16.7 Prokaryotes have inhabited Earth for billions of years

The fossil record shows that prokaryotes were abundant 3.5 billion years ago. They continued to evolve all alone on Earth for the next 1.5 billion years. Today, prokaryotes are found wherever there is life, and they outnumber all eukaryotes combined. More prokaryotes inhabit a handful of fertile soil or the mouth of a human than the total number of people who have ever lived. Prokaryotes also thrive in habitats too cold, too hot, too salty, too acidic, or too alkaline for any eukaryote. You can get an idea of the size of most prokaryotes from Figure 16.7, a colorized scanning electron micrograph of the point of a pin (purple), covered with numerous bacteria (orange). Most prokaryotic cells have diameters in the range of 1–10 μm, much smaller than most eukaryotic cells (typically 10–100 μm).

Despite their small size, prokaryotes have an immense impact on our world. We hear most about a few species that cause serious illnesses. During the fourteenth century, Black Death—bubonic plague, a bacterial disease—spread across Europe, killing an estimated 25% of the human population. Tuberculosis, cholera, and various sexually transmissible diseases, and certain types of food poisoning are also caused by bacteria. In addition, bacteria cause many kinds of diseases in other animals and in plants. We focus on bacterial diseases in Module 16.14.

Far more common than harmful bacteria are those that are benign or beneficial. We have bacteria in our intestines that provide us with important vitamins, and others living in our mouth help prevent harmful fungi from growing there. Essential to all life on Earth are prokaryotes that decompose dead organisms. Found in soil and at the bottom of lakes, rivers, and oceans, these prokaryotes—bacteria and archaea—return vital chemical elements to the environment in the form of inorganic compounds that can be used by plants, which in turn feed animals. If prokaryotic decomposers were to disappear, the chemical cycles that sustain life would halt, and all forms of eukaryotic life would be doomed. In contrast, prokaryotic life would undoubtably persist in the absence of eukaryotes, as it once did for billions of years.

16.8 Archaea and bacteria are the two main branches of prokaryotic evolution

Prokaryotes have a cellular organization fundamentally different from that of eukaryotes, as we saw in Modules 4.4 and 4.5. Whereas eukaryotic cells have a membrane-enclosed nucleus and numerous other membrane-enclosed organelles, prokaryotic cells lack these structural features.

As we discussed in earlier chapters, however, two very different kinds of prokaryotes, classified in the domains Bacteria and Archaea, are found on Earth today. The name Archaea comes from the Greek archaios ("ancient"), and most biologists believe that these prokaryotes and bacteria diverged from each other in very ancient times.

The most fundamental differences between the organisms of these two domains are in their nucleic acids. Researchers first focused on one type of ribosomal RNA (rRNA), a type found in all prokaryotes and eukaryotes. Comparing the nucleotide sequences, they made some interesting discoveries. For instance, near nucleotide number 910 (of 1,500) in this rRNA, they found the following difference in sequence:

- Bacteria: AACUCUAAA
- Archaea: AACUUAAAAG

Researchers have identified a dozen such short rRNA sequences that distinguish bacteria from archaea. Intriguingly, in a number of cases, the archaean sequence is identical to that of eukaryotes.

More recently, researchers have focused on DNA and have completely sequenced a number of bacterial and archaean genomes (see Module 12.14). When compared to each other and with the genomes of eukaryotic yeasts, these genome sequences strongly support the archaean domain view of life. Some genes of archaean are similar to bacterial genes and others to eukaryotic genes; still others seem unique to archaean.

The table on the next page summarizes some of the most fundamental differences between bacteria and archaea. In addition to rRNA sequences, several other differences involve the cellular machinery for gene expression. These include differences in RNA polymerases (enzymes catalyzing the synthesis of RNA), in the presence of introns within genes, and in sensitivity to certain antibiotics that inhibit protein synthesis. Subtle differences between archaean and bacteria ribosomes—in both rRNA and proteins—undoubtedly account for the insensitivity of archaean to these antibiotics.
Other differences between bacteria and archaea show up in their cell walls and membranes. Nearly all prokaryotes have a cell wall outside their plasma membrane. As in plants, the wall maintains cell shape and provides physical protection. Bacterial cell walls contain a unique material called peptidoglycan, a polymer of sugars cross-linked by short polypeptides. No archaea have true peptidoglycan. Furthermore, the lipids forming the backbone of plasma membranes differ between the two domains.

