in the cytoplasm or nuclear DNA, but no complete viral particles or viral release can be detected. (The latent phase is similar to the lysogenic cycle that is part of the life cycle of some bacteriophages.) At some point, the latent phase may end as the viral DNA is replicated in quantity, coat proteins are made, and completed viral particles are released from the cell. The herpesviruses causing oral and genital ulcers in humans remains in a latent phase of this type in the cytoplasm of some body cells for the life of the individual. At times, particularly during periods of metabolic stress, the virus becomes active in some cells, directing viral replication and causing ulcers to form as cells break down during viral release.

Infection of Plant Cells. Plant viruses may be rodlike or polyhedral; although most include RNA as their nucleic acid, some contain DNA. None of the known plant viruses have envelopes. Plant viruses enter cells through mechanical injuries to leaves and stems or through transmission from plant to plant by biting and feeding insects such as leaf hoppers and aphids, by nematode worms, and by pollen during fertilization. Plant viruses can also be transmitted from generation to generation in seeds. Once inside a cell, plant viruses replicate in the same patterns as animal viruses. Within plants, virus particles pass from infected to healthy cells through plasmodesmata, the openings in cell walls that directly connect plant cells, and through the vascular system.

Plant viruses are generally named and classified by the type of plant they infect and their most visible effects. *Tomato bushy stunt virus,* for example, causes dwarfing and overgrowth of leaves and stems of tomato plants, and *tobacco mosaic virus* causes a mosaic-like pattern of spots on leaves of tobacco plants. Most species of crop plants can be infected by at least one destructive virus.

The tobacco mosaic virus was the first virus to be isolated, crystallized, disassembled, and reassembled in the test tube, and the first viral structure to be established in full molecular detail (see Figure 25.18a).

Viral Infections Are Typically Difficult to Treat

Viral infections are unaffected by the antibiotics and other treatment methods used for bacterial infections. As a result, many viral infections are allowed to run

their course, with treatment limited to relieving the symptoms while the natural immune defenses of the patient attack the virus. Some viruses, however, cause serious and sometimes deadly symptoms upon infection and, consequently, researchers have spent considerable effort to develop antiviral drugs to treat them. Many of these drugs fight the virus directly by targeting a stage of the viral life cycle; they include amantidine (inhibits hepatitis B and hepatitis C virus entry into cells), acyclovir (analog of nucleosides [*analog* means it is chemically similar] that inhibits replication of the genomes of herpesviruses), and zanamivir (inhibits release of influenza virus particles from cells).

The influenza virus illustrates the difficulties inherent in treating viral diseases. The influenza type A virus (see Figure 25.19) causes flu epidemics that sweep over the world each year. It has many unusual features that tend to keep it a step ahead of efforts to counteract its infections. One is the genome of the virus, which consists of eight separate pieces of RNA. When two different influenza viruses infect the same individual, the pieces can assemble in random combinations derived from either parent virus. The new combinations can change the protein coat of the virus, making it unrecognizable to antibodies developed against either parent virus. Antibodies are highly specific protein molecules produced by the immune system that recognize and bind to foreign proteins originating from a pathogen (see Chapter 43). The invisibility to antibodies means that new virus strains can infect people who have already had the flu or who have had flu shots that stimulate the formation of antibodies effective only against the earlier strains of the virus. Random mutations in the RNA genome of the virus add to the variations in the coat proteins that make previously formed antibodies ineffective.

Luckily, most flu infections, although debilitating, are not dangerous, except for individuals who are very young or very old or who have compromised immune systems. However, some flu epidemics have been devastatingly lethal. The worst recorded example is the epidemic of 1918. A strain of influenza virus known as the Spanish flu infected approximately 20% of the world's 1.8 billion people, killing about 50 million.

