27

Bacteria and Archaea

▲ **Figure 27.1 Why is this lake's water pink?**

EVOLUTION

KEY CONCEPTS

OVERVIEW

Masters of Adaptation

In the heat of summer, parts of Utah's Great Salt Lake turn pink **(Figure 27.1)**, a sign of waters so salty that they would dehydrate your skin if you took a dip. The salt concentration can reach 32%, nearly ten times that of seawater. Yet despite these harsh conditions, the dramatic color of these waters is caused not by minerals or other nonliving sources, but by living things. What organisms can live in such an inhospitable environment, and how do they do it?

The pink color in the Great Salt Lake comes from trillions of prokaryotes in the domains Archaea and Bacteria, including archaea in the genus *Halobacterium*. These archaea have red membrane pigments, some of which capture the light energy that drives ATP synthesis. *Halobacterium* species are among the most salt-tolerant organisms on Earth; they thrive in salinities that dehydrate and kill other cells. *Halobacterium* compensates for water lost through osmosis by pumping potassium ions (K^+) into the cell until the ionic concentration inside the cell matches the concentration outside.

Like *Halobacterium*, many other prokaryotes can tolerate extreme conditions. Examples include *Deinococcus radiodurans*, which can survive 3 million rads of radiation (3,000 times the dose fatal to humans), and *Picrophilus oshimae*, which can grow at a pH of 0.03 (acidic enough to dissolve metal). Other prokaryotes live in environments that are too cold or too hot for most other organisms, and some have even been found living in rocks 3.2 km (2 miles) below Earth's surface.

Prokaryotic species are also very well adapted to more "normal" habitats—the lands and waters in which most other species are found. Their ability to adapt to a broad range of habitats helps explain why prokaryotes are the most abundant organisms on Earth: The number of prokaryotes in a handful of fertile soil is greater than the number of people who have ever lived. In this chapter, we'll examine the adaptations, diversity, and enormous ecological impact of these tiny organisms.

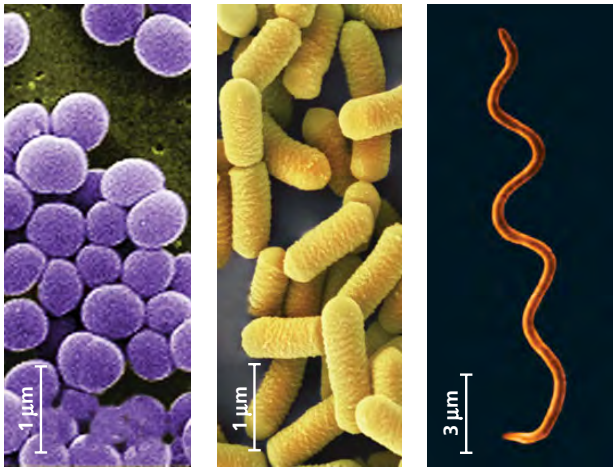
CONCEPT 27.1

Structural and functional adaptations contribute to prokaryotic success

As you read in Chapter 25, the first organisms to inhabit Earth were likely prokaryotes. Throughout their long evolutionary history, prokaryotic populations have been (and continue to be) subjected to natural selection in all kinds of environments, resulting in their enormous diversity today.

We'll begin by describing prokaryotes. Most prokaryotes are unicellular, although the cells of some species remain attached to each other after cell division. Prokaryotic cells typically have diameters of 0.5–5 μm, much smaller than the

10–100 µm diameter of many eukaryotic cells. (One notable exception, *Thiomargarita namibiensis*, can be 750 µm across—bigger than the dot on this i.) Prokaryotic cells have a variety of shapes **(Figure 27.2)**. Finally, although they are unicellular and small, prokaryotes are well organized, achieving all of an organism's life functions within a single cell.



(a) Spherical **(b) Rod-shaped** **(c) Spiral**

▲ **Figure 27.2 The most common shapes of prokaryotes.** **(a)** Cocci (singular, *coccus*) are spherical prokaryotes. They occur singly, in pairs (diplococci), in chains of many cells (streptococci), and in clusters resembling bunches of grapes (staphylococci). **(b)** Bacilli (singular, *bacillus*) are rod-shaped prokaryotes. They are usually solitary, but in some forms the rods are arranged in chains (streptobacilli). **(c)** Spiral prokaryotes include spirilla, which range from comma-like shapes to loose coils, and spirochetes (shown here), which are corkscrew-shaped (colorized SEMs).

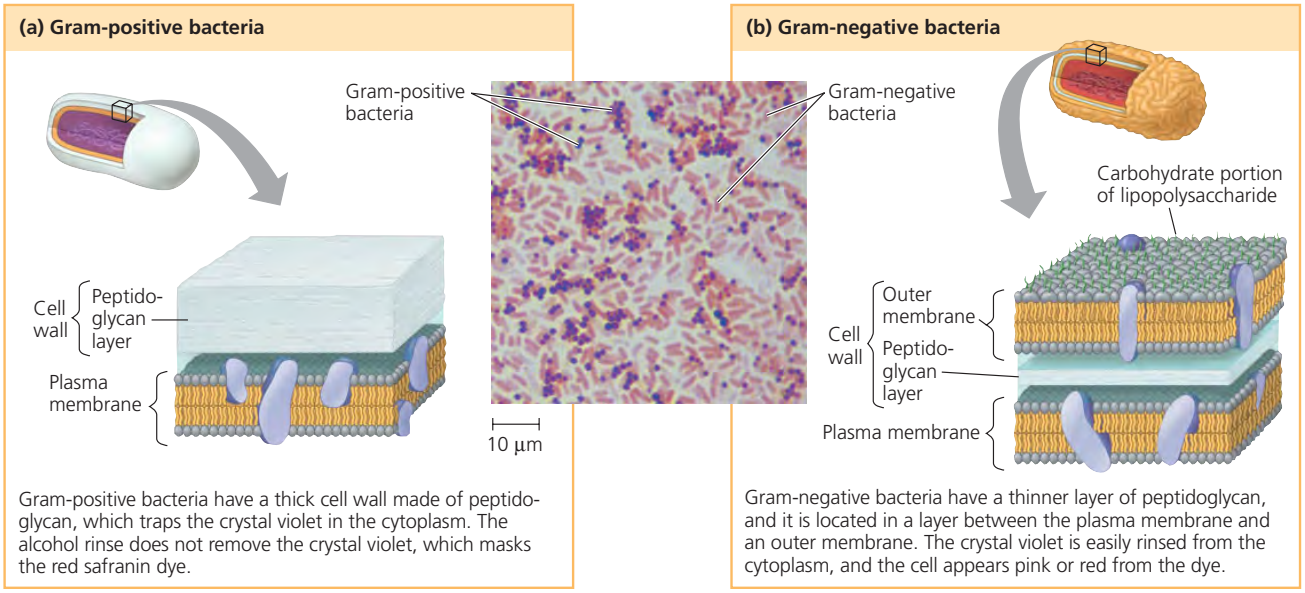
Cell-Surface Structures

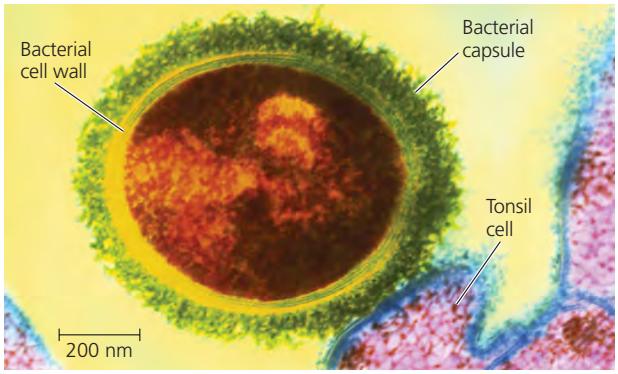
A key feature of nearly all prokaryotic cells is the cell wall, which maintains cell shape, protects the cell, and prevents it from bursting in a hypotonic environment (see Chapter 7). In a hypertonic environment, most prokaryotes lose water and shrink away from their wall (plasmolyze), like other walled cells. Such water losses can inhibit cell reproduction. Thus, salt can be used to preserve foods because it causes prokaryotes to lose water, preventing them from rapidly multiplying.

The cell walls of prokaryotes differ in structure from those of eukaryotes. In eukaryotes that have cell walls, such as plants and fungi, the walls are usually made of cellulose or chitin (see Chapter 5). In contrast, most bacterial cell walls contain **peptidoglycan**, a polymer composed of modified sugars cross-linked by short polypeptides. This molecular fabric encloses the entire bacterium and anchors other molecules that extend from its surface. Archaeal cell walls contain a variety of polysaccharides and proteins but lack peptidoglycan.

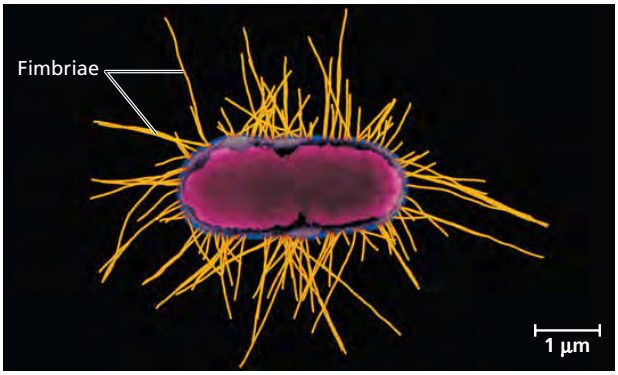
Using a technique called the **Gram stain**, developed by the nineteenth-century Danish physician Hans Christian Gram, scientists can classify many bacterial species into two groups based on differences in cell wall composition. Samples are first stained with crystal violet dye and iodine, then rinsed in alcohol, and finally stained with a red dye such as safranin. The structure of a bacterium's cell wall determines the staining response **(Figure 27.3)**. **Gram-positive** bacteria have simpler walls with a relatively large amount of peptidoglycan. **Gram-negative** bacteria have less peptidoglycan and are structurally more complex, with an outer membrane that contains lipopolysaccharides (carbohydrates bonded to lipids).

▼ **Figure 27.3 Gram staining.**





▲ **Figure 27.4 Capsule.** The polysaccharide capsule around this *Streptococcus* bacterium enables the prokaryote to attach to cells in the respiratory tract—in this colorized TEM, a tonsil cell.



▲ **Figure 27.5 Fimbriae.** These numerous protein-containing appendages enable some prokaryotes to attach to surfaces or to other cells (colorized TEM).

Gram staining is a valuable tool in medicine for quickly determining if a patient's infection is due to gram-negative or to gram-positive bacteria. This information has treatment implications. The lipid portions of the lipopolysaccharides in the walls of many gram-negative bacteria are toxic, causing fever or shock. Furthermore, the outer membrane of a gram-negative bacterium helps protect it from the body's defenses. Gram-negative bacteria also tend to be more resistant than gram-positive species to antibiotics because the outer membrane impedes entry of the drugs. However, certain gram-positive species have virulent strains that are resistant to one or more antibiotics. (Figure 22.14 discusses one example: multidrug-resistant *Staphylococcus aureus*, which can cause lethal skin infections.)