Notice that in most of the features in the table, archaea are more like eukaryotes than like bacteria. In fact, archaea have at least as much in common with eukaryotes as they do with bacteria, the other prokaryotes. As you saw in Figure 15.14B, a current hypothesis is that modern archaea and eukaryotes evolved from a common ancestor. But the situation is complicated by evidence of gene swapping among the three domains.

The main point here is to realize that there are two very different kinds of prokaryotic organisms. We will discuss the diversity within these two groups after a look at some more general features of prokaryotes.

### 16.9 Prokaryotes come in a variety of shapes

Determining cell shape by microscopic examination is an important step in identifying prokaryotes. The micrographs below show three of their most common cell shapes. Spherical prokaryotic cells are called cocci (from the Greek word for "berries"). Cocci (singular, coccus) that occur in clusters, like the ones in Figure 16.9A, are called staphylococci (from the Greek staphyle, cluster of grapes). Other cocci occur in chains; they are called streptococci (from the Greek strepto-, twisted). The bacterium that causes strep throat in humans is a streptococcus.

Figure 16.9B shows rod-shaped prokaryotes, which are called bacilli (singular, bacillus). Most bacilli occur singly, but the cells of some species occur in pairs (diplobacilli) and in chains (streptobacilli). The species shown here, which is common in fertile soil, exists as solitary cells.

A third prokaryotic cell shape is curved or spiral. Some bacteria in this category resemble commas and are called vibrios. Other bacteria and archaea have a helical shape, like a corkscrew. Helical prokaryotes that are relatively short and rigid are called spirilla; those with longer, more flexible cells are called spirchetes (Figure 16.9C). The bacterium that causes syphilis, for example, is a spirochete. Spirochetes include some giants by prokaryotic standards—cells 0.5 mm long (though very thin).
16.10 Prokaryotes obtain nourishment in a variety of ways

When classifying diverse organisms, biologists often use the phrase “mode of nutrition” to describe how an organism obtains two main resources: carbon (for synthesizing organic compounds) and energy. As a group, prokaryotes exhibit much more nutritional diversity than eukaryotes.

**Types of Nutrition** Many prokaryotes are **autotrophs** (“self-feeders”), making their own organic compounds from inorganic sources. As shown in the top half of the table here, autotrophs obtain their carbon atoms from carbon dioxide (CO₂). They get their energy from sunlight or from inorganic chemicals, such as hydrogen sulfide (H₂S), elemental sulfur (S), or compounds containing iron (Fe). Autotrophs that harness sunlight for energy and use CO₂ for carbon, such as the cyanobacteria, do so by photosynthesis; they are called **photoautotrophs**. (Cyanobacteria use H₂O as a source of electrons for photosynthesis and produce O₂ as a waste product, just like plants.) Autotrophic organisms that obtain energy from inorganic chemicals instead of sunlight are called **chemoautotrophs**.

Most prokaryotes are **heterotrophs** (“other-feeders”), meaning they obtain their carbon atoms from organic compounds. Some heterotrophs, called **photoheterotrophs**, can obtain energy from sunlight. By far the largest group of prokaryotes, however, are nutritionally similar to animals in that they obtain both energy and carbon from organic molecules. Called **chemoheterotrophs**, these bacteria are so diverse that almost any organic molecule can serve as food for some species. Many species, such as *Escherichia coli*, a resident of the human intestine, can thrive on a variety of organic nutrients. The photograph in Figure 16.10 shows a culture of *E. coli* grown with only glucose as an organic nutrient. Each round spot in the culture dish is a colony, a clone of millions of bacterial cells.