The exact type of virus responsible for this deadly epidemic was finally determined in 2005, when researchers led by Jeffrey Taubenberger at the U.S. Armed Forces Institute of Pathology reconstructed the genome of the virus and produced infectious, pathogenic viruses in the laboratory. The team worked mainly with tissue from a 1918 flu victim found in permafrost in Alaska. Using modern DNA technology (see Chapter 18), they pieced together the sequences of the virus's eight genes and characterized their protein products. They also transformed clones of the genes into animal cells and were able to produce complete virus particles. These newly reconstructed 1918 viruses are about 50 times more virulent than modern-day human influenza viruses; they kill a higher percentage of mice and kill them much more quickly, for instance. (All of these experiments were done with appropriate approval and under highly controlled experimental conditions.) By studying the 1918 virus genome and its pathogenicity, the researchers are learning how highly virulent viruses can be produced. What they have learned so far is that the 1918 virus had mutations in polymerase genes for replicating the viral genome in host cells, likely making this strain capable of replicating more efficiently. Some of the mutations are similar to those found in bird flu viruses, including the one causing human deaths in Asia. The scientists believe that the 1918 flu virus likely arose directly from a bird flu virus and not from an assembly of RNA genome segments from a bird flu virus and a human flu virus in the same cell. If this is true, the concern about a devastating bird flu epidemic in the near future is well founded.

Other human viruses are also considered to have evolved from a virus that previously infected other animals. HIV is one of these; until the second half of the twentieth century, infections of this virus were apparently restricted almost entirely to African monkeys. Now the virus infects nearly 40 million people worldwide, with the greatest concentration of infected individuals in sub-Saharan Africa.

Viruses May Have Evolved from Fragments of Cellular DNA or RNA

Where did viruses come from? Because viruses can duplicate only by infecting a host cell, they probably evolved after cells appeared. They may represent fragments of DNA molecules that once formed part of the genetic material of living cells, or an RNA copy of such a fragment. In some way, the fragments became surrounded by a protective layer of protein with recognition functions and escaped from their parent cells. As viruses evolved, the information encoded in the core of the virus became reduced to a set of directions for producing more viral particles of the same kind.

Viroids and Prions Are Infective Agents Even Simpler in Structure than Viruses

Viroids, first discovered in 1971, are plant pathogens that consist of strands or circles of RNA, smaller than any viral DNA or RNA molecule, that have no protein coat. Some of the infective RNAs acting as viroids contain fewer than 300 nucleotides. Infection by viroids can rapidly destroy entire fields of citrus, potatoes, tomatoes, coconut palms, and other crop plants.

The manner in which viroids cause disease remains ill defined. In fact, researchers believe that there is more than one mechanism. Some recent research has defined one pathway to disease in which viroid RNA activates a protein kinase (an enzyme that adds phosphate groups to proteins) in plants. This process

leads to a reduction in protein synthesis and protein activity, and disease symptoms result.

Prions, named by Stanley Prusiner of the University of California San Francisco in 1982 as a loose acronym for *pro*teinaceous *in*fectious particles, are the only known infectious agents that do not include a nucleic acid molecule.

Prions have been identified as the causal agents of certain diseases that degenerate the nervous system in mammals. One of these diseases is *scrapie,* a brain disease that causes sheep to rub against fences, rocks, or trees until they scrape off most of their wool. Another prion-based disease is bovine spongiform encephalopathy (BSE), also called *mad cow disease* **(Figure 25.20)**. The disease produces spongy holes and deposits of proteinaceous material in brain tissue. In 1996, 150,000 cattle in Great Britain died from an outbreak of BSE, which was traced to cattle feed containing ground-up tissues of sheep that had died of scrapie. Humans are subject to a fatal prion infection called *Creutzfeldt-Jakob disease (CJD)*. The symptoms of CJD include rapid mental deterioration, loss of vision and speech, and paralysis; autopsies show spongy holes and deposits in brain tissue similar to those of cattle with BSE. Classic CJD occurs as a result of the spontaneous transformation of normal proteins into prion proteins. Fewer than 300 cases a year occur in the United States. Variant CJD

