

34

Bacteria

Concept Outline

34.1 Bacteria are the smallest and most numerous organisms.

The Prevalence of Bacteria. The simplest of organisms, bacteria are thought to be the most ancient. They are the most abundant living organisms. Bacteria lack the high degree of internal compartmentalization characteristic of eukaryotes.

34.2 Bacterial cell structure is more complex than commonly supposed.

The Bacterial Surface. Some bacteria have a secondary membranelike covering outside of their cell wall.

The Cell Interior. While bacteria lack extensive internal compartments, they may have complex internal membranes.

34.3 Bacteria exhibit considerable diversity in both structure and metabolism.

Bacterial Diversity. There are at least 16 phyla of bacteria, although many more remain to be discovered.

Bacterial Variation. Mutation and recombination generate enormous variation within bacterial populations.

Bacterial Metabolism. Bacteria obtain carbon atoms and energy from a wide array of sources. Some can thrive in the absence of other organisms, while others must obtain their energy and carbon atoms from other organisms.

34.4 Bacteria are responsible for many diseases but also make important contributions to ecosystems.

Human Bacterial Diseases. Many serious human diseases are caused by bacteria, some of them responsible for millions of deaths each year.

Importance of Bacteria. Bacteria have had a profound impact on the world's ecology, and play a major role in modern medicine and agriculture.



FIGURE 34.1

A colony of bacteria. With their enormous adaptability and metabolic versatility, bacteria are found in every habitat on earth, carrying out many of the vital processes of ecosystems, including photosynthesis, nitrogen fixation, and decomposition.

The simplest organisms living on earth today are bacteria, and biologists think they closely resemble the first organisms to evolve on earth. Too small to see with the unaided eye, bacteria are the most abundant of all organisms (figure 34.1) and are the only ones characterized by prokaryotic cellular organization. Life on earth could not exist without bacteria because bacteria make possible many of the essential functions of ecosystems, including the capture of nitrogen from the atmosphere, decomposition of organic matter, and, in many aquatic communities, photosynthesis. Indeed, bacterial photosynthesis is thought to have been the source for much of the oxygen in the earth's atmosphere. Bacterial research continues to provide extraordinary insights into genetics, ecology, and disease. An understanding of bacteria is thus essential.

34.1 Bacteria are the smallest and most numerous organisms.

The Prevalence of Bacteria

Bacteria are the oldest, structurally simplest, and the most abundant forms of life on earth. They are also the only organisms with prokaryotic cellular organization. Represented in the oldest rocks from which fossils have been obtained, 3.5 to 3.8 billion years old, bacteria were abundant for over 2 billion years before eukaryotes appeared in the world (see figure 4.11). Early photosynthetic bacteria (cyanobacteria) altered the earth's atmosphere with the production of oxygen which led to extreme bacterial and eukaryotic diversity. Bacteria play a vital role both in productivity and in cycling the substances essential to all other life-forms. Bacteria are the only organisms capable of fixing atmospheric nitrogen.

About 5000 different kinds of bacteria are currently recognized, but there are doubtless many thousands more awaiting proper identification (figure 34.2). Every place microbiologists look, new species are being discovered, in some cases altering the way we think about bacteria. In the 1970s and 80s a new type of bacterium was analyzed that eventually led to the classification of a new prokaryotic cell type, the archeobacteria (or Archaea). Even when viewed with an electron microscope, the structural differences between different bacteria are minor compared to other groups of organisms. Because the structural differences are so slight, bacteria are classified based primarily upon their metabolic and genetic characteristics. Bacteria can be characterized properly only when they are grown on a defined medium because the characteristics of these organisms often change, depending on their growth conditions.

Bacteria are ubiquitous on Earth, and live everywhere eukaryotes do. Many of the other more extreme environments in which bacteria are found would be lethal to any other form of life. Bacteria live in hot springs that would cook other organisms, hypersaline environments that would dehydrate other cells, and in atmospheres rich in toxic gases like methane or hydrogen sulfide that would kill most other organisms. These harsh environments may be similar to the conditions present on the early Earth, when life first began. It is likely that bacteria evolved to dwell in these harsh conditions early on and have retained the ability to exploit these areas as the rest of the atmosphere has changed.