When nutrients are available, *E. coli* and other prokaryotes multiply exponentially. One cell divides to form 2, 2 cells form 4, 4 form 8, and so on. With generation times as short as a few hours or less, prokaryotes have enormous growth potential. Their actual growth is limited by environmental factors (such as nutrient availability) and by the buildup of toxic metabolic wastes from the microbes themselves.

**The Early Evolution of Nutrition** Chemoheterotrophs are the dominant prokaryotes today—and may have been since the dawn of life. However, there are other possibilities. Earlier, we proposed that the first life-forms were prokaryotes that evolved from membrane-enclosed molecular co-ops. The first prokaryote would undoubtedly have had a very simple metabolism requiring only a few enzymes. Its environment contained almost no O₂, so its metabolism would have been anaerobic. It is unlikely that the earliest organisms were able to use sunlight as an energy source, because doing so requires a very complex set of enzymes. More likely, early life-forms would have simply obtained their carbon and energy from the rich soup of molecules and ions in which they evolved.

One hypothesis is that the earliest life-form was a chemoheterotroph that obtained its energy from chemical reactions involving inorganic sulfur and iron compounds. These chemicals were abundant in the ocean—especially in the hot vents near the deep-sea hydrothermal vents where life may have first arisen. Dissolved CO₂ or perhaps abiotically formed organic molecules may have served as the carbon source.

Scientists got the idea for this hypothesis from the metabolic activities of certain archaea living on Earth today, which we discuss next.

**Web/CD Thinking as a Scientist What Are the Modes of Nutrition in Prokaryotes?**

A bacterium requires only the amino acid methionine as an organic nutrient and lives deep in the soil where no light penetrates. Based on its mode of nutrition, this bacterium would be classified as a **_______**.
Archaea thrive in extreme environments—and in the ocean

Archaea are abundant in many habitats, including places where few other organisms can survive. The archaean inhabitants of extreme environments have unusual proteins and other molecular adaptations that enable them to metabolize and reproduce effectively. Scientists are only beginning to learn about these adaptations.

A group of archaea called the **extreme halophiles** ("salt lovers") thrive in very salty places, such as the Great Salt Lake in Utah, the Dead Sea, and seawater-evaporating ponds used to produce salt. Figure 16.11A shows some ponds of this sort next to San Francisco Bay. The colors of the ponds result from the dense growth of the archaea that thrive when the salinity of the water reaches 15–20%. (Before evaporation, seawater has a salt concentration of about 3%.) The purplish color of the ponds near the top of the photo is due to an archaean called *Halobacterium halobium*. A unique photosynthesizer, *H. halobium* lacks chlorophyll; instead, it has a purple molecule called bacteriorhodopsin that traps solar energy.

Another group of archaea, the **extreme thermophiles** ("heat lovers"), thrive in very hot water; some even live near deep-ocean vents where temperatures are above 100°C, the boiling point of water at sea level! Other hyperthermophiles thrive in acid. Many hot, acidic pools in Yellowstone National Park harbor such archaea, which give the pools a vivid greenish color (Figure 16.11B). One of these organisms, *Sulfolobus*, can obtain energy by oxidizing sulfur or a compound of sulfur and iron; the mechanisms involved may be similar to those used billions of years ago by the first cells.

A third group of archaea, the **methanogens**, live in anaerobic environments and give off methane as a waste product. Many thrive in anaerobic mud at the bottom of lakes and swamps. You may have seen methane, also called marsh gas, bubbling up from a swamp. Great numbers of methanogens do inhabit the digestive tracts of animals. In humans, most of the intestinal gas is largely the result of their metabolism. More importantly, methanogens aid digestion in cattle, deer, and other animals that depend heavily on cellulose for their nutrition. Normally, bloating does not occur, because these animals regularly belch out large volumes of gas produced by methanogens and other microorganisms that enable them to digest cellulose.

Acquainted to thinking of archaea as mostly "extremophiles," scientists have been surprised to discover their abundance in more moderate environments, especially in the oceans. Archaea live at all depths, making up a substantial fraction of the prokaryotes in waters below 150 m and equaling bacteria in numbers below 1,000 m. Archaea are the most abundant cell types in the Earth's largest habitat.