The effectiveness of certain antibiotics, such as penicillin, derives from their inhibition of peptidoglycan cross-linking. The resulting cell wall may not be functional, particularly in gram-positive bacteria. Such drugs destroy many species of pathogenic bacteria without adversely affecting human cells, which do not have peptidoglycan.

The cell wall of many prokaryotes is surrounded by a sticky layer of polysaccharide or protein. This layer is called a **capsule** if it is dense and well-defined **(Figure 27.4)** or a *slime layer* if it is less well organized. Both kinds of sticky outer layers enable prokaryotes to adhere to their substrate or to other individuals in a colony. Some capsules and slime layers protect against dehydration, and some shield pathogenic prokaryotes from attacks by their host's immune system.

Some prokaryotes stick to their substrate or to one another by means of hairlike appendages called **fimbriae** (singular, *fimbria*) **(Figure 27.5)**. For example, the bacterium that causes gonorrhea, *Neisseria gonorrhoeae*, uses fimbriae to fasten itself to the mucous membranes of its host. Fimbriae are usually shorter and more numerous than **pili** (singular, *pilus*), appendages that pull two cells together prior to DNA transfer from one cell to the other (see Figure 27.12); pili are sometimes referred to as *sex pili*.

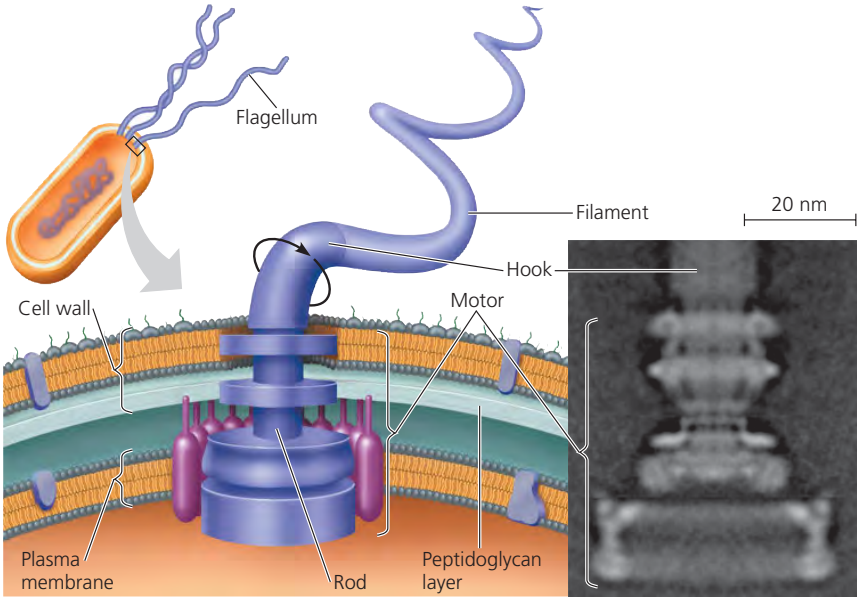
Motility

About half of all prokaryotes are capable of **taxis**, a directed movement toward or away from a stimulus (from the Greek *taxis*, to arrange). For example, prokaryotes that exhibit *chemotaxis* change their movement pattern in response to chemicals. They may move *toward* nutrients or oxygen (positive chemotaxis) or *away from* a toxic substance (negative chemotaxis). Some species can move at velocities exceeding 50 µm/sec—up to 50 times their body length per second. For perspective, consider that a person 1.7 m tall moving that fast would be running 306 km (190 miles) per hour!

Of the various structures that enable prokaryotes to move, the most common are flagella **(Figure 27.6)**. Flagella (singular, *flagellum*) may be scattered over the entire surface of the cell or concentrated at one or both ends. Prokaryotic flagella differ greatly from eukaryotic flagella: They are one-tenth the width and are not covered by an extension of the plasma membrane (see Figure 6.24). The flagella of prokaryotes are also very different in their molecular composition and their mechanism of propulsion. Among prokaryotes, bacterial and archaeal flagella are similar in size and rotation mechanism, but they are composed of different proteins. Overall, these structural and molecular comparisons suggest that the flagella of bacteria, archaea, and eukaryotes arose independently. Since the flagella of organisms in the three domains perform similar functions but probably are not related by common descent, it is likely that they are analogous, not homologous, structures.

Evolutionary Origins of Bacterial Flagella

The bacterial flagellum shown in Figure 27.6 has three main parts (the motor, hook, and filament) that are themselves composed of 42 different kinds of proteins. How could such a complex structure evolve? In fact, much evidence indicates that bacterial flagella originated as simpler structures that were modified in a stepwise fashion over time. As in the case of the



▲ **Figure 27.6 A prokaryotic flagellum.** The motor of a prokaryotic flagellum consists of a system of rings embedded in the cell wall and plasma membrane (TEM). ATP-driven pumps in the motor transport protons out of the cell. The diffusion of protons back into the cell provides the force that turns a curved hook and thereby causes the attached filament to rotate and propel the cell. (This diagram shows flagellar structures characteristic of gram-negative bacteria.)

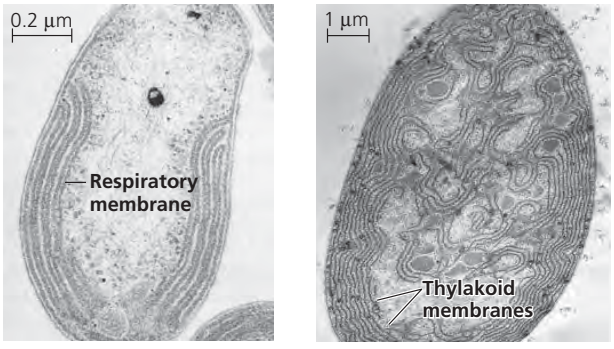
human eye (see Concept 25.6), biologists asked whether a less complex version of the flagellum could still benefit its owner. Analyses of hundreds of bacterial genomes indicate that only half of the flagellum's protein components appear to be necessary for it to function; the others are inessential or not encoded in the genomes of some species. Of the 21 proteins required by all species studied to date, 19 are modified versions of proteins that perform other tasks in bacteria. For example, a set of 10 proteins in the motor are homologous to 10 similar proteins in a secretory system found in bacteria. (A secretory system is a protein complex that enables a cell to secrete certain macromolecules.)

Two other proteins in the motor are homologous to proteins that function in ion transport. The proteins that comprise the rod, hook, and filament are all related to each other and are descended from an ancestral protein that formed a pilus-like tube. These findings suggest that the bacterial flagellum evolved as other proteins were added to an ancestral secretory system. This is an example of *exaptation*, the process in which existing structures take on new functions through descent with modification.

Internal Organization and DNA

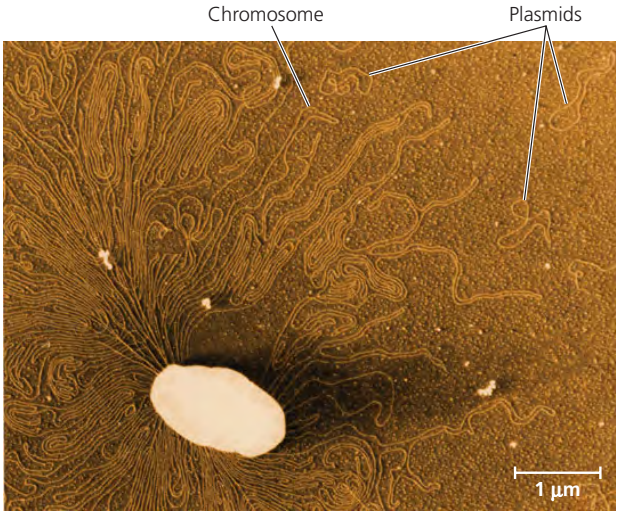
The cells of prokaryotes are simpler than those of eukaryotes in both their internal structure and the physical arrangement of their DNA (see Figure 6.5). Prokaryotic cells lack the complex compartmentalization found in eukaryotic cells. However, some prokaryotic cells do have specialized membranes that perform metabolic functions **(Figure 27.7)**. These membranes are usually infoldings of the plasma membrane.

The genome of a prokaryote is structurally different from a eukaryotic genome and in most cases has considerably less DNA. In the majority of prokaryotes, the genome consists of a circular chromosome with many fewer proteins than found in the linear chromosomes of eukaryotes **(Figure 27.8)**. Also



(a) Aerobic prokaryote **(b) Photosynthetic prokaryote**

▲ **Figure 27.7 Specialized membranes of prokaryotes.** **(a)** Infoldings of the plasma membrane, reminiscent of the cristae of mitochondria, function in cellular respiration in some aerobic prokaryotes (TEM). **(b)** Photosynthetic prokaryotes called cyanobacteria have thylakoid membranes, much like those in chloroplasts (TEM).



▲ **Figure 27.8 A prokaryotic chromosome and plasmids.** The thin, tangled loops surrounding this ruptured *E. coli* cell are parts of the cell's large, circular chromosome (colorized TEM). Three of the cell's plasmids, the much smaller rings of DNA, are also shown.

unlike eukaryotes, prokaryotes lack a membrane-bounded nucleus; their chromosome is located in the **nucleoid**, a region of cytoplasm that appears lighter than the surrounding cytoplasm in electron micrographs. In addition to its single chromosome, a typical prokaryotic cell may also have much smaller rings of independently replicating DNA molecules called **plasmids** (see Figure 27.8), most carrying only a few genes.

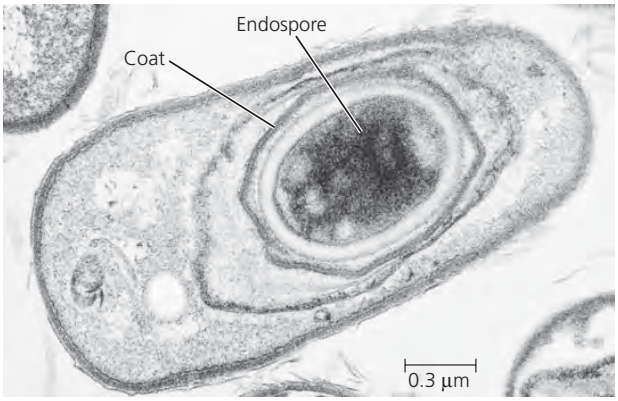
As explained in Chapters 16 and 17, DNA replication, transcription, and translation are fundamentally similar processes in prokaryotes and eukaryotes, although there are some differences. For example, prokaryotic ribosomes are slightly smaller than eukaryotic ribosomes and differ in their protein and RNA content. These differences allow certain antibiotics, such as erythromycin and tetracycline, to bind to ribosomes and block protein synthesis in prokaryotes but not in eukaryotes. As a result, people can use these antibiotics to kill or inhibit the growth of bacteria without harming themselves.

Reproduction and Adaptation

Prokaryotes are highly successful in part because of their potential to reproduce quickly in a favorable environment. By *binary fission* (see Figure 12.12), a single prokaryotic cell divides into 2 cells, which then divide into 4, 8, 16, and so on. Under optimal conditions, many prokaryotes can divide every 1–3 hours; some species can produce a new generation in only 20 minutes. If reproduction continued unchecked at this rate, a single prokaryotic cell could give rise to a colony outweighing Earth in only two days!