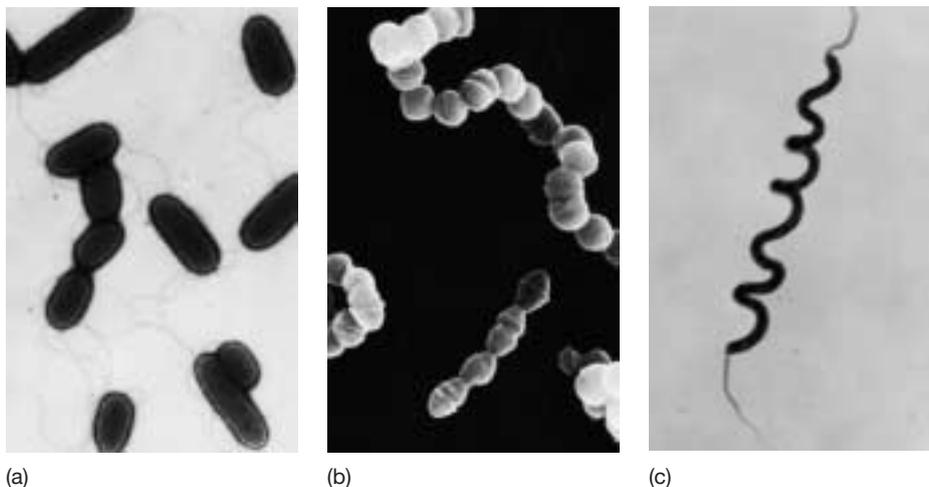


FIGURE 34.2

The diversity of bacteria. (a) *Pseudomonas aeruginosa*, a rod-shaped, flagellated bacterium (bacillus). *Pseudomonas* includes the bacteria that cause many of the most serious plant diseases. (b) *Streptococcus*. The spherical individual bacteria (cocci) adhere in chains in the members of this genus (34,000 \times). (c) *Spirillum volutans*, one of the spirilla. This large bacterium, which occurs in stagnant fresh water, has a tuft of flagella at each end (500 \times).

Bacterial Form

Bacteria are mostly simple in form and exhibit one of three basic structures: **bacillus** (plural, **bacilli**) straight and rod-shaped, **coccus** (plural, **cocci**) spherical-shaped, and **spirillus** (plural, **spirilla**) long and helical-shaped, also called spirochetes. Spirilla bacteria generally do not form associations with other cells and swim singly through their environments. They have a complex structure within their cell membranes that allow them to spin their corkscrew-shaped bodies which propels them along. Some rod-shaped and spherical bacteria form colonies, adhering end-to-end after they have divided, forming chains (see figure 34.2). Some bacterial colonies change into stalked structures, grow long, branched filaments, or form erect structures that release **spores**, single-celled bodies that grow into new bacterial individuals. Some filamentous bacteria are capable of gliding motion, often combined with rotation around a longitudinal axis. Biologists have not yet determined the mechanism by which they move.

Prokaryotes versus Eukaryotes

Prokaryotes—eubacteria and archaea—differ from eukaryotes in numerous important features. These differences represent some of the most fundamental distinctions that separate any groups of organisms.

1. **Multicellularity.** All prokaryotes are fundamentally single-celled. In some types, individual cells adhere to

FIGURE 34.3
Approaches to multicellularity in bacteria.

Chondromyces crocatus, one of the gliding bacteria. The rod-shaped individuals move together, forming the composite spore-bearing structures shown here. Millions of spores, which are basically individual bacteria, are released from these structures.



each other within a matrix and form filaments, however the cells retain their individuality. Cyanobacteria, in particular, are likely to form such associations but their cytoplasm is not directly interconnected, as often is the case in multicellular eukaryotes. The activities of a bacterial colony are less integrated and coordinated than those in multicellular eukaryotes. A primitive form of colonial organization occurs in gliding bacteria, which move together and form spore-bearing structures (figure 34.3). Such coordinated multicellular forms are rare among bacteria.

- 2. Cell size.** As new species of bacteria are discovered, we are finding that the size of prokaryotic cells varies tremendously, by as much as five orders of magnitude. Most prokaryotic cells are only 1 micrometer or less in diameter. Most eukaryotic cells are well over 10 times that size.
- 3. Chromosomes.** Eukaryotic cells have a membrane-bound nucleus containing chromosomes made up of both nucleic acids and proteins. Bacteria do not have membrane-bound nuclei, nor do they have chromosomes of the kind present in eukaryotes, in which DNA forms a structural complex with proteins. Instead, their naked circular DNA is localized in a zone of the cytoplasm called the **nucleoid**.
- 4. Cell division and genetic recombination.** Cell division in eukaryotes takes place by mitosis and involves spindles made up of microtubules. Cell division in bacteria takes place mainly by binary fission (see chapter 11). True sexual reproduction occurs only in eukaryotes and involves syngamy and meiosis, with an alternation of diploid and haploid forms. Despite their lack of sexual reproduction, bacteria do have mechanisms that lead to the transfer of genetic material. These mecha-

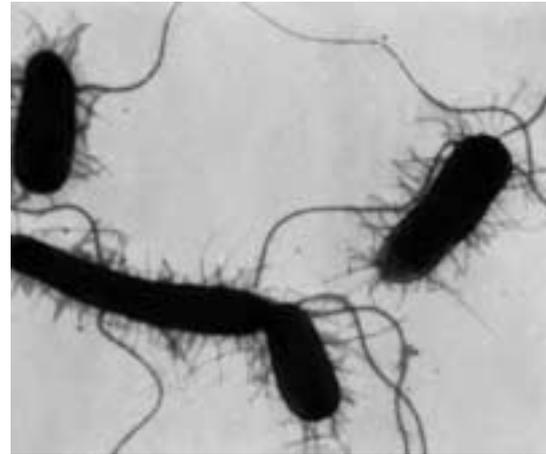


FIGURE 34.4
Flagella in the common intestinal bacterium, *Escherichia coli*.
The long strands are flagella, while the shorter hairlike outgrowths are called pili.

nisms are far less regular than those of eukaryotes and do not involve the equal participation of the individuals between which the genetic material is transferred.