Because bacteria have been the subjects of most prokaryotic research throughout the history of microbiology, much more is known about them than about archaea. Now that the evolutionary and ecological importance of archaea has come into focus, we can expect research on this domain to turn up many more surprises about the history of life and the roles of microbes in ecosystems.

**Some archaea are referred to as "extremophiles." Why?**

Once the archaean species were isolated and grown in pure culture, they were compared with known bacteria. The enzymes of archaea were often found to be too stable and too heat resistant to be produced by bacteria. Therefore, the archaean species were classified as an "archaeal" domain.
16.12 Diverse structural features help prokaryotes thrive almost everywhere

In this module, we discuss some of the structural features that help prokaryotes—bacteria and archaea—thrive in a great variety of environments.

Many bacteria and archaea are equipped with flagella, which enable them to move about. Prokaryotes with flagella can move toward more favorable places or away from less favorable ones. Flagella may be scattered over the entire cell surface or concentrated at one or both ends of the cell. Entirely different in structure from the flagellum of eukaryotic cells (described in Module 4.18), the prokaryotic flagellum (often called the bacterial flagellum) is a naked protein structure that lacks microtubules. It is attached to the cell surface by a system of rotating rings anchored in the plasma membrane and cell wall. The rings give the flagellum a propeller-like rotary movement, as shown in Figure 16.12A. The flagellated organism in the photo is the bacterium *Proteus*, an especially fast swimmer.

Shorter and thinner than flagella are the appendages called pili (singular, *pilus*). Pili are not visible in the Figure 16.12A micrograph but show up clearly in the more highly magnified micrograph of another bacterium in Figure 16.12B. Pili help bacteria stick to each other and to surfaces, such as rocks in flowing streams or the lining of human intestines. Special pili called sex pili are required for initiating bacterial “mating” (conjugation) (see Module 12.1). Sex pili are fewer and longer than ordinary pili.

Although few bacteria can thrive in the extreme environments favored by many archaea, bacteria of several genera can survive extended periods of very harsh conditions by forming specialized “resting” cells. Figure 16.12C (top of the facing page) shows an example of such an organism, *Bacillus anthracis*, the bacterium that produces the deadly disease called anthrax in cattle, sheep, and humans. There are actually two cells here, one inside the other. The outer cell produced the specialized inner cell, called an *endospore*. The endospore has a thick, protective coat, its cytoplasm is dehydrated, and it does not metabolize. Under harsh conditions, the outer cell may disintegrate, but the endospore survives all sorts of trauma, including lack of water and nutrients, extreme heat or cold, and most poisons. When the environment becomes more hospitable, the endospore absorbs water and resumes growth.

Some endospores can remain dormant for centuries. Not even boiling water kills most of these resistant cells. To sterilize laboratory equipment, microbiologists use an autoclave, a pressure cooker that kills endospores by heating to a temperature of 121°C (250°F) with high-pressure steam. The food-canning industry uses similar methods to kill endospores of dangerous bacteria such as *Clostridium botulinum*, the source of the potentially fatal disease botulism.

The mass of branching cell chains (filaments) in Figure 16.12D is a structural feature unique to the bacterial group called actinomycetes. These bacteria are very common in soil, where they break down organic substances. The filaments enable the organism to bridge dry gaps between soil particles. Actinomycetes were once mistaken for fungi, which also grow in branching filaments; this similarity explains the name, which is from the Greek for “ray fungus.” The actinomycete in Figure 16.12D is of the genus *Streptomyces*, a common soil organism. *Streptomyces* secretes the antibiotic streptomycin and a number of other antibiotics, which inhibit the growth of competing bacteria. Pharmaceutical companies use various species of actinomycetes to produce many antibiotics.
Branching chains of cells are unusual, but many other prokaryotes, both bacteria and archaea, grow in unbranched chains. Next we look at a cyanobacterium that grows in unbranched filaments and at the effect it can have on a polluted lake.