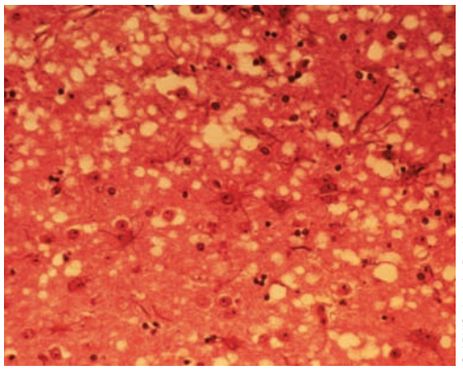


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Figure 25.20
Bovine spongiform encephalopathy (BSE). The light-colored patches in this section from a brain damaged by BSE are areas where tissue has been destroyed.

Unanswered Questions

Do viruses infect archaeans?

Viruses of bacteria, and of the many types of eukaryotes, are well defined morphologically and molecularly. Do viruses infect members of the Archaea? If so, do these viruses resemble known viruses?

Mark Young's research group at Montana State University has focused on characterizing viruses from extreme thermophilic archaeans belonging to Crenoarchaeota. The researchers have discovered a number of viruses in archaeans from Yellowstone National Park acidic thermal areas. The morphology and molecular features of some of these viruses are novel and unrelated to those of any other known viruses. Young's group has sequenced the genomes of several of these new viruses, and their results indicate that the genes they carry have little or no similarity to known genes. Another archaean virus from the same area has a morphology also found in viruses of Bacteria and Eukarya. This result is of evolutionary significance because it suggests that the structure of the virus particle existed before the separation of each domain. The long-term goal of the research is to determine the mechanisms by which the viruses replicate in their extremely hot environment and to use them as tools for characterizing the special mechanisms the organisms use to survive at high temperatures. The research will also contribute to our understanding of the role viruses played in evolution.

How can West Nile virus be controlled?

West Nile virus is typically spread by mosquitoes. Usually, a mosquito becomes a carrier after biting a bird infected with the virus, and it then transmits the virus to other birds. Infected mosquitoes can also transmit the virus to humans and a number of other hosts, such as horses.

West Nile virus first entered the United States in 1999, and a number of humans have been infected. Humans infected with West Nile virus usually have mild symptoms such as fever, headache, body aches, rash, and swollen lymph glands. In some infected individuals, though, the virus enters the brain, where it can cause meningitis (inflammation of the lining of the brain and spinal cord) or encephalitis (inflammation of the brain), both of which can be fatal.

Researchers are trying to understand the infection cycle of the virus and how the virus causes disease. Specific research questions include how the virus replicates in the host and how the virus spreads through the body. Answers to these questions should aid efforts to develop effective vaccines and drugs to prevent and treat this disease. (At present, there is no vaccine for humans; one is available for horses.)

How do prion proteins move within the brain?

The brain-wasting diseases caused by prions are not well understood, despite much research. We know that prion proteins invade nerve cells and ultimately lead to fatal degeneration of the nervous system. To understand disease progression, scientists have investigated how prion proteins move through the nervous system. Using labeled-protein techniques, researchers have tracked infectious prion proteins from sites of infection up to the brain. Recently, the research groups of Bryon Caughey at the Rocky Mountain Laboratories in Montana, and Marco Prado at the University of Minas Gerais, Brazil, followed prion proteins as they invaded mouse brain cells growing in tissue culture. One exciting observation in these experiments was that prion proteins moved through the wirelike projections of the nerve cells to points of contact with other cells. Perhaps in a living organism, the prion proteins would be able to cross into the adjacent cell. The results are heralded as a significant step toward developing therapies to stop the spread of brain-wasting diseases by blocking the pathways by which prion proteins invade cells, replicate, move within the cell, and invade adjacent cells.