- 5. Internal compartmentalization.** In eukaryotes, the enzymes for cellular respiration are packaged in mitochondria. In bacteria, the corresponding enzymes are not packaged separately but are bound to the cell membranes (see chapters 5 and 9). The cytoplasm of bacteria, unlike that of eukaryotes, contains no internal compartments or cytoskeleton and no organelles except ribosomes.
- 6. Flagella.** Bacterial flagella are simple in structure, composed of a single fiber of the protein flagellin (figure 34.4; see also chapter 5). Eukaryotic flagella and cilia are complex and have a 9 + 2 structure of microtubules (see figure 5.27). Bacterial flagella also function differently, spinning like propellers, while eukaryotic flagella have a whiplike motion.
- 7. Metabolic diversity.** Only one kind of photosynthesis occurs in eukaryotes, and it involves the release of oxygen. Photosynthetic bacteria have several different patterns of anaerobic and aerobic photosynthesis, involving the formation of end products such as sulfur, sulfate, and oxygen (see chapter 10). Prokaryotic cells can also be chemoautotrophic, using the energy stored in chemical bonds of inorganic molecules to synthesize carbohydrates; eukaryotes are not capable of this metabolic process.

Bacteria are the oldest and most abundant organisms on earth. Bacteria, or prokaryotes, differ from eukaryotes in a wide variety of characteristics, a degree of difference as great as any that separates any groups of organisms.

34.2 Bacterial cell structure is more complex than commonly supposed.

The Bacterial Surface

The bacterial **cell wall** is an important structure because it maintains the shape of the cell and protects the cell from swelling and rupturing. The cell wall usually consists of **peptidoglycan**, a network of polysaccharide molecules connected by polypeptide cross-links. In some bacteria, the peptidoglycan forms a thick, complex network around the outer surface of the cell. This network is interlaced with peptide chains. In other bacteria a thin layer of peptidoglycan is found sandwiched between two plasma membranes. The outer membrane contains large molecules of lipopolysaccharide, lipids with polysaccharide chains attached. These two major types of bacteria can be identified using a staining process called a **Gram stain**. **Gram-positive** bacteria have the thicker peptidoglycan wall and stain a purple color (figure 34.5). The more common **gram-negative** bacteria contain less peptidoglycan and do not retain the purple-colored dye. Gram-negative bacteria stain red. The outer membrane layer makes gram-negative bacteria resistant to many antibiotics that interfere with cell wall synthesis in gram-positive bacteria. In some kinds of bacteria, an additional gelatinous layer, the capsule, surrounds the cell wall.

Many kinds of bacteria have slender, rigid, helical **flagella** (singular, **flagellum**) composed of the protein flagellin (figure 34.6). These flagella range from 3 to 12 micrometers in length and are very thin—only 10 to 20 nanometers thick. They are anchored in the cell wall and spin, pulling the bacteria through the water like a propeller.

Pili (singular, **pilus**) are other hairlike structures that occur on the cells of some bacteria (see figure 34.4). They are shorter than bacterial flagella, up to several micrometers long, and about 7.5 to 10 nanometers thick. Pili help the bacterial cells attach to appropriate substrates and exchange genetic information.

Some bacteria form thick-walled **endospores** around their chromosome and a small portion of the surrounding cytoplasm when they are exposed to nutrient-poor conditions. These endospores are highly resistant to environmental stress, especially heat, and can germinate to form new individuals after decades or even centuries.

Bacteria are encased within a cell wall composed of one or more polysaccharide layers. They also may contain external structures such as flagella and pili.