In reality, of course, prokaryotic reproduction is limited. The cells eventually exhaust their nutrient supply, poison themselves with metabolic wastes, face competition from other microorganisms, or are consumed by other organisms. For example, the well-studied bacterium *Escherichia coli* can divide every 20 minutes under ideal lab conditions, one reason it is used as a model organism in research. However, when growing in a human intestine, one of its natural environments, *E. coli* cells divide only once every 12–24 hours. But whether cell division occurs every 20 minutes or every few days, reproduction in prokaryotes draws attention to three key features of their biology: *They are small, they reproduce by binary fission, and they have short generation times*. As a result, prokaryotic populations can consist of many trillions of individuals—far more than populations of multicellular eukaryotes, such as plants and animals.

The ability of some prokaryotes to withstand harsh conditions also contributes to their success. Some, like *Halobacterium*, can survive in harsh environments because of particular biochemical adaptations; others, because of particular structural adaptations. Certain bacteria, for example, develop resistant cells called **endospores** when they lack an essential nutrient **(Figure 27.9)**. The original cell produces a copy of its chromosome and surrounds it with a tough multilayered structure,



▲ **Figure 27.9 An endospore.** *Bacillus anthracis*, the bacterium that causes the disease anthrax, produces endospores (TEM). An endospore's protective, multilayered coat helps it survive in the soil for years.

forming the endospore. Water is removed from the endospore, and its metabolism halts. The original cell then lyses, releasing the endospore. Most endospores are so durable that they can survive in boiling water; killing them requires heating lab equipment to 121°C under high pressure. In less hostile environments, endospores can remain dormant but viable for centuries, able to rehydrate and resume metabolism when their environment improves.

Finally, in part because of their short generation times, prokaryotic populations can evolve substantially in short periods of time. For example, in a remarkable study that spanned 20,000 generations (roughly eight years) of evolution, researchers at Michigan State University documented adaptive evolution in bacterial populations **(Figure 27.10)**. The ability of prokaryotes to adapt rapidly to new conditions highlights the point that although the structure of their cells is simpler than that of eukaryotic cells, prokaryotes are not "primitive" or "inferior" in an evolutionary sense. They are, in fact, highly evolved: For over 3.5 billion years, prokaryotic populations have responded successfully to many different types of environmental challenges. As we will see, one reason for this is that their populations harbor high levels of genetic diversity on which selection can act.

CONCEPT CHECK 27.1

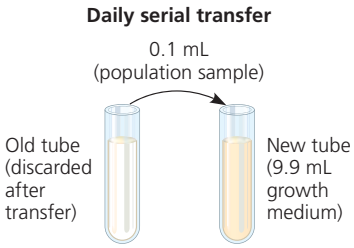
1. Identify and explain at least two adaptations that enable prokaryotes to survive in environments too harsh for other organisms.
2. Contrast the cellular and DNA structures of prokaryotes and eukaryotes.
3. **MAKE CONNECTIONS** Suggest a hypothesis to explain why the thylakoid membranes of chloroplasts resemble those of cyanobacteria. Refer to Figure 6.18 (p. 111) and Figure 26.21 (p. 552).

For suggested answers, see Appendix A.

▼ Figure 27.10 **INQUIRY**

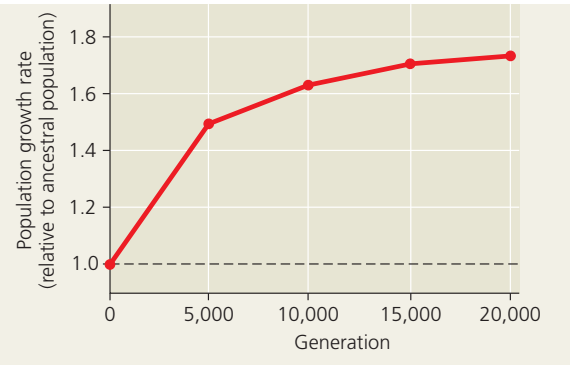
Can prokaryotes evolve rapidly in response to environmental change?

EXPERIMENT Vaughn Cooper and Richard Lenski, of Michigan State University, tested the ability of *E. coli* populations to adapt to a new environment. They established 12 populations, each founded by a single cell from an *E. coli* strain, and followed these populations for 20,000 generations (3,000 days). To maintain a continual supply of resources, each day the researchers performed a *serial transfer*: They transferred 0.1 mL of each population to a new tube containing 9.9 mL of fresh growth medium. The growth medium used throughout the experiment provided a challenging environment that contained only low levels of glucose and other resources needed for growth.



Samples were periodically removed from the 12 populations and grown in competition with the common ancestral strain in the experimental (low-glucose) environment.

RESULTS The fitness of the experimental populations, as measured by the rate at which each population grew, increased rapidly for the first 5,000 generations (two years) and more slowly for the next 15,000 generations. The graph below shows the averages for the 12 populations.



CONCLUSION Populations of *E. coli* continued to accumulate beneficial mutations for 20,000 generations, allowing rapid evolution of improved performance in their new environment.

SOURCE V. S. Cooper and R. E. Lenski, The population genetics of ecological specialization in evolving *Escherichia coli* populations, *Nature* 407:736–739 (2000).

WHAT IF? Suggest possible functions of the genes whose sequence or expression was altered as the experimental populations evolved in the low-glucose environment.

CONCEPT 27.2

Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes

As we discussed in Unit Four, genetic variation is a prerequisite for natural selection to occur in a population. The diverse adaptations exhibited by prokaryotes suggest that their populations must have considerable genetic variation—and they do. For example, a ribosomal RNA gene can differ more between two strains of *E. coli* than it does between a human and a platypus. In this section, we'll examine three factors that give rise to high levels of genetic diversity in prokaryotes: rapid reproduction, mutation, and genetic recombination.

Rapid Reproduction and Mutation

In sexually reproducing species, the generation of a novel allele by a new mutation is rare for any particular gene. Instead, most of the genetic variation in sexual populations results from the way existing alleles are arranged in new combinations during meiosis and fertilization (see Chapter 13). Prokaryotes do not reproduce sexually, so at first glance their extensive genetic variation may seem puzzling. In fact, this variation can result from prokaryotes' rapid reproduction and mutation.

Consider a prokaryote reproducing by binary fission. After repeated rounds of division, most of the offspring cells are genetically identical to the original parent cell. However, if errors occur during DNA replication—such as insertions, deletions, or base-pair substitutions—some of the offspring cells may differ genetically. The probability of a spontaneous mutation occurring in a given *E. coli* gene averages only about one in 10 million (1×10^{-7}) per cell division. But among the 2×10^{10} new *E. coli* cells that arise each day in a person's intestine, there will be approximately $(2 \times 10^{10}) \times (1 \times 10^{-7}) = 2{,}000$ bacteria that have a mutation in that gene. The total number of mutations when all 4,300 *E. coli* genes are considered is about $4{,}300 \times 2{,}000 = 9$ million per day per human host.

The key point is that new mutations, though rare, can increase genetic diversity quickly in species with short generation times and large populations. This diversity, in turn, can lead to rapid evolution: Individuals that are genetically better equipped for their environment tend to survive and reproduce more prolifically than less fit individuals (see Figure 27.10).

Genetic Recombination

Although new mutations are a major source of variation in prokaryotic populations, additional diversity arises from *genetic recombination*, the combining of DNA from two sources. In eukaryotes, the sexual processes of meiosis and fertilization combine DNA from two individuals in a single zygote. But meiosis and fertilization do not occur in prokaryotes. Instead,

three other mechanisms—transformation, transduction, and conjugation—can bring together prokaryotic DNA from different individuals (that is, cells). When the individuals are members of different species, this movement of genes from one organism to another is called *horizontal gene transfer*. Although scientists have found evidence that each of these mechanisms can transfer DNA within and between species in both domain Bacteria and domain Archaea, to date most of our knowledge comes from research on bacteria.

Transformation and Transduction

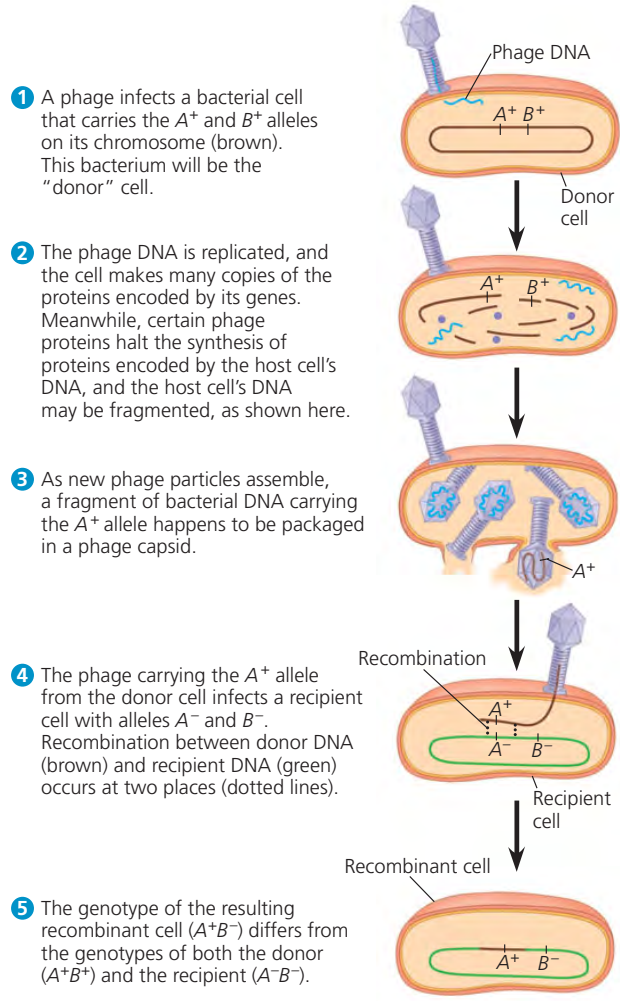
In **transformation**, the genotype and possibly phenotype of a prokaryotic cell are altered by the uptake of foreign DNA from its surroundings. For example, a harmless strain of *Streptococcus pneumoniae* can be transformed into pneumonia-causing cells if the cells are placed in a medium containing DNA from a pathogenic strain (see p. 306). This transformation occurs when a nonpathogenic cell takes up a piece of DNA carrying the allele for pathogenicity and replaces its own allele with the foreign allele, an exchange of homologous DNA segments. The cell is now a recombinant: Its chromosome contains DNA derived from two different cells.

For many years after transformation was discovered in laboratory cultures, most biologists thought the process to be too rare and haphazard to play an important role in natural bacterial populations. But researchers have since learned that many bacteria have cell-surface proteins that recognize DNA from closely related species and transport it into the cell. Once inside the cell, the foreign DNA can be incorporated into the genome by homologous DNA exchange.

In **transduction**, phages (from "bacteriophages," the viruses that infect bacteria) carry prokaryotic genes from one host cell to another. In most cases, transduction results from accidents that occur during the phage replicative cycle **(Figure 27.11)**. A virus that carries prokaryotic DNA may not be able to replicate because it lacks some or all of its own genetic material. However, the virus can attach to another prokaryotic cell (a recipient) and inject prokaryotic DNA acquired from the first cell (the donor). If some of this DNA is then incorporated into the recipient cell's chromosome by DNA recombination, a recombinant cell is formed.