Peter J. Russell

is a form of the disease caused by eating nervous tissue containing meat or meat products from cattle with BSE. Another prion-based disease of humans, *kuru,* originally spread among cannibals in New Guinea, who became infected by eating raw human brain during ritual feasts following the death of an individual.

For several decades, scientists had hypothesized that a slow virus—a disease-causing virus with a long incubation period and gradual onset of pathogenicity—was responsible for these diseases. Prusiner was the first to hypothesize that infectious proteins were responsible. The research community mostly rejected this hypothesis out of hand because they held to the dogma that infectious agents required genes in the form of DNA or RNA to cause disease. Prusiner obtained experimental data supporting his hypothesis, and showed that prions are proteins normally made in the cell that misfold and cause other proteins of the same type to misfold, thereby "replicating" structural information from one molecule to the next. Typically, the misfolded prion proteins aggregate, whereas the normal proteins do not. If a misfolded prion protein is transferred from one animal to another, infection occurs; the transferred prions cause the recipient's proteins to misfold and eventually symptoms of the neurodegenerative disease characteristic of the prion will develop. Proteins with prion behavior are also found naturally in yeast and other fungi; no diseases are associated with these prions. Prusiner received a Nobel Prize in 1997 for his discovery of prions.

The diseases caused by prions share symptoms that include loss of motor control, dementia, and eventually death. Progression of the disease is slow but there is no present cure. Under the microscope, aggregates of misfolded proteins called amyloid fibers are seen in brain tissues; the accumulation of these proteins in the brain is the likely cause of the brain damage in animals with prion diseases. The normal forms of the prion proteins are found on the surface of many types of cells, including brain cells. However, scientists do not know the function of the protein's normal form.

We began this chapter with prokaryotes, the simplest living organisms, and we end with still simpler entities, viruses, viroids, and prions, which are derived from living organisms and retain only some of the properties of life. In the next six chapters we turn to life at its most complex: the eukaryotic kingdoms of protists, plants, fungi, and animals.

Study Break

Distinguish between a virus, a viroid, and a prion.

Review

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25.1 Prokaryotic Structure and Function

- Three shapes are common in prokaryotes: spherical, rodlike, and spiral (Figure 25.2).
- Prokaryotic genomes typically consist of a single, circular DNA molecule packaged into the nucleoid. Many prokaryotic species also contain plasmids, which replicate independently of the main DNA (Figure 25.3).
- Gram-positive bacteria have a cell wall consisting of a thick peptidoglycan layer. Gram-negative bacteria have a thin peptidoglycan layer. The thin cell wall is surrounded by an outer membrane (Figure 25.4).
- A polysaccharide capsule or slime layer surrounds many bacteria. This sticky, slimy layer both protects the bacteria and helps them adhere to surfaces (Figure 25.5).
- Some prokaryotes have flagella, corkscrew-shaped protein fibers that rotate like propellers, and pili, protein shafts that help bacterial cells adhere to each other or to eukaryotic cells (Figure 25.7).
- Prokaryotes show great diversity in their modes of obtaining energy and carbon. Chemoautotrophs obtain energy by oxidizing inorganic substrates and use carbon dioxide as their carbon source. Chemoheterotrophs obtain both energy and carbon from organic molecules. Photoautotrophs are photosynthetic organisms that use light as a source of energy and carbon dioxide as their carbon source. Photoheterotrophs use light as a source of energy and obtain their carbon from organic molecules (Figure 25.8).
- Some prokaryotes are capable of nitrogen fixation, the conversion of atmospheric nitrogen to ammonia; others are responsible for nitrification, the two-step conversion of ammonium to nitrate.
- Prokaryotes normally reproduce asexually by binary fission. Some prokaryotes are capable of conjugation, in which part of the DNA of one cell is transferred to another cell.
- In nature, prokaryotes may live in an interacting community, such as a biofilm. Biofilms have both detrimental and beneficial consequences; they can harm human health, but they also can be effective in, for example, bioremediation (Figure 25.10).