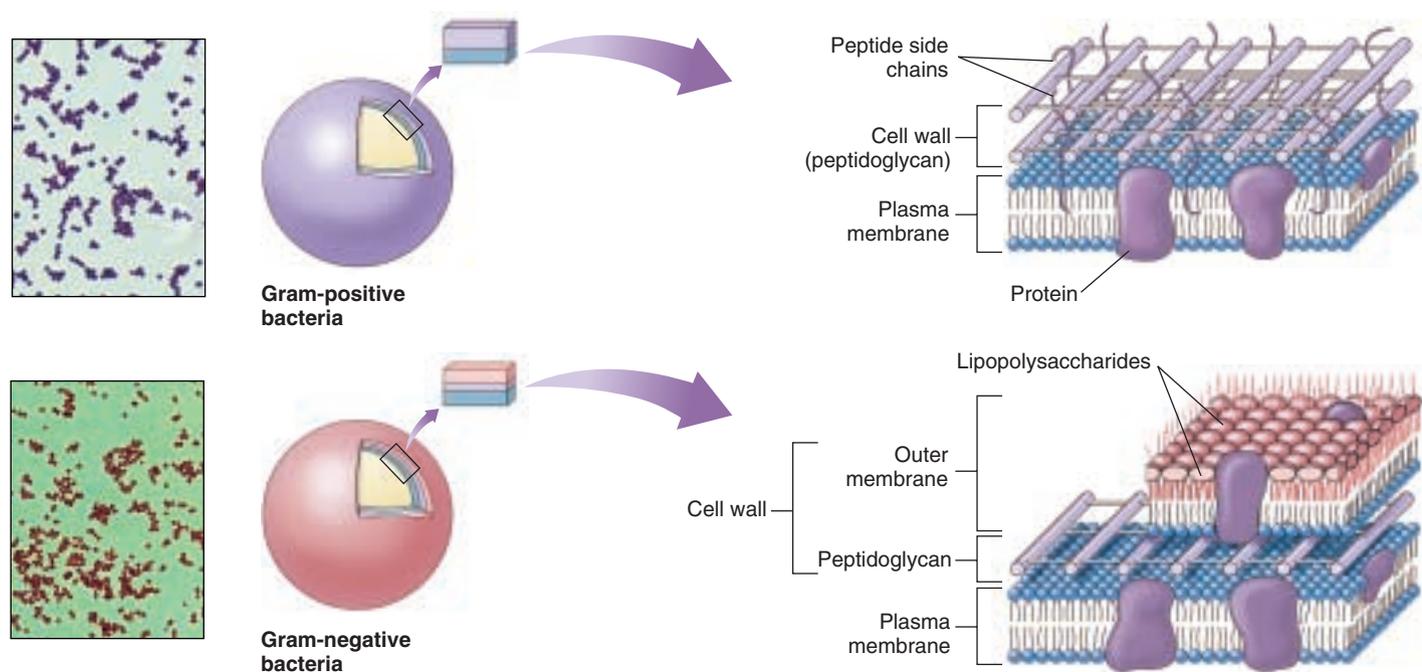


FIGURE 34.5

The Gram stain. The peptidoglycan layer encasing gram-positive bacteria traps crystal violet dye, so the bacteria appear purple in a Gram-stained smear (named after Hans Christian Gram, who developed the technique). Because gram-negative bacteria have much less peptidoglycan (located between the plasma membrane and an outer membrane), they do not retain the crystal violet dye and so exhibit the red background stain (usually a safranin dye).

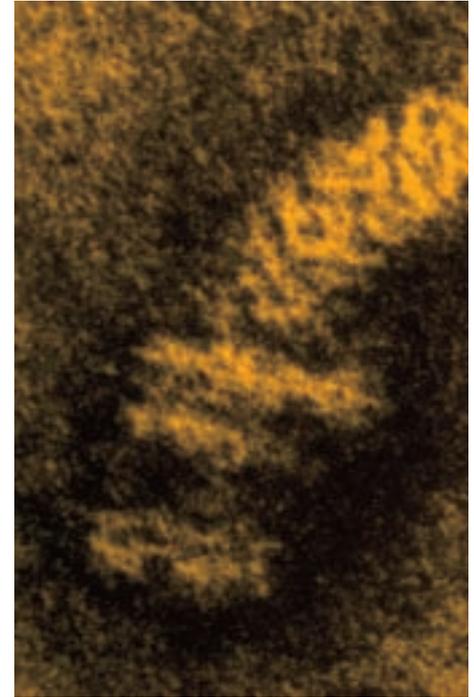
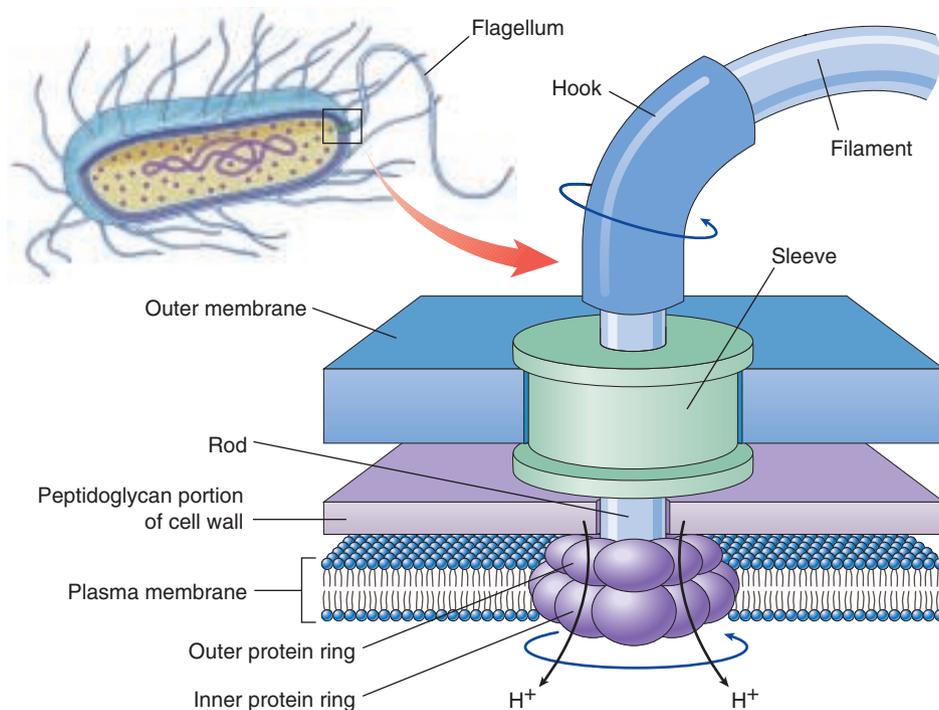


FIGURE 34.6

The flagellar motor of a gram-negative bacterium. A protein filament, composed of the protein flagellin, is attached to a protein shaft that passes through a sleeve in the outer membrane and through a hole in the peptidoglycan layer to rings of protein anchored in the cell wall and plasma membrane, like rings of ballbearings. The shaft rotates when the inner protein ring attached to the shaft turns with respect to the outer ring fixed to the cell wall. The inner ring is an H^+ ion channel, a proton pump that uses the passage of protons into the cell to power the movement of the inner ring past the outer one.