**CONNECTION**

**16.13 Cyanobacteria sometimes “bloom” in aquatic environments**

The larger lake pictured in Figure 16.13A below is undergoing a population explosion—often called a “bloom”—of cyanobacteria. The blue-green color results from the presence of trillions of cyanobacterial cells. Figure 16.13B is a micrograph of Anabaena, the predominant cyanobacterium in the lake.

Cyanobacteria make up one group of photosynthetic bacteria. They are common in lakes, ponds, and tropical oceans. Extensive blooms of cyanobacteria in a lake usually indicate polluted water conditions. In the case shown here, the water was loaded with organic wastes from agricultural runoff. Phosphates and nitrates from the waste material acted as fertilizers, stimulating explosive multiplication of the cyanobacteria.

This lake’s condition may be reminiscent of the age of cyanobacteria, a time when these prokaryotes dominated Earth. At that time, from about 3.0 to 1.5 billion years ago, ancient cyanobacteria gave Earth its first greenish coat, generated the stromatolites we discussed in the chapter introduction, and made the atmosphere aerobic. Some of the molecular machinery for photosynthesis housed in cyanobacteria today may be much like that which first added \( \text{O}_2 \) to Earth’s atmosphere.
16.14 Some bacteria cause disease

All organisms, humans included, are almost constantly exposed to bacteria, some of which are potentially harmful. In fact, most of us are well most of the time only because our body defenses check the growth of bacterial pathogens, disease-causing agents. Occasionally, the balance shifts in favor of a pathogen, and we become ill. Even some of the bacteria that are normal residents of the human body can make us ill when our defenses have been weakened by poor nutrition or by a viral infection.

Pathogenic bacteria cause about half of all human diseases. Most cause disease by producing poisons, which are of two types: exotoxins and endotoxins. Exotoxins, toxic proteins secreted by bacterial cells, include some of the most potent poisons known. A single gram of the exotoxin that causes botulism, for instance, could kill a million people.

The culture dish in Figure 16.14A shows yellow colonies of Staphylococcus aureus, another exotoxin producer (the name is from the Latin aureus, golden). S. aureus is a common, usually harmless resident of our skin surface. If it enters the body through a cut or other wound, however, or is swallowed in contaminated food, it can cause serious diseases. One type of S. aureus produces exotoxins that cause layers of skin to slough off; another can cause vomiting and severe diarrhea; yet another can produce the potentially deadly toxic shock syndrome.

Bacterial species that are generally harmless can also develop strains that cause illness. Since first identified in 1982, a group of pathogenic, exotoxin-producing strains of E. coli designated O157:H7 have caused a number of outbreaks of severe illness and thousands of deaths. These strains have emerged as threats to public health worldwide. Commonly found in cattle, the bacteria do not hurt the cattle, but in infected humans the exotoxin selectively enters the cells that line blood vessels and kills them. Bloody diarrhea ensues and, in extreme cases, kidney failure. The recently sequenced genome of an O157:H7 strain may provide clues for vaccine development or treatments. For now, the best preventive measure is to avoid eating undercooked meat.

In contrast to exotoxins, endotoxins are not cell secretions, but components of the cell walls of certain bacteria. Endotoxins are glycolipids, large molecular complexes of polysaccharides and lipids. All endotoxins induce the same general symptoms: fever, aches, and sometimes a dangerous drop in blood pressure (shock). The severity of symptoms varies with the host's condition and with the bacterium. Different species of Salmonella, for example, produce endotoxins that cause food poisoning and typhoid fever.

During the last 10 years, following the discovery that "germs" cause disease, the incidence of bacterial diseases has declined, particularly in developed nations. Sanitation is generally the most effective way to prevent bacterial diseases, and the installation of water treatment and sewage systems continues to be a public health priority throughout the world. Antibiotics can cure most bacterial diseases, but many pathogenic bacteria have evolved resistance to widely used antibiotics, becoming newly dangerous (see Module 13.22).