Animation: Prokaryotic body plan

Animation: Gram staining

Animation: Prokaryotic fission

Animation: Prokaryotic conjunction

25.2 The Domain Bacteria

- Bacteria are divided into more than a dozen evolutionary branches (Figure 25.11).
- The proteobacteria are Gram-negative bacteria that include purple sulfur (photoautotrophic) and nonsulfur (photoheterotrophic) photosynthetic species, and nonphotosynthetic species. Free-living proteobacteria include the spore-forming myxobacteria and species that fix nitrogen (Figure 25.12).
- The green bacteria are Gram-negative and include sulfur (photoautotrophic) and nonsulfur (photoheterotrophic) photosynthetic bacteria.

- The cyanobacteria are Gram-negative photoautotrophs that carry out photosynthesis and release oxygen as a by-product (Figure 25.13).
- The Gram-positive bacteria are primarily chemoheterotrophs that include many pathogenic species (Figure 25.14).
- The spirochetes are spiral-shaped bacteria that are propelled by twisting movements produced by the rotation of flagella.
- Chlamydias are Gram-negative intracellular parasites that cause various diseases in animals. They have cell walls with an outer membrane, but they lack peptidoglycans (Figure 25.15).
- Bacteria cause disease through exotoxins, endotoxins, and exoenzymes.
- Pathogenic bacteria may develop resistance to antibiotics through mutation of their own genes, or by acquiring resistance genes from other bacteria or plasmids.

Animation: Examples of Eubacteria

25.3 The Domain Archaea

- The Archaea have some features that are like those of bacteria, others that are eukaryotic, and some that are uniquely archaean (Table 25.1).
- The archaean plasma membrane contains unusual lipid molecules. The cell walls of archaeans consist of distinct molecules similar to peptidoglycans, or of protein or polysaccharide molecules.
- The Archaea are classified into three groups. The Euryarchaeota include the methanogens, the extreme halophiles, and some extreme thermophiles. The Crenarchaeota contain most of the archaean extreme thermophiles, as well as psychrophiles and mesophiles. Obligate anaerobes, facultative anaerobes, and aerobes are found among the Crenarchaeota. The Korarchaeota are recognized only on the basis of sequences in DNA samples.

25.4 Viruses, Viroids, and Prions

- Viruses are nonliving infective agents. A free virus particle consists of a nucleic acid genome enclosed in a protein coat. Recognition proteins enabling the virus to attach to host cells extend from the surface of infectious viruses (Figure 25.18).
- Viruses reproduce by entering a host cell and directing the cellular machinery to make new particles of the same kind.
- Viruses are unaffected by antibiotics and most other treatment methods; hence, infections caused by them are difficult to treat.
- Viroids, which infect crop plants, consist only of a very small, single-stranded RNA molecule. Prions, which cause brain diseases in some animals, are infectious proteins with no associated nucleic acid. Prions are misfolded versions of normal cellular proteins that can induce other normal proteins to misfold.