The Cell Interior

The most fundamental characteristic of bacterial cells is their prokaryotic organization. Bacterial cells lack the extensive functional compartmentalization seen within eukaryotic cells.

Internal membranes. Many bacteria possess invaginated regions of the plasma membrane that function in respiration or photosynthesis (figure 34.7).

Nucleoid region. Bacteria lack nuclei and do not possess the complex chromosomes characteristic of eukaryotes. Instead, their genes are encoded within a single double-stranded ring of DNA that is crammed into one region of the cell known as the **nucleoid region**. Many bacterial cells also possess small, independently replicating circles of DNA called plasmids. Plasmids contain only a few genes, usually not essential for the cell's survival. They are best thought of as an excised portion of the bacterial chromosome.

Ribosomes. Bacterial ribosomes are smaller than those of eukaryotes and differ in protein and RNA content. Antibiotics such as tetracycline and chloramphenicol can tell the difference—they bind to bacterial ribosomes and block protein synthesis, but do not bind to eukaryotic ribosomes.

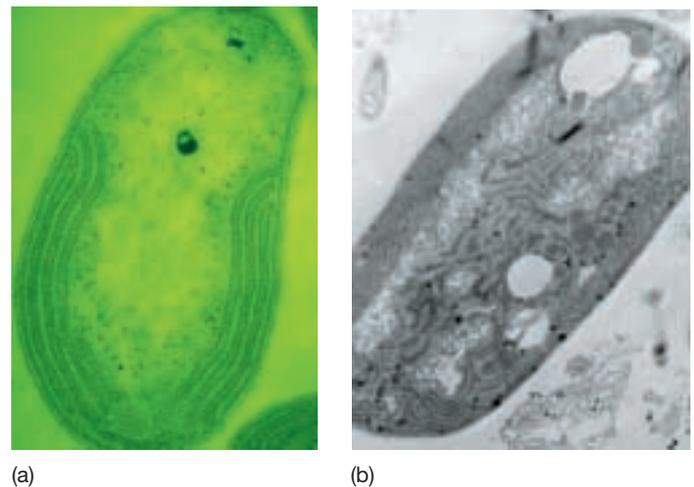


FIGURE 34.7

Bacterial cells often have complex internal membranes. This aerobic bacterium (*a*) exhibits extensive respiratory membranes within its cytoplasm not unlike those seen in mitochondria. This cyanobacterium (*b*) has thylakoid-like membranes that provide a site for photosynthesis.

The interior of a bacterial cell may possess internal membranes and a nucleoid region.

34.3 Bacteria exhibit considerable diversity in both structure and metabolism.

Bacterial Diversity

Bacteria are not easily classified according to their forms, and only recently has enough been learned about their biochemical and metabolic characteristics to develop a satisfactory overall classification comparable to that used for other organisms. Early systems for classifying bacteria relied on differential stains such as the Gram stain. Key bacterial characteristics used in classifying bacteria were:

1. Photosynthetic or nonphotosynthetic
2. Motile or nonmotile
3. Unicellular or multicellular
4. Formation of spores or dividing by transverse binary fission

With the development of genetic and molecular approaches, bacterial classifications can at last reflect true evolutionary relatedness. Molecular approaches include: (1) the analysis of the amino acid sequences of key proteins; (2) the analysis of nucleic acid base sequences by establishing the percent of guanine (G) and cytosine (C); (3) nucleic acid hybridization, which is essentially the mixing of single-stranded DNA from two species and determining the amount of base-pairing (closely related species will have more bases pairing); and (4) nucleic acid sequencing especially looking at ribosomal RNA. Lynn Margulis and Karlene Schwartz proposed a useful classification system that divides bacteria into 16 phyla, according to their most significant features. Table 34.1 outlines some of the major features of the phyla we describe.

Kinds of Bacteria

Although they lack the structural complexity of eukaryotes, bacteria have diverse internal chemistries, metabolisms and unique functions. Bacteria have adapted to many kinds of environments, including some you might consider harsh. They have successfully invaded very salty waters, very acidic or alkaline environments, and very hot or cold areas. They are found in hot springs where the temperatures exceed 78°C (172°F) and have been recovered living beneath 435 meters of ice in Antarctica!

Much of what we know of bacteria we have learned from studies in the laboratory. It is important to understand the limits this has placed on our knowledge: we have only been able to study those bacteria that can be cultured in laboratories. Field studies suggest that these represent but a small fraction of the kinds of bacteria that occur in soil, most of which cannot be cultured with existing tech-

niques. We clearly have only scraped the surface of bacterial diversity.

As we learned in chapter 32, bacteria split into two lines early in the history of life, so different in structure and metabolism that they are as different from each other as either is from eukaryotes. The differences are so fundamental that biologists assign the two groups of bacteria to separate domains. One domain, the Archaea, consists of the archaeobacteria (“ancient bacteria”—although they are actually not as ancient as the other bacterial domain). It was once thought that survivors of this group were confined to extreme environments that may resemble habitats on the early earth. However, the use of genetic screening has revealed that these “ancient” bacteria live in nonextreme environments as well. The other more ancient domain, the Bacteria, consists of the eubacteria (“true bacteria”). It includes nearly all of the named species of bacteria.