Conjugation and Plasmids

In a process called **conjugation**, DNA is transferred between two prokaryotic cells (usually of the same species) that are temporarily joined. In bacteria, the DNA transfer is always one-way: One cell donates the DNA, and the other receives it. The best-understood mechanism is that used by *E. coli*, and we will focus on this organism for the rest of this section. In *E. coli*, a pilus of the donor cell attaches to the recipient **(Figure 27.12)**. The pilus then retracts, pulling the two cells together, much like a grappling hook. The next step is thought



▲ **Figure 27.11 Transduction.** Phages may carry pieces of a bacterial chromosome from one cell (the donor) to another (the recipient). If recombination occurs after the transfer, genes from the donor may be incorporated into the recipient's genome.

? *Under what circumstances would transduction result in horizontal gene transfer?*

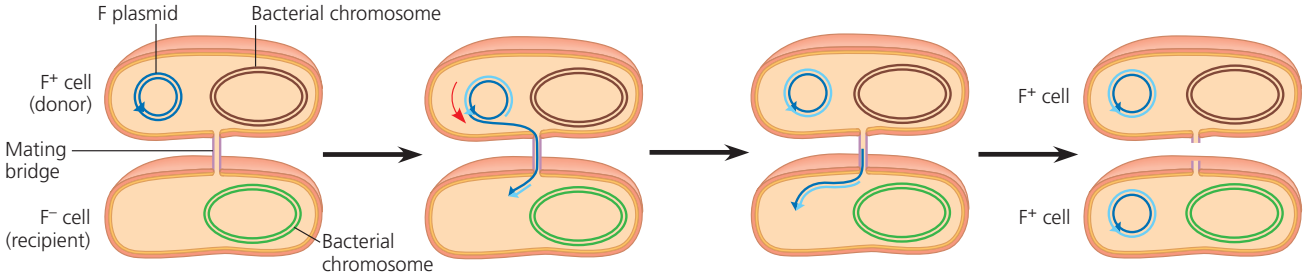
▲ **Figure 27.12 Bacterial conjugation.** The *E. coli* donor cell (left) extends a pilus that attaches to a recipient cell, a key first step in the transfer of DNA. The pilus is a flexible tube of protein subunits (TEM).

to be the formation of a temporary "mating bridge" between the two cells, through which the donor may transfer DNA to the recipient. This is an unsettled issue, however, and recent evidence indicates that DNA may pass directly through the pilus, which is hollow.

In either case, the ability to form pili and donate DNA during conjugation results from the presence of a particular piece of DNA called the **F factor** (F for *f*ertility). The F factor of *E. coli* consists of about 25 genes, most required for the production of pili. The F factor can exist either as a plasmid or as a segment of DNA within the bacterial chromosome.

The F Factor as a Plasmid The F factor in its plasmid form is called the **F plasmid**. Cells containing the F plasmid, designated F^+ cells, function as DNA donors during conjugation. Cells lacking the F factor, designated F^-, function as DNA recipients during conjugation. The F^+ condition is transferable in the sense that an F^+ cell converts an F^- cell to F^+ if a copy of the entire F^+ plasmid is transferred **(Figure 27.13a)**.

The F Factor in the Chromosome Chromosomal genes can be transferred during conjugation when the donor cell's F factor is integrated into the chromosome. A cell with the F factor built into its chromosome is called an *Hfr cell* (for *h*igh *f*requency of *r*ecombination). Like an F^+ cell, an Hfr cell functions as a donor during conjugation with an F^- cell **(Figure 27.13b)**. When chromosomal DNA from an Hfr cell enters an F^- cell, homologous regions of the Hfr and F^- chromosomes may align, allowing segments of their DNA to be exchanged. This results in the production of a recombinant bacterium that has genes derived from two different cells—a new genetic variant on which evolution can act.



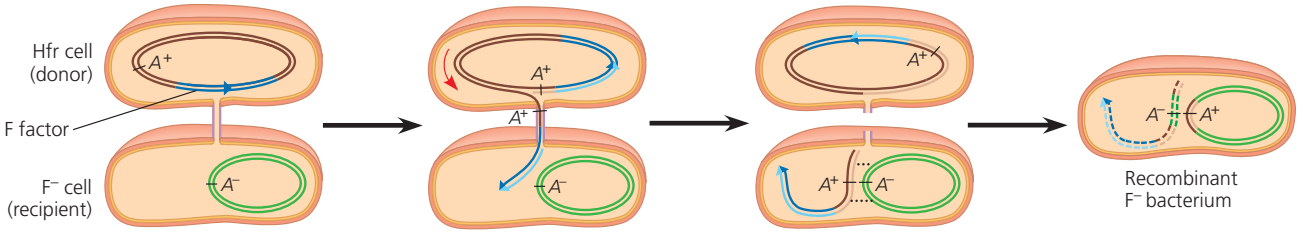
1 A cell carrying an F plasmid (an F^+ cell) forms a mating bridge with an F^- cell. One strand of the plasmid's DNA breaks at the point marked by the arrowhead.

2 Using the unbroken strand as a template, the cell synthesizes a new strand (light blue). Meanwhile, the broken strand peels off (red arrow), and one end enters the F^- cell. There synthesis of its complementary strand begins.

3 DNA replication continues in both donor and recipient cells, as the transferred plasmid strand moves farther into the recipient cell.

4 Once DNA transfer and synthesis are completed, the plasmid in the recipient cell circularizes. Now both cells are F^+ cells.

(a) Conjugation and transfer of an F plasmid



1 In an Hfr cell, the F factor (dark blue) is integrated into the bacterial chromosome. Since an Hfr cell has all of the F-factor genes, it can form a mating bridge with an F^- cell and transfer DNA.

2 A single strand of the F factor breaks and begins to move through the bridge. DNA replication occurs in both donor and recipient cells, resulting in double-stranded DNA (daughter strands shown in lighter color).

3 The mating bridge usually breaks before the entire chromosome is transferred. DNA recombination (indicated by dotted lines) can result in the exchange of homologous genes between the transferred DNA (brown) and the recipient's chromosome (green).

4 Cellular enzymes degrade any linear DNA not incorporated into the chromosome. The recipient cell, with a new combination of genes but no F factor, is now a recombinant F^- cell.

(b) Conjugation and transfer of part of an Hfr bacterial chromosome, resulting in recombination

▲ **Figure 27.13 Conjugation and recombination in *E. coli*.** The DNA replication that accompanies transfer of an F plasmid or part of an Hfr bacterial chromosome is called *rolling circle replication*. In effect, the intact circular parental DNA strand "rolls" as its other strand peels off and a new complementary strand is synthesized.

R Plasmids and Antibiotic Resistance During the 1950s in Japan, physicians started noticing that some hospital patients with bacterial dysentery, which produces severe diarrhea, did not respond to antibiotics that had generally been effective in the past. Apparently, resistance to these antibiotics had evolved in certain strains of *Shigella*, the bacterium that causes the disease.

Eventually, researchers began to identify the specific genes that confer antibiotic resistance in *Shigella* and other pathogenic bacteria. Sometimes, mutation in a chromosomal gene of the pathogen can confer resistance. For example, a mutation in one gene may make it less likely that the pathogen will transport a particular antibiotic into its cell. Mutation in a different gene may alter the intracellular target protein for an antibiotic molecule, reducing its inhibitory effect. In other cases, bacteria have "resistance genes," which code for enzymes that specifically destroy or otherwise hinder the effectiveness of certain antibiotics, such as tetracycline or ampicillin. Such resistance genes are carried by plasmids known as **R plasmids** (R for *r*esistance).

Exposing a bacterial population to a specific antibiotic, whether in a laboratory culture or within a host organism, will kill antibiotic-sensitive bacteria but not those that happen to have R plasmids with genes that counter the antibiotic. Under these circumstances, we would predict that natural selection would cause the fraction of the bacterial population carrying genes for antibiotic resistance to increase, and that is exactly what happens. The medical consequences are also predictable: As you've read, resistant strains of pathogens are becoming more common, making the treatment of certain bacterial infections more difficult. The problem is compounded by the fact that many R plasmids, like F plasmids, have genes that encode pili and enable DNA transfer from one bacterial cell to another by conjugation. Making the problem still worse, some R plasmids carry as many as ten genes for resistance to that many antibiotics.

CONCEPT CHECK 27.2

1. What features of prokaryotes make it likely that considerable genetic variation will be added to their populations in each generation?
2. Distinguish between the three mechanisms of transferring DNA from one bacterial cell to another.
3. In a rapidly changing environment, which bacterial population would likely be more successful, one that includes individuals capable of conjugation or one that does not? Explain.
4. **WHAT IF?** If a nonpathogenic bacterium were to acquire resistance to antibiotics, could this strain pose a health risk to people? Explain. In general, how does DNA transfer among bacteria affect the spread of resistance genes?

For suggested answers, see Appendix A.

CONCEPT 27.3

Diverse nutritional and metabolic adaptations have evolved in prokaryotes

The extensive genetic variation found in prokaryotic populations is reflected in the diverse nutritional adaptations of prokaryotes. Like all organisms, prokaryotes can be categorized by how they obtain energy and the carbon used in building the organic molecules that make up cells. Every type of nutrition observed in eukaryotes is represented among prokaryotes, along with some nutritional modes unique to prokaryotes. In fact, prokaryotes have an astounding range of metabolic adaptations, much broader than that found in eukaryotes.

Organisms that obtain energy from light are called *phototrophs*, and those that obtain energy from chemicals are called *chemotrophs*. Organisms that need only CO_2 in some form as a carbon source are called *autotrophs*. In contrast, *heterotrophs* require at least one organic nutrient, such as glucose, to make other organic compounds. Combining possible energy sources and carbon sources results in four major modes of nutrition, summarized in **Table 27.1**.

The Role of Oxygen in Metabolism

Prokaryotic metabolism also varies with respect to oxygen (O_2). **Obligate aerobes** must use O_2 for cellular respiration (see Chapter 9) and cannot grow without it. **Obligate anaerobes**, on the other hand, are poisoned by O_2. Some obligate anaerobes live exclusively by fermentation; others extract chemical energy by **anaerobic respiration**, in which substances other than O_2, such as nitrate ions (NO_3^-) or sulfate ions (SO_4^{2-}), accept electrons at the "downhill" end of electron transport chains. **Facultative anaerobes** use O_2 if it is present but can also carry out fermentation or anaerobic respiration in an anaerobic environment.

Nitrogen Metabolism

Nitrogen is essential for the production of amino acids and nucleic acids in all organisms. Whereas eukaryotes can obtain nitrogen from only a limited group of nitrogen compounds, prokaryotes can metabolize nitrogen in a wide variety of forms. For example, some cyanobacteria and some methanogens (a group of archaea) convert atmospheric nitrogen (N_2) to ammonia (NH_3), a process called **nitrogen fixation**. The cells can then incorporate this "fixed" nitrogen into amino acids and other organic molecules. In terms of their nutrition, nitrogen-fixing cyanobacteria are some of the most self-sufficient organisms, since they need only light, CO_2, N_2, water, and some minerals to grow.