Animation: Body plans of viruses

Animation: Bacteriophage multiplication cycles

Questions

Self-Test Questions

1. A urologist identifies cells in a man's urethra as bacterial. Which of the following descriptions applies to the cells?
   a. They have sex pili, which give them motility.
   b. They have flagella, which allow them to remain in one position in the urethral tube.
   c. They are covered by a capsule, which enables them to multiply quickly.
   d. They are covered by pili, which keep them attached to the urethral walls.
   e. They contain a peptidoglycan cell wall, which gives them buoyancy to float in the fluids of the urethra.
2. A bacterium that uses nitrites as its only energy source was found in a deep salt mine. It is a:
   a. chemoautotroph.
   b. parasite.
   c. photoautotroph.
   d. heterotroph.
   e. photoheterotroph.
3. The _____ are all oxygen-producing photoautotrophs.
   a. spirochetes
   b. chlamydias
   c. cyanobacteria
   d. Gram-positive bacteria
   e. proteobacteria
4. At the health center, a fecal sample was taken from a feverish student. Organisms with corkscrew-like flagella and no endomembranes but with cell walls were isolated as the cause for the illness. These organisms belong to the group:
   a. protists with nuclei.
   b. bacteria with ribosomes.
   c. fungi with endoplasmic reticulum.
   d. plants with chloroplasts
   e. Archaea with Golgi bodies.
5. Which of the following is *not* a property of an endospore?
   a. resistant to boiling—must be autoclaved to be killed
   b. metabolically inactive
   c. can survive millions of years
   d. provides a method to preserve bacterial DNA under harsh conditions
   e. is a means that bacterial cells use to multiply
6. Each bacterial cell is traditionally thought to act independently of others. An exception to this is:
   a. biofilm aggregates.
   b. photosynthesis.
   c. peptidoglycan layering.
   d. toxin release.
   e. facultative anaerobic metabolism.
7. Penicillin, an antibiotic, inhibits the formation of cross-links between sugar groups in peptidoglycan. Bacteria treated with penicillin should be:
   a. aerobic.
   b. anaerobic.
   c. Gram-negative.
   d. Gram-positive.
   e. flagellated.
8. The best choice when using/prescribing antibiotics is to:
   a. increase the dosage when the original amount does not work.
   b. determine the kind of bacterium causing the problem.
   c. stop taking the antibiotic when you feel better but the prescription has not run out.
   d. ask the doctor to prescribe a drug as a precaution for an infection you do not have.
   e. choose soaps that are labeled "antibacterial."
9. When a virus enters the lysogenic stage:
   a. the viral DNA is replicated outside the host cell.
   b. it enters the host cell and kills it immediately.
   c. it enters the host cell, picks up host DNA, and leaves the cell unharmed.
   d. it sits on the host cell plasma membrane with which it covers itself and then leaves the cell.
   e. The viral DNA integrates into the host genome.
10. An infectious material is isolated from a nerve cell. It contains protein with amino acid sequences identical to the host protein but no nucleic acids. It belongs to the group:
    a. prions.
    b. Archaea.
    c. toxin producers.
    d. viroids.
    e. sporeformers.

Questions for Discussion

1. The digestive tract of newborn chicks is free of bacteria until they eat food that has been exposed to the feces of adult chickens. The ingested bacteria establishes a population in the digestive tract that is beneficial for the digestion of food. However, if *Salmonella* are present in the adult feces, this bacterium, which can be pathogenic for humans who ingest it, may become established in the digestive tracts of the chicks. To eliminate the possibility that *Salmonella* might become established, should farmers feed newborn chicks a mixture of harmless known bacteria from a lab culture, or a mixture of unknown fecal bacteria from healthy adult chickens? Design an experiment to answer this question.
2. Investigators in Australia found that mats of pond scum formed by the bacterium *Botyrococcus braunii* decayed into a substance resembling crude oil when the ponds dried up. Formulate a hypothesis explaining how this process may have contributed to Earth's oil deposits.
3. What rules would you suggest to prevent the spread of mad cow disease (BSE)?

Experimental Analysis

Suppose you isolate a previously unknown virus that has caused infection in humans. Describe how you would show experimentally to what virus genus and species this new virus is most closely related.

Evolution Link

Prion diseases cause similar fatal brain degeneration in a large number of animals, including human, baboon, chimpanzee, mule deer, cow, sheep, pig, golden hamster, rat, mouse, and rabbit. Can you make any evolutionary hypotheses based on this observation? How might you determine the evolutionary relationships of prion proteins?

How Would You Vote?

Eliminating mosquitoes is the best defense against West Nile virus. Many local agencies are spraying pesticides wherever mosquitoes are likely to breed. Some people fear ecological disruptions and bad effects on health and say spraying will never eliminate all mosquitoes anyway. Would you support a spraying program in your community? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.