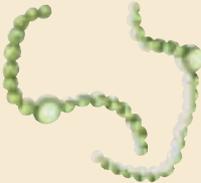
Comparing Archaeobacteria and Eubacteria

Archaeobacteria and eubacteria are similar in that they both have a prokaryotic cellular but they vary considerably at the biochemical and molecular level. There are four key areas in which they differ:

1. **Cell wall.** Both kinds of bacteria typically have cell walls covering the plasma membrane that strengthen the cell. The cell walls of eubacteria are constructed of carbohydrate-protein complexes called peptidoglycan, which link together to create a strong mesh that gives the eubacterial cell wall great strength. The cell walls of archaeobacteria lack peptidoglycan.
2. **Plasma membranes.** All bacteria have plasma membranes with a lipid-bilayer architecture (as described in chapter 6). The plasma membranes of eubacteria and archaeobacteria, however, are made of very different kinds of lipids.
3. **Gene translation machinery.** Eubacteria possess ribosomal proteins and an RNA polymerase that are distinctly different from those of eukaryotes. However, the ribosomal proteins and RNA of archaeobacteria are very similar to those of eukaryotes.
4. **Gene architecture.** The genes of eubacteria are not interrupted by introns, while at least some of the genes of archaeobacteria do possess introns.

While superficially similar, bacteria differ from one another in a wide variety of characteristics.

Table 34.1 Bacteria

Major Group	Typical Examples		Key Characteristics
Archaeobacteria	Methanogens, thermophiles, halophiles		ARCHAEBACTERIA Bacteria that are not members of the kingdom Eubacteria. Mostly anaerobic with unusual cell walls. Some produce methane. Others reduce sulfur.
Actinomycetes	<i>Streptomyces</i> , <i>Actinomyces</i>		EUBACTERIA Gram-positive bacteria. Form branching filaments and produce spores; often mistaken for fungi. Produce many commonly used antibiotics, including streptomycin and tetracycline. One of the most common types of soil bacteria; also common in dental plaque.
Chemoautotrophs	Sulfur bacteria, <i>Nitrobacter</i> , <i>Nitrosomonas</i>		Bacteria able to obtain their energy from inorganic chemicals. Most extract chemical energy from reduced gases such as H ₂ S (hydrogen sulfide), NH ₃ (ammonia), and CH ₄ (methane). Play a key role in the nitrogen cycle.
Cyanobacteria	<i>Anabaena</i> , <i>Nostoc</i>		A form of photosynthetic bacteria common in both marine and freshwater environments. Deeply pigmented; often responsible for “blooms” in polluted waters.
Enterobacteria	<i>Escherichia coli</i> , <i>Salmonella</i> , <i>Vibrio</i>		Gram-negative, rod-shaped bacteria. Do not form spores; usually aerobic heterotrophs; cause many important diseases, including bubonic plague and cholera.
Gliding and budding bacteria	Myxobacteria, <i>Cbondromyces</i>		Gram-negative bacteria. Exhibit gliding motility by secreting slimy polysaccharides over which masses of cells glide; some groups form upright multicellular structures carrying spores called fruiting bodies.
Pseudomonads	<i>Pseudomonas</i>		Gram-negative heterotrophic rods with polar flagella. Very common form of soil bacteria; also contain many important plant pathogens.
Rickettsias and chlamydias	<i>Rickettsia</i> , <i>Chlamydia</i>		Small, gram-negative intracellular parasites. <i>Rickettsia</i> life cycle involves both mammals and arthropods such as fleas and ticks; <i>Rickettsia</i> are responsible for many fatal human diseases, including typhus (<i>Rickettsia prowazekii</i>) and Rocky Mountain spotted fever. Chlamydial infections are one of the most common sexually transmitted diseases.
Spirochaetes	<i>Treponema</i>		Long, coil-shaped cells. Common in aquatic environments; a parasitic form is responsible for the disease syphilis.

Bacterial Variation

Bacteria reproduce rapidly, allowing genetic variations to spread quickly through a population. Two processes create variation among bacteria: mutation and genetic recombination.

Mutation

Mutations can arise spontaneously in bacteria as errors in DNA replication occur. Certain factors tend to increase the likelihood of errors occurring such as radiation, ultraviolet light, and various chemicals. In a typical bacterium such as *Escherichia coli* there are about 5000 genes. It is highly probable that one mutation will occur by chance in one out of every million copies of a gene. With 5000 genes in a bacterium, the laws of probability predict that 1 out of every 200 bacteria will have a mutation (figure 34.8). A spoonful of soil typically contains over a billion bacteria and therefore should contain something on the order of 5 million mutant individuals!

With adequate food and nutrients, a population of *E. coli* can double in under 20 minutes. Because bacteria multiply so rapidly, mutations can spread rapidly in a population and can change the characteristics of that population.

The ability of bacteria to change rapidly in response to new challenges often has adverse effects on humans. Recently a number of strains of *Staphylococcus aureus* associated with serious infections in hospitalized patients have appeared, some of them with alarming frequency. Unfortunately, these strains have acquired resistance to penicillin and a wide variety of other antibiotics, so that infections caused by them are very difficult to treat. *Staphylococcus* infections provide an excellent example of the way in which mutation and intensive selection can bring about rapid change in bacterial populations. Such changes have serious medical implications when, as in the case of *Staphylococcus*, strains of bacteria emerge that are resistant to a variety of antibiotics.