Nitrogen fixation by prokaryotes has a large impact on other organisms. For example, nitrogen-fixing prokaryotes can increase the nitrogen available to plants, which cannot use

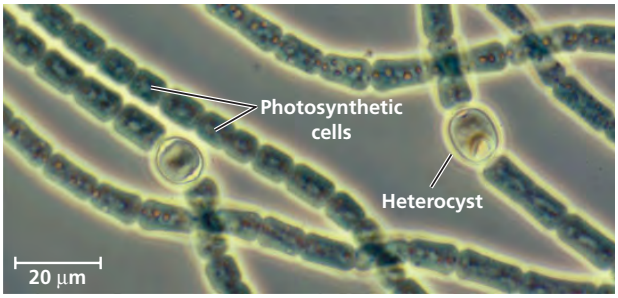
Table 27.1 Major Nutritional Modes

Mode	Energy Source	Carbon Source	Types of Organisms
AUTOTROPH			
Photoautotroph	Light	CO_2, HCO_3^-, or related compound	Photosynthetic prokaryotes (for example, cyanobacteria); plants; certain protists (for example, algae)
Chemoautotroph	Inorganic chemicals (such as H_2S, NH_3, or Fe^{2+})	CO_2, HCO_3^-, or related compound	Unique to certain prokaryotes (for example, *Sulfolobus*)
HETEROTROPH			
Photoheterotroph	Light	Organic compounds	Unique to certain aquatic and salt-loving prokaryotes (for example, *Rhodobacter*, *Chloroflexus*)
Chemoheterotroph	Organic compounds	Organic compounds	Many prokaryotes (for example, *Clostridium*) and protists; fungi; animals; some plants

atmospheric nitrogen but can use the nitrogen compounds that the prokaryotes produce from ammonia. Chapter 55 discusses this and other essential roles that prokaryotes play in the nitrogen cycles of ecosystems.

Metabolic Cooperation

Cooperation between prokaryotic cells allows them to use environmental resources they could not use as individual cells. In some cases, this cooperation takes place between specialized cells of a filament. For instance, the cyanobacterium *Anabaena* has genes that encode proteins for photosynthesis and for nitrogen fixation, but a single cell cannot carry out both processes at the same time. The reason is that photosynthesis produces O_2, which inactivates the enzymes involved in nitrogen fixation. Instead of living as isolated cells, *Anabaena* forms filamentous chains **(Figure 27.14)**. Most cells in a filament carry out only photosynthesis, while a few specialized cells called **heterocysts** (sometimes called *heterocytes*) carry out only nitrogen fixation. Each heterocyst is surrounded by a thickened cell wall that restricts entry of O_2 produced by neighboring photosynthetic cells. Intercellular connections allow heterocysts to transport fixed nitrogen to neighboring cells and to receive carbohydrates.



▲ **Figure 27.14 Metabolic cooperation in a prokaryote.** In the filamentous cyanobacterium *Anabaena*, cells called heterocysts fix nitrogen, while the other cells carry out photosynthesis (LM). *Anabaena* is found in many freshwater lakes.

Metabolic cooperation between different prokaryotic species often occurs in surface-coating colonies known as **biofilms**. Cells in a biofilm secrete signaling molecules that recruit nearby cells, causing the colonies to grow. The cells also produce polysaccharides and proteins that stick the cells to the substrate and to one another. Channels in the biofilm allow nutrients to reach cells in the interior and wastes to be expelled. Biofilms are common in nature, but they can cause problems by contaminating industrial products and medical equipment and contributing to tooth decay and more serious health problems. Altogether, damage caused by biofilms costs billions of dollars annually.

In another example of cooperation between prokaryotes, sulfate-consuming bacteria coexist with methane-consuming archaea in ball-shaped aggregates on the ocean floor. The bacteria appear to use the archaea's waste products, such as organic compounds and hydrogen. In turn, the bacteria produce sulfur compounds that the archaea use as oxidizing agents when they consume methane in the absence of oxygen. This partnership has global ramifications: Each year, these archaea consume an estimated 300 billion kilograms of methane, a major contributor to the greenhouse effect (see Chapter 55).

CONCEPT CHECK 27.3

1. Distinguish between the four major modes of nutrition, noting which are unique to prokaryotes.
2. A bacterium requires only the amino acid methionine as an organic nutrient and lives in lightless caves. What mode of nutrition does it employ? Explain.
3. **WHAT IF?** Describe what you might eat for a typical meal if humans, like cyanobacteria, could fix nitrogen.

For suggested answers, see Appendix A.

CONCEPT 27.4

Molecular systematics is illuminating prokaryotic phylogeny

Until the late 20th century, systematists based prokaryotic taxonomy on phenotypic criteria such as shape, motility, nutritional mode, and response to Gram staining. These criteria are still valuable in certain contexts, such as the rapid identification of pathogenic bacteria cultured from a patient's blood. But

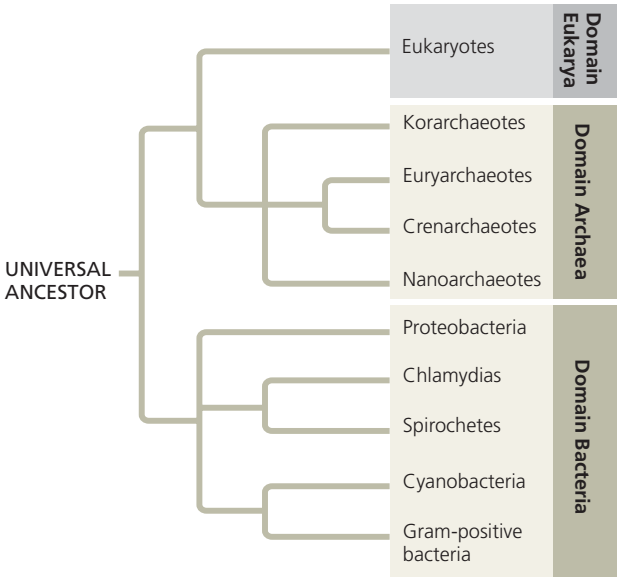
when it comes to prokaryotic phylogeny, comparing these characteristics does not reveal a clear evolutionary history. Applying molecular systematics to the investigation of prokaryotic phylogeny, however, has led to some dramatic conclusions.

Lessons from Molecular Systematics

As discussed in Chapter 26, microbiologists began comparing the sequences of prokaryotic genes in the 1970s. Using small-subunit ribosomal RNA as a marker for evolutionary relationships, Carl Woese and his colleagues concluded that many prokaryotes once classified as bacteria are actually more closely related to eukaryotes and belong in a domain of their own: Archaea. Microbiologists have since analyzed larger amounts of genetic data—including hundreds of entire genomes—and have concluded that a few traditional taxonomic groups, such as cyanobacteria, do appear to be monophyletic. However, other groups, such as gram-negative bacteria, are scattered throughout several lineages. **Figure 27.15** shows one phylogenetic hypothesis for some of the major taxa of prokaryotes based on molecular systematics.

One lesson from studying prokaryotic phylogeny is that the genetic diversity of prokaryotes is immense. When researchers began to sequence the genes of prokaryotes, they could investigate only the small fraction of species that could be cultured in the laboratory. In the 1980s, researchers began using the polymerase chain reaction (PCR; see Chapter 20) to analyze the genes of prokaryotes collected from the environment (such as from soil or water samples). Such "genetic prospecting" is now widely used; in fact, today entire prokaryotic genomes can be obtained from environmental samples using *metagenomics* (see Chapter 21). Each year these techniques add new branches to the tree of life. While only about 7,800 prokaryotic species have been assigned scientific names, a single handful of soil could contain 10,000 prokaryotic species by some estimates. Taking full stock of this diversity will require many years of research.

Another important lesson from molecular systematics is the apparent significance of horizontal gene transfer in the evolution of prokaryotes. Over hundreds of millions of years, prokaryotes have acquired genes from even distantly related species, and they continue to do so today. As a result, significant portions of the genomes of many prokaryotes are actually mosaics of genes imported from other species. As we saw in Chapter 26, such gene transfers can make it difficult to determine the root of the tree of life. Still, it is clear that for billions of years, the prokaryotes have evolved in two separate lineages, the archaea and the bacteria (see Figure 27.15).



▲ **Figure 27.15 A simplified phylogeny of prokaryotes.** This phylogenetic tree based on molecular data shows one of several debated hypotheses of the relationships between the major prokaryotic groups discussed in this chapter. Within Archaea, the placement of the korarchaeotes and nanoarchaeotes remains unclear.

Archaea

Archaea share certain traits with bacteria and other traits with eukaryotes **(Table 27.2)**. However, archaea also have many unique characteristics, as we would expect in a taxon that has followed a separate evolutionary path for so long.

Table 27.2 A Comparison of the Three Domains of Life

CHARACTERISTIC	DOMAIN		
	Bacteria	**Archaea**	**Eukarya**
Nuclear envelope	Absent	Absent	Present
Membrane-enclosed organelles	Absent	Absent	Present
Peptidoglycan in cell wall	Present	Absent	Absent
Membrane lipids	Unbranched hydrocarbons	Some branched hydrocarbons	Unbranched hydrocarbons
RNA polymerase	One kind	Several kinds	Several kinds
Initiator amino acid for protein synthesis	Formyl-methionine	Methionine	Methionine
Introns in genes	Very rare	Present in some genes	Present in many genes
Response to the antibiotics streptomycin and chloramphenicol	Growth inhibited	Growth not inhibited	Growth not inhibited
Histones associated with DNA	Absent	Present in some species	Present
Circular chromosome	Present	Present	Absent
Growth at temperatures > 100°C	No	Some species	No

The first prokaryotes assigned to domain Archaea live in environments so extreme that few other organisms can survive there. Such organisms are called **extremophiles**, meaning "lovers" of extreme conditions (from the Greek *philos*, lover), and include extreme halophiles and extreme thermophiles.

Extreme halophiles (from the Greek *halo*, salt) live in highly saline environments, such as the Great Salt Lake and the Dead Sea (see Figure 27.1). Some species merely tolerate salinity, while others require an environment that is several times saltier than seawater (which has a salinity of 3.5%). For example, the proteins and cell wall of *Halobacterium* have unusual features that improve function in extremely salty environments but render these organisms incapable of survival if the salinity drops below 9%.

Extreme thermophiles (from the Greek *thermos*, hot) thrive in very hot environments **(Figure 27.16)**. For example, archaea in the genus *Sulfolobus* live in sulfur-rich volcanic springs as hot as 90°C. At temperatures this high, the cells of most organisms die because, for example, their DNA does not remain in a double helix and many of their proteins denature. *Sulfolobus* and other extreme thermophiles avoid this fate because their DNA and proteins have adaptations that make them stable at high temperatures. One extreme thermophile that lives near deep-sea hot springs called *hydrothermal vents* is informally known as "strain 121," since it can reproduce even at 121°C. Another extreme thermophile, *Pyrococcus furiosus*, is used in biotechnology as a source of DNA polymerase for the PCR technique (see Chapter 20).

Other archaea live in more moderate environments. Consider the **methanogens**, archaea that release methane as a byproduct of their unique ways of obtaining energy. Many methanogens use CO_2 to oxidize H_2, a process that produces both energy and methane waste. Among the strictest of anaerobes, methanogens are poisoned by O_2. Although some methanogens live in extreme environments, such as under kilometers of ice in Greenland, others live in swamps and marshes where other microorganisms have consumed all the O_2. The "marsh gas" found in such environments is the methane released by these archaea. Other species of methanogens inhabit the anaerobic environment within the guts of cattle, termites, and other herbivores, playing an essential role in the nutrition of these animals. Methanogens also have an important application as decomposers in sewage treatment facilities.