Recently, concern has arisen over the prevalence of antibacterial soaps in the marketplace. They are marketed as a means of protecting your family from harmful bacteria; however, it is likely that their routine use will favor bacteria that have mutations making them immune to the antibiotics contained in them. Ultimately, extensive use of antibacterial soaps could have an adverse effect on our ability to treat common bacterial infections.

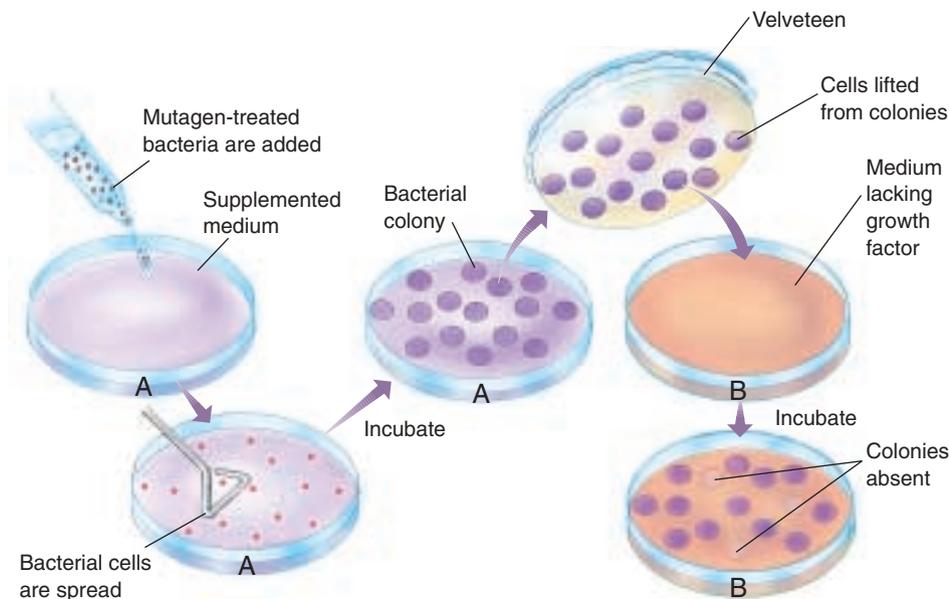


FIGURE 34.8

A mutant hunt in bacteria. Mutations in bacteria can be detected by a technique called replica plating, which allows the genetic characteristics of the colonies to be investigated without destroying them. The bacterial colonies, growing on a semisolid agar medium, are transferred from A to B using a sterile velveteen disc pressed on the plate. Plate A has a medium that includes special growth factors, while B has a medium that lacks some of these growth factors. Bacteria that are not mutated can produce their own growth factors and do not require them to be added to the medium. The colonies absent in B were unable to grow on the deficient medium and were thus mutant colonies; they were already present but undetected in A.

Genetic Recombination

Another source of genetic variation in populations of bacteria is recombination, discussed in detail in chapter 18. Bacterial recombination occurs by the transfer of genes from one cell to another by viruses, or through conjugation. The rapid transfer of newly produced, antibiotic-resistant genes by plasmids has been an important factor in the appearance of the resistant strains of *Staphylococcus aureus* discussed earlier. An even more important example in terms of human health involves the Enterobacteriaceae, the family of bacteria to which the common intestinal bacterium, *Escherichia coli*, belongs. In this family, there are many important pathogenic bacteria, including the organisms that cause dysentery, typhoid, and other major diseases. At times, some of the genetic material from these pathogenic species is exchanged with or transferred to *E. coli* by plasmids. Because of its abundance in the human digestive tract, *E. coli* poses a special threat if it acquires harmful traits.

Because of the short generation time of bacteria, mutation and recombination play an important role in generating genetic diversity.

Bacterial Metabolism

Bacteria have evolved many mechanisms to acquire the energy and nutrients they need for growth and reproduction. Many are **autotrophs**, organisms that obtain their carbon from inorganic CO₂. Autotrophs that obtain their energy from sunlight are called *photoautotrophs*, while those that harvest energy from inorganic chemicals are called *chemoautotrophs*. Other bacteria are **heterotrophs**, organisms that obtain at least some of their carbon from organic molecules like glucose. Heterotrophs that obtain their energy from sunlight are called *photoheterotrophs*, while those that harvest energy from organic molecules are called *chemoheterotrophs*.

Photoautotrophs. Many bacteria carry out photosynthesis, using the energy of sunlight to build organic molecules from carbon dioxide. The cyanobacteria use chlorophyll *a* as the key light-capturing pigment and use H₂O as an electron donor, releasing oxygen gas as a by-product. Other bacteria use bacteriochlorophyll as their pigment and H₂S as an electron donor, leaving elemental sulfur as the by-product.

Chemoautotrophs. Some bacteria obtain their energy by oxidizing inorganic substances. Nitrifiers, for example, oxidize ammonia or nitrite to obtain energy, producing the nitrate that is taken up by plants. This process is called nitrogen fixation and is essential in terrestrial ecosystems as plants can only absorb nitrogen in the form of nitrate. Other bacteria oxidize sulfur, hydrogen gas, and other inorganic molecules. On the dark ocean floor at depths of 2500 meters, entire ecosystems subsist on bacteria that oxidize hydrogen sulfide as it escapes from thermal vents.

Photoheterotrophs. The so-called purple nonsulfur bacteria use light as their source of energy but obtain carbon from organic molecules such as carbohydrates or alcohols that have been produced by other organisms.

Chemoheterotrophs. Most bacteria obtain both carbon atoms and energy from organic molecules. These include decomposers and most pathogens.

How Heterotrophs Infect Host Organisms

In the 1980s, researchers studying the disease-causing species of *Yersinia*, a group of gram-negative bacteria, found that they produced and secreted large amounts of proteins. Most proteins secreted by gram-negative bacteria have special signal sequences that allow them to pass through the bacterium's double membrane. This key signal sequence was missing the proteins being secreted by *Yersinia*. These proteins lacked a signal sequence that two known secretion mechanisms require for transport across the double membrane of gram-negative bacteria. The proteins must therefore have

been secreted by a third type of system, which researchers called the *type III system*.

As more bacteria species are studied, the genes coding for the type III system are turning up in other gram-negative animal pathogens, and even in more distantly related plant pathogens. The genes seem to be more closely related to one another than do the bacteria. Furthermore, the genes are similar to those that code for bacterial flagella.

The role of these proteins is still under investigation, but it seems that some of the proteins are used to transfer other virulence proteins into nearby eukaryotic cells. Given the similarity of the type III genes to the genes that code for flagella, some scientists hypothesize that the transfer proteins may form a flagellum-like structure that shoots virulence proteins into the host cells. Once in the eukaryotic cells, the virulence proteins may determine the host's response to the pathogens. In *Yersinia*, proteins secreted by the type III system are injected into macrophages; they disrupt signals that tell the macrophages to engulf bacteria. *Salmonella* and *Shigella* use their type III proteins to enter the cytoplasm of eukaryotic cells and thus are protected from the immune system of their host. The proteins secreted by *E. coli* alter the cytoskeleton of nearby intestinal eukaryotic cells, resulting in a bulge onto which the bacterial cells can tightly bind.

Currently, researchers are looking for a way to disarm the bacteria using knowledge of their internal machinery, possibly by causing the bacteria to release the virulence proteins before they are near eukaryotic cells. Others are studying the eukaryotic target proteins and the process by which they are affected.

Bacteria as Plant Pathogens

Many costly diseases of plants are associated with particular heterotrophic bacteria. Almost every kind of plant is susceptible to one or more kinds of bacterial disease. The symptoms of these plant diseases vary, but they are commonly manifested as spots of various sizes on the stems, leaves, flowers, or fruits. Other common and destructive diseases of plants, including blights, soft rots, and wilts, also are associated with bacteria. Fire blight, which destroys pears, apple trees, and related plants, is a well-known example of bacterial disease. Most bacteria that cause plant diseases are members of the group of rod-shaped bacteria known as pseudomonads (see figure 34.2a).

While bacteria obtain carbon and energy in many ways, most are chemoheterotrophs. Some heterotrophs have evolved sophisticated ways to infect their hosts.

34.4 Bacteria are responsible for many diseases but also make important contributions to ecosystems.

Human Bacterial Diseases

Bacteria cause many diseases in humans, including cholera, leprosy, tetanus, bacterial pneumonia, whooping cough, diphtheria and Lyme disease (table 34.2). Members of the genus *Streptococcus* (see figure 34.2b) are associated with scarlet fever, rheumatic fever, pneumonia, and other infections. Tuberculosis (TB), another bacterial disease, is still a leading cause of death in humans. Some of these diseases like TB are mostly spread through the air in water vapor. Other bacterial diseases are dispersed in food or water, including typhoid fever, paratyphoid fever, and bacillary dysentery. Typhus is spread among rodents and humans by insect vectors.

Tuberculosis

Tuberculosis has been one of the great killer diseases for thousands of years. Currently, about one-third of all people worldwide are infected with *Mycobacterium tuberculosis*, the tuberculosis bacterium (figure 34.9). Eight million new cases crop up each year, with about 3 million people dying from the disease annually (the World Health Organization predicts 4 million deaths a year by 2005). In fact, in 1997, TB was the leading cause of death from a *single infectious agent* worldwide. Since the mid-1980s, the United States has been experiencing a dramatic resurgence of tuberculosis. TB afflicts the respiratory system and is easily transmitted from person to person through the air. The causes of this current resurgence of TB include social factors such as poverty, crowding, homelessness, and incarceration (these factors have always promoted the spread of TB). The increasing prevalence of HIV infections is also a significant contributing factor. People with AIDS are much more likely to develop TB than people with healthy immune systems.

In addition to the increased numbers of cases—more than 25,000 nationally as of March 1995—there have been alarming outbreaks of multidrug-resistant strains of tuberculosis—strains resistant to the best available anti-TB medications. Multidrug-resistant TB is particularly concerning because it requires much more time to treat, is more expensive to treat, and may prove to be fatal.

The basic principles of TB treatment and control are to make sure all patients complete a full course of medication so that all of the bacteria causing the infection are killed and drug-resistant strains do not develop. Great efforts are being made to ensure that high-risk individuals who are infected but not yet sick receive preventative therapy, which is 90% effective in reducing the likelihood of developing active TB.