▲ **Figure 27.16 Extreme thermophiles.** Orange and yellow colonies of thermophilic prokaryotes grow in the hot water of a Nevada geyser.

MAKE CONNECTIONS *Review the discussion of enzymes in Concept 8.4 (pp. 155–156). How might the enzymes of thermophiles differ from those of other organisms?*

Many extreme halophiles and all known methanogens are archaea in the clade Euryarchaeota (from the Greek *eurys*, broad, a reference to the habitat range of these prokaryotes). The euryarchaeotes also include some extreme thermophiles, though most thermophilic species belong to a second clade, Crenarchaeota (*cren* means "spring," such as a hydrothermal spring). Recently, genetic prospecting has revealed many species of euryarchaeotes and crenarchaeotes that are not extremophiles. These archaea exist in habitats ranging from farm soils to lake sediments to the surface waters of the open ocean.

New findings continue to update the picture of archaeal phylogeny. In 1996, researchers sampling a hot spring in Yellowstone National Park discovered archaea that do not appear to belong to either Euryarchaeota or Crenarchaeota. They placed these archaea in a new clade, Korarchaeota (from the Greek *koron*, young man). In 2002, researchers exploring hydrothermal vents off the coast of Iceland discovered archaeal cells only 0.4 µm in diameter attached to a much larger crenarchaeote. The genome of the smaller archaean is one of the smallest known of any organism, containing only 500,000 base pairs. Genetic analysis indicates that this prokaryote belongs to a fourth archaeal clade, Nanoarchaeota (from the Greek *nanos*, dwarf). Within a year after this clade was named, three other DNA sequences from nanoarchaeote species were isolated: one from Yellowstone's hot springs, one from hot springs in Siberia, and one from a hydrothermal vent in the Pacific. As prospecting continues, it seems likely that the tree in Figure 27.15 will undergo further changes.

Bacteria

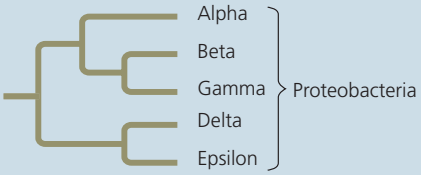
Bacteria include the vast majority of prokaryotic species of which most people are aware, from the pathogenic species that cause strep throat and tuberculosis to the beneficial species used to make Swiss cheese and yogurt. Every major mode of nutrition and metabolism is represented among bacteria, and even a small taxonomic group of bacteria may contain species exhibiting many different nutritional modes. As we'll see, the diverse nutritional and metabolic capabilities of bacteria—and archaea—are behind the great impact of these tiny organisms on Earth and its life. Examine **Figure 27.17**, on the following two pages, for a closer look at several major groups of bacteria.

▼ Figure 27.17

Exploring Major Groups of Bacteria

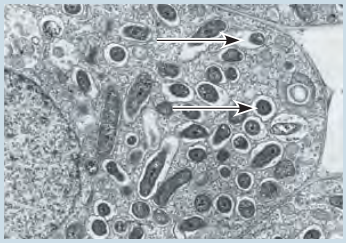
Proteobacteria

This large and diverse clade of gram-negative bacteria includes photoautotrophs, chemoautotrophs, and heterotrophs. Some proteobacteria are anaerobic, while others are aerobic. Molecular systematists currently recognize five subgroups of proteobacteria; the phylogenetic tree at right shows their relationships based on molecular data.



Subgroup: Alpha Proteobacteria

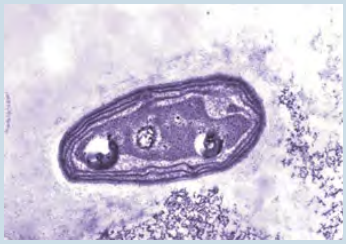
Many of the species in this subgroup are closely associated with eukaryotic hosts. For example, *Rhizobium* species live in nodules within the roots of legumes (plants of the pea/bean family), where the bacteria convert atmospheric N_2 to compounds the host plant can use to make proteins. Species in the genus *Agrobacterium* produce tumors in plants; genetic engineers use these bacteria to carry foreign DNA into the genomes of crop plants (see Figure 20.26). As explained in Chapter 25, scientists hypothesize that mitochondria evolved from aerobic alpha proteobacteria through endosymbiosis.



Rhizobium (arrows) inside a root cell of a legume (TEM)

Subgroup: Beta Proteobacteria

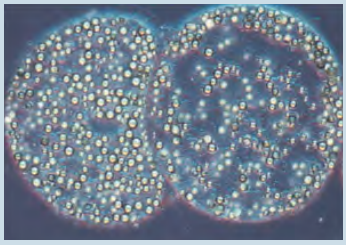
This nutritionally diverse subgroup includes *Nitrosomonas*, a genus of soil bacteria that play an important role in nitrogen recycling by oxidizing ammonium (NH_4^+), producing nitrite (NO_2^-) as a waste product.



Nitrosomonas (colorized TEM)

Subgroup: Gamma Proteobacteria

This subgroup's autotrophic members include sulfur bacteria such as *Thiomargarita namibiensis* (see p. 557), which obtain energy by oxidizing H_2S, producing sulfur as a waste product (the small globules in the photograph at right). Some heterotrophic gamma proteobacteria are pathogens; for example, *Legionella* causes Legionnaires' disease, *Salmonella* is responsible for some cases of food poisoning, and *Vibrio cholerae* causes cholera. *Escherichia coli*, a common resident of the intestines of humans and other mammals, normally is not pathogenic.



Thiomargarita namibiensis containing sulfur wastes (LM)

Subgroup: Delta Proteobacteria

This subgroup includes the slime-secreting myxobacteria. When the soil dries out or food is scarce, the cells congregate into a fruiting body that releases resistant "myxospores." These cells found new colonies in favorable environments. Another group of delta proteobacteria, the bdellovibrios, attack other bacteria, charging at up to 100 µm/sec (comparable to a human running 240 km/hr). The attack begins when a bdellovibrio attaches to specific molecules found on the outer covering of some bacterial species. The bdellovibrio then drills into its prey by using digestive enzymes and spinning at 100 revolutions per second.

Fruiting bodies of *Chondromyces crocatus*, a myxobacterium (SEM)

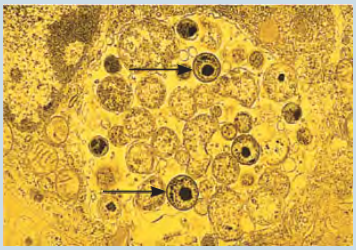
Subgroup: Epsilon Proteobacteria

Most species in this subgroup are pathogenic to humans or other animals. Epsilon proteobacteria include *Campylobacter*, which causes blood poisoning and intestinal inflammation, and *Helicobacter pylori*, which causes stomach ulcers.

Helicobacter pylori (colorized TEM)

Chlamydias

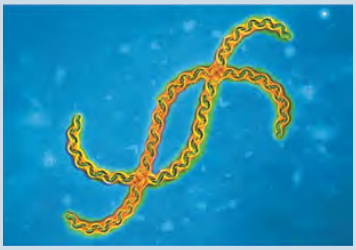
These parasites can survive only within animal cells, depending on their hosts for resources as basic as ATP. The gram-negative walls of chlamydias are unusual in that they lack peptidoglycan. One species, *Chlamydia trachomatis*, is the most common cause of blindness in the world and also causes nongonococcal urethritis, the most common sexually transmitted disease in the United States.



Chlamydia (arrows) inside an animal cell (colorized TEM)

Spirochetes

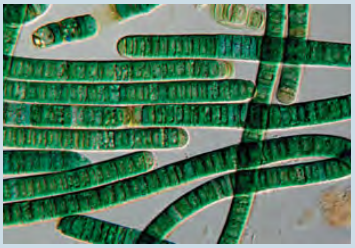
These helical heterotrophs spiral through their environment by means of rotating, internal, flagellum-like filaments. Many spirochetes are free-living, but others are notorious pathogenic parasites: *Treponema pallidum* causes syphilis, and *Borrelia burgdorferi* causes Lyme disease (see Figure 27.20).



Leptospira, a spirochete (colorized TEM)

Cyanobacteria

These photoautotrophs are the only prokaryotes with plantlike, oxygen-generating photosynthesis. (In fact, as we'll discuss in Chapter 28, chloroplasts likely evolved from an endosymbiotic cyanobacterium.) Both solitary and filamentous cyanobacteria are abundant components of freshwater and marine *phytoplankton*, the collection of photosynthetic organisms that drift near the water's surface. Some filaments have cells specialized for nitrogen fixation, the process that incorporates atmospheric N_2 into inorganic compounds that can be used in the synthesis of amino acids and other organic molecules (see Figure 27.14).



Oscillatoria, a filamentous cyanobacterium

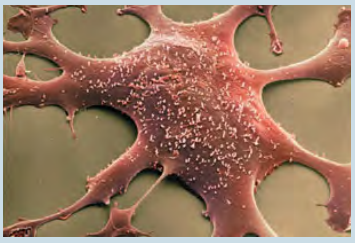
Gram-Positive Bacteria

Gram-positive bacteria rival the proteobacteria in diversity. Species in one subgroup, the actinomycetes (from the Greek *mykes,* fungus, for which these bacteria were once mistaken), form colonies containing branched chains of cells. Two species of actinomycetes cause tuberculosis and leprosy. However, most actinomycetes are free-living species that help decompose the organic matter in soil; their secretions are partly responsible for the "earthy" odor of rich soil. Soil-dwelling species in the genus *Streptomyces* (top) are cultured by pharmaceutical companies as a source of many antibiotics, including streptomycin.

Gram-positive bacteria include many solitary species, such as *Bacillus anthracis* (see Figure 27.9), which causes anthrax, and *Clostridium botulinum*, which causes botulism. The various species of *Staphylococcus* and *Streptococcus* are also gram-positive bacteria.

Mycoplasmas (bottom) are the only bacteria known to lack cell walls. They are also the tiniest known cells, with diameters as small as 0.1 µm, only about five times as large as a ribosome. Mycoplasmas have small genomes—*Mycoplasma genitalium* has only 517 genes, for example. Many mycoplasmas are free-living soil bacteria, but others are pathogens.

Streptomyces, the source of many antibiotics (SEM)



Hundreds of mycoplasmas covering a human fibroblast cell (colorized SEM)

CONCEPT CHECK 27.4

1. Explain how molecular systematics has contributed to our understanding of prokaryotic phylogeny.
2. How has genetic prospecting contributed to our understanding of prokaryotic diversity and phylogeny?
3. **WHAT IF?** What would the discovery of a bacterial species that is a methanogen imply about the evolution of the methane-producing pathway?

For suggested answers, see Appendix A.

CONCEPT 27.5

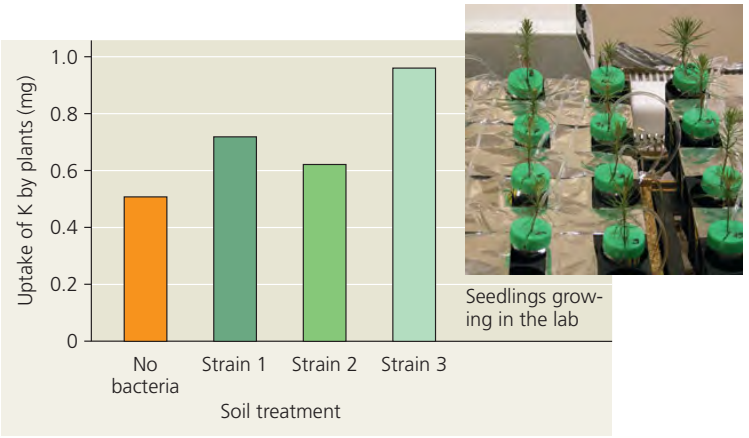
Prokaryotes play crucial roles in the biosphere

If humans were to disappear from the planet tomorrow, life on Earth would change for many species, but few would be driven to extinction. In contrast, prokaryotes are so important to the biosphere that if they were to disappear, the prospects of survival for many other species would be dim.

Chemical Recycling

The atoms that make up the organic molecules in all living things were at one time part of inorganic substances in the soil, air, and water. Sooner or later, those atoms will return there. Ecosystems depend on the continual recycling of chemical elements between the living and nonliving components of the environment, and prokaryotes play a major role in this process. For example, chemoheterotrophic prokaryotes function as **decomposers**, breaking down dead organisms as well as waste products and thereby unlocking supplies of carbon, nitrogen, and other elements. Without the actions of prokaryotes and other decomposers such as fungi, all life would cease. (See Chapter 55 for a detailed discussion of chemical cycles.)

Prokaryotes also convert some molecules to forms that can be taken up by other organisms. Cyanobacteria and other autotrophic prokaryotes use CO_2 to make organic compounds such as sugars, which are then passed up through food chains. Cyanobacteria also produce atmospheric O_2, and a variety of prokaryotes fix atmospheric nitrogen (N_2) into forms that other organisms can use to make the building blocks of proteins and nucleic acids. Under some conditions, prokaryotes can increase the availability of nutrients that plants require for growth, such as nitrogen, phosphorus, and potassium **(Figure 27.18)**. Prokaryotes can also *decrease* the availability of key plant nutrients; this occurs when prokaryotes "immobilize" nutrients by using them to synthesize molecules that remain within their cells. Thus, prokaryotes can have complex effects on soil nutrient concentrations. In marine environments, a 2005 study found that an archaean from the clade Crenarchaeota can perform nitrification, a key step in the nitrogen cycle (see Figure 55.14). Crenarchaeotes dominate the oceans by numbers, comprising an estimated 10^{28} cells. The sheer abundance of these organisms suggests that they may have a large impact on the global nitrogen cycle; scientists are investigating this possibility.



▲ **Figure 27.18 Impact of bacteria on soil nutrient availability.** Pine seedlings grown in sterile soils to which one of three strains of the bacterium *Burkholderia glathei* had been added absorbed more potassium (K) than did seedlings grown in soil without any bacteria. Other results (not shown) demonstrated that strain 3 increased the amount of K released from mineral crystals to the soil.

WHAT IF? *Estimate the average uptake of K for seedlings in soils with bacteria. What would you expect this average to be if bacteria had no effect on nutrient availability?*

Ecological Interactions

Prokaryotes play a central role in many ecological interactions. Consider **symbiosis** (from a Greek word meaning "living together"), an ecological relationship in which two species live in close contact with each other. Prokaryotes often form symbiotic associations with much larger organisms. In general, the larger organism in a symbiotic relationship is known as the **host**, and the smaller is known as the **symbiont**. There are many cases in which a prokaryote and its host participate in **mutualism**, an ecological interaction between two species in which both benefit **(Figure 27.19)**. Other interactions take the form of **commensalism**, an ecological relationship in which one species benefits while the other is not harmed or helped in any significant way. For example, more than 150 bacterial species live on the surface of your body, covering portions of your skin with up to 10 million cells per square centimeter. Some of these species are commensalists: You provide them with food, such as the oils that exude from your pores, and a place to live, while they do not harm or benefit you. Finally, some prokaryotes engage in **parasitism**, an ecological relationship in which a **parasite** eats the cell contents, tissues, or body fluids of its host; as a group, parasites harm but usually do not kill their host, at least not immediately (unlike a predator). Parasites that cause disease are known as **pathogens**, many of which are prokaryotic.

▲ **Figure 27.19 Mutualism: bacterial "headlights."** The glowing oval below the eye of the flashlight fish (*Photoblepharon palpebratus*) is an organ harboring bioluminescent bacteria. The fish uses the light to attract prey and to signal potential mates. The bacteria receive nutrients from the fish.

(We'll discuss mutualism, commensalism, and parasitism in greater detail in Chapter 54.)

The very existence of an ecosystem can depend on prokaryotes. For example, consider the diverse ecological communities found at hydrothermal vents. These communities are densely populated by many different kinds of animals, including worms, clams, crabs, and fishes. But since sunlight does not penetrate to the deep ocean floor, the community does not include photosynthetic organisms. Instead, the energy that supports the community is derived from the metabolic activities of chemoautotrophic bacteria. These bacteria harvest chemical energy from compounds such as hydrogen sulfide (H_2S) that are released from the vent. An active hydrothermal vent may support hundreds of eukaryotic species, but when the vent stops releasing chemicals, the chemoautotrophic bacteria cannot survive. As a result, the entire vent community collapses.

CONCEPT CHECK 27.5

1. Explain how prokaryotes, though small, can be considered giants in their collective impact on Earth and its life.
2. **MAKE CONNECTIONS** After reviewing photosynthesis in Figure 10.6 (p. 188), summarize the main steps by which cyanobacteria produce O_2 and use CO_2 to make organic compounds.

For suggested answers, see Appendix A.

CONCEPT 27.6

Prokaryotes have both beneficial and harmful impacts on humans

Though the best-known prokaryotes tend to be the bacteria that cause illness in humans, these pathogens represent only a small fraction of prokaryotic species. Many other prokaryotes have positive interactions with humans, and some play essential roles in agriculture and industry.

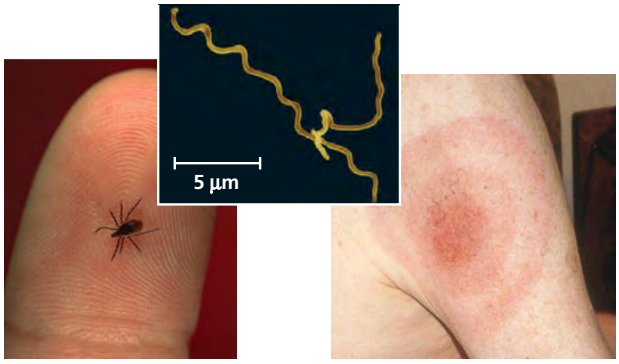
Mutualistic Bacteria

As is true for many other eukaryotes, human well-being can depend on mutualistic prokaryotes. For example, our intestines are home to an estimated 500–1,000 species of bacteria; their cells outnumber all human cells in the body by a factor of ten. Different species live in different portions of the intestines, and they vary in their ability to process different foods. Many of these species are mutualists, digesting food that our own intestines cannot break down. In 2003, scientists published the first complete genome of one of these gut mutualists, *Bacteroides thetaiotaomicron*. The genome includes a large array of genes involved in synthesizing carbohydrates, vitamins, and other nutrients needed by humans. Signals from the bacterium activate human genes that build the network of intestinal blood vessels necessary to absorb nutrient molecules. Other signals induce human cells to produce antimicrobial compounds to which *B. thetaiotaomicron* is not susceptible. This action may reduce the population sizes of other, competing species, thus potentially benefiting both *B. thetaiotaomicron* and its human host.

Pathogenic Bacteria

All the pathogenic prokaryotes known to date are bacteria, and they deserve their negative reputation. Bacteria cause about half of all human diseases. Roughly 2 million people die each year of the lung disease tuberculosis, caused by *Mycobacterium tuberculosis*. And another 2 million people die each year from diarrheal diseases caused by various bacteria.

Some bacterial diseases are transmitted by other species, such as fleas or ticks. In the United States, the most widespread pest-carried disease is Lyme disease, which infects 15,000 to 20,000 people each year **(Figure 27.20)**. Caused by a bacterium carried by ticks that live on deer and field mice,



▲ **Figure 27.20 Lyme disease.** Ticks in the genus *Ixodes* spread the disease by transmitting the spirochete *Borrelia burgdorferi* (colorized SEM). A rash may develop at the site of the tick's bite; the rash may be large and ring-shaped (as shown) or much less distinctive.

Lyme disease can result in debilitating arthritis, heart disease, nervous disorders, and death if untreated.

Pathogenic prokaryotes usually cause illness by producing poisons, which are classified as exotoxins or endotoxins. **Exotoxins** are proteins secreted by certain bacteria and other organisms. Cholera, a dangerous diarrheal disease, is caused by an exotoxin secreted by the proteobacterium *Vibrio cholerae*. The exotoxin stimulates intestinal cells to release chloride ions into the gut, and water follows by osmosis. In another example, the potentially fatal disease botulism is caused by botulinum toxin, an exotoxin secreted by the gram-positive bacterium *Clostridium botulinum* as it ferments various foods, including improperly canned meat, seafood, and vegetables. Like other exotoxins, the botulinum toxin can produce disease even if the bacteria that manufacture it are not present. In one such case, eight people contracted botulism after eating salted fish that did not contain any *C. botulinum* bacteria, but did contain the botulinum toxin. Even though the bacterium was no longer present, at some point in the fish preparation process, the bacterium had been able to grow and secrete the toxin.

Endotoxins are lipopolysaccharide components of the outer membrane of gram-negative bacteria. In contrast to exotoxins, endotoxins are released only when the bacteria die and their cell walls break down. Endotoxin-producing bacteria include species in the genus *Salmonella*, such as *Salmonella typhi*, which causes typhoid fever. You might have heard of food poisoning caused by other *Salmonella* species that are frequently found in poultry.

Since the 19th century, improved sanitation systems in the industrialized world have greatly reduced the threat of pathogenic bacteria. Antibiotics have saved a great many lives and reduced the incidence of disease. However, resistance to antibiotics is currently evolving in many bacterial strains. As you read earlier, the rapid reproduction of bacteria enables cells carrying resistance genes to quickly give rise to large populations as a result of natural selection, and these genes can also spread to other species by horizontal gene transfer.

Horizontal gene transfer can also spread genes associated with virulence, turning normally harmless bacteria into potent pathogens. *E. coli*, for instance, is ordinarily a harmless symbiont in the human intestines, but pathogenic strains that cause bloody diarrhea have emerged. One of the most dangerous strains, called O157:H7, is a global threat; in the United States alone, there are 75,000 cases of O157:H7 infection per year, often from contaminated beef or produce. In 2001, scientists sequenced the genome of O157:H7 and compared it with the genome of a harmless strain of *E. coli* called K-12. They discovered that 1,387 out of the 5,416 genes in O157:H7 have no counterpart in K-12. Many of these 1,387 genes are found in chromosomal regions that include phage DNA. This result suggests that at least some of the 1,387 genes were incorporated into the genome of O157:H7 through phage-mediated horizontal gene transfer (transduction). Some of the genes found only in O157:H7 are associated with virulence, including genes that code for adhesive fimbriae that enable O157:H7 to attach itself to the intestinal wall and extract nutrients.

Pathogenic bacteria also pose a potential threat as weapons of bioterrorism. For example, endospores of *Bacillus anthracis* sent through the mail in 2001 caused 18 people to develop inhalation anthrax, which was fatal in 5 of the cases. Such scenarios have stimulated more research on pathogenic prokaryotic species in the hope of developing new vaccines and antibiotics.

Prokaryotes in Research and Technology

On a positive note, we reap many benefits from the metabolic capabilities of both bacteria and archaea. For example, humans have long used bacteria to convert milk to cheese and yogurt. In recent years, our greater understanding of prokaryotes has led to an explosion of new applications in biotechnology; two examples are the use of *E. coli* in gene cloning (see Figure 20.2) and the use of *Agrobacterium tumefaciens* in producing transgenic plants such as Golden Rice (see Figure 20.26 and p. 816).

Bacteria may soon figure prominently in a major industry: plastics. Globally, each year about 350 billion pounds of plastic are produced from petroleum and used to make toys, storage containers, soft drink bottles, and many other items. These products degrade slowly, creating environmental problems. Bacteria can now be used to make natural plastics **(Figure 27.21a)**. For example, some bacteria synthesize a type of polymer known as PHA (polyhydroxyalkanoate), which they use to store chemical energy. The PHA they produce can be extracted, formed into pellets, and used to make durable, biodegradable plastics.

▲ **Figure 27.21 Some applications of prokaryotes. (a)** These bacteria synthesize and store PHA, which can be extracted and used to make biodegradable plastic products. **(b)** Spraying fertilizers on an oil-soaked area stimulates growth of native bacteria that metabolize the oil, speeding the natural breakdown process up to fivefold. **(c)** Current research seeks to develop bacteria that produce ethanol (E-85) fuel efficiently from renewable plant products.

Another way to harness prokaryotes is in **bioremediation**, the use of organisms to remove pollutants from soil, air, or water. For example, anaerobic bacteria and archaea decompose the organic matter in sewage, converting it to material that can be used as landfill or fertilizer after chemical sterilization. Other bioremediation applications include cleaning up oil spills **(Figure 27.21b)** and precipitating radioactive material (such as uranium) out of groundwater.

Through genetic engineering, humans can now modify bacteria to produce vitamins, antibiotics, hormones, and other products (see Chapter 20). Researchers are seeking to reduce fossil fuel use by engineering bacteria that can produce ethanol from various forms of biomass, including agricultural waste, switchgrass, municipal waste (such as paper products that are not recycled), and corn **(Figure 27.21c)**.

The usefulness of prokaryotes largely derives from their diverse forms of nutrition and metabolism. All this metabolic versatility evolved prior to the appearance of the structural novelties that heralded the evolution of eukaryotic organisms, to which we devote the remainder of this unit.

CONCEPT CHECK 27.6

1. Identify at least two ways that prokaryotes have affected you positively today.
2. A pathogenic bacterium's toxin causes symptoms that increase the bacterium's chance of spreading from host to host. Does this information indicate whether the poison is an exotoxin or endotoxin? Explain.
3. **WHAT IF?** How might a sudden and dramatic change in your diet affect the diversity of prokaryotic species that live in your digestive tract?

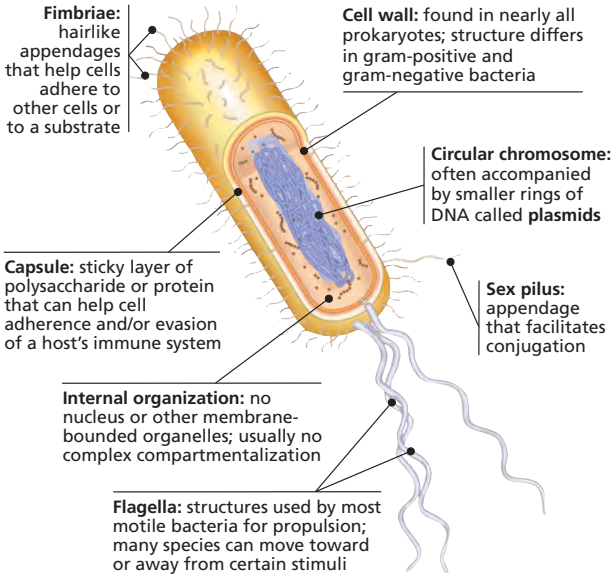
For suggested answers, see Appendix A.

27 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 27.1

Structural and functional adaptations contribute to prokaryotic success (pp. 556–561)



- Prokaryotes can reproduce quickly by binary fission. Some form endospores, which can remain viable in harsh conditions for centuries. Prokaryotic populations can evolve in short periods of time in response to changing environmental conditions.

? *Describe features of prokaryotes that enable them to thrive in many different environments.*

CONCEPT 27.2

Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes (pp. 561–564)

- Because prokaryotes can often proliferate rapidly, mutations can quickly increase a population's genetic variation, making adaptive evolution possible.
- Genetic diversity in prokaryotes also can arise by recombination of the DNA from two different cells (via transformation, transduction, or conjugation). By transferring advantageous alleles, such as ones for antibiotic resistance, genetic recombination can promote adaptive evolution in prokaryotic populations.

? *Mutations are rare and prokaryotes reproduce asexually; yet their populations can have high genetic diversity. Explain how this can occur.*

CONCEPT 27.3

Diverse nutritional and metabolic adaptations have evolved in prokaryotes (pp. 564–565)

- Nutritional diversity is much greater in prokaryotes than in eukaryotes. As a group, prokaryotes perform all four modes of nutrition: **photoautotrophy**, **chemoautotrophy**, **photoheterotrophy**, and **chemoheterotrophy**.
- Among prokaryotes, **obligate aerobes** require O_2, **obligate anaerobes** are poisoned by O_2, and **facultative anaerobes** can survive with or without O_2.
- Unlike eukaryotes, prokaryotes can metabolize nitrogen in many different forms. Some can convert atmospheric nitrogen to ammonia, a process called **nitrogen fixation**.
- Prokaryotic cells and even species may cooperate metabolically. In *Anabaena*, photosynthetic cells and nitrogen-fixing cells exchange metabolic products. Metabolic cooperation also occurs in surface-coating **biofilms** that include different species.

? *Describe the range of prokaryotic metabolic adaptations.*

CONCEPT 27.4

Molecular systematics is illuminating prokaryotic phylogeny (pp. 565–570)

- Molecular systematics is leading to a phylogenetic classification of prokaryotes, allowing systematists to identify major new clades.
- Some archaea, such as extreme thermophiles and extreme halophiles, live in extreme environments. Other archaea live in moderate environments such as soils and lakes.
- Diverse nutritional types are scattered among the major groups of bacteria. The two largest groups are the proteobacteria and the gram-positive bacteria.

? *What impact have molecular data had on constructing prokaryotic phylogeny?*

CONCEPT 27.5

Prokaryotes play crucial roles in the biosphere (pp. 570–571)

- Decomposition by heterotrophic prokaryotes and the synthetic activities of autotrophic and nitrogen-fixing prokaryotes contribute to the recycling of elements in ecosystems.
- Many prokaryotes have a symbiotic relationship with a host; the relationships between prokaryotes and their hosts range from mutualism to commensalism to parasitism.

? *In what ways are prokaryotes key to the survival of many species?*

CONCEPT 27.6

Prokaryotes have both beneficial and harmful impacts on humans (pp. 571–573)

- Humans depend on mutualistic prokaryotes, including hundreds of species that live in our intestines and help digest food.
- Pathogenic bacteria typically cause disease by releasing **exotoxins** or **endotoxins** and are potential weapons of bioterrorism. Horizontal gene transfer can spread genes associated with virulence to harmless species or strains.
- Experiments with bacteria such as *E. coli* have led to important advances in DNA technology. Prokaryotes can be used in bioremediation, production of biodegradable plastics, and the synthesis of vitamins, antibiotics, and other products.

? *Describe beneficial and harmful impacts of prokaryotes on humans.*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Genetic variation in bacterial populations cannot result from
   a. transduction.
   b. transformation.
   c. conjugation.
   d. mutation.
   e. meiosis.

2. Photoautotrophs use
   a. light as an energy source and CO_2 as a carbon source.
   b. light as an energy source and methane as a carbon source.
   c. N_2 as an energy source and CO_2 as a carbon source.
   d. CO_2 as both an energy source and a carbon source.
   e. H_2S as an energy source and CO_2 as a carbon source.

3. Which of the following statements is *not* true?
   a. Archaea and bacteria have different membrane lipids.
   b. Both archaea and bacteria generally lack membrane-enclosed organelles.
   c. The cell walls of archaea lack peptidoglycan.
   d. Only bacteria have histones associated with DNA.
   e. Only some archaea use CO_2 to oxidize H_2, releasing methane.

4. Which of the following involves metabolic cooperation among prokaryotic cells?
   a. binary fission
   b. endospore formation
   c. endotoxin release
   d. biofilms
   e. photoautotrophy

5. Bacteria perform the following ecological roles. Which role typically does *not* involve symbiosis?
   a. skin commensalist
   b. decomposer
   c. aggregate with methane-consuming archaea
   d. gut mutualist
   e. pathogen

6. Plantlike photosynthesis that releases O_2 occurs in
   a. cyanobacteria.
   b. chlamydias.
   c. archaea.
   d. actinomycetes.
   e. chemoautotrophic bacteria.

LEVEL 2: APPLICATION/ANALYSIS

7. **EVOLUTION CONNECTION**
   In patients infected with nonresistant strains of the tuberculosis bacterium, antibiotics can relieve symptoms in a few weeks. However, it takes much longer to halt the infection, and patients may discontinue treatment while bacteria are still present. How might this result in the evolution of drug-resistant pathogens?

LEVEL 3: SYNTHESIS/EVALUATION

8. **SCIENTIFIC INQUIRY**
   DRAW IT The nitrogen-fixing bacterium *Rhizobium* infects the roots of some plant species, forming a mutualism in which the bacterium provides nitrogen, and the plant provides carbohydrates. Scientists measured the 12-week growth of one such plant species (*Acacia irrorata*) when infected by six different *Rhizobium* strains. (a) Graph the data. (b) Interpret your graph.

Rhizobium strain	1	2	3	4	5	6
Plant mass (g)	0.91	0.06	1.56	1.72	0.14	1.03

Source: J. J. Burdon et al., Variation in the effectiveness of symbiotic associations between native rhizobia and temperate Australian *Acacia*: within species interactions, *Journal of Applied Ecology* 36:398–408 (1999).
Note: Without *Rhizobium*, after 12 weeks, *Acacia* plants have a mass of about 0.1 g.

9. **WRITE ABOUT A THEME**
   Energy Transfer In a short essay (about 100–150 words), discuss how prokaryotes and other members of hydrothermal vent communities transfer and transform energy.

For selected answers, see Appendix A.

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1. MasteringBiology® Assignments

Make Connections Tutorial Bacterial Conjugation (Chapter 27) and Binary Fission (Chapter 12)
Tutorial Diversity in Bacteria
Activities Classification of Prokaryotes • The Tree of Life • Discovery Channel Videos: Bacteria; Antibiotics; Tasty Bacteria
Questions Student Misconceptions • Reading Quiz • Multiple Choice • End-of-Chapter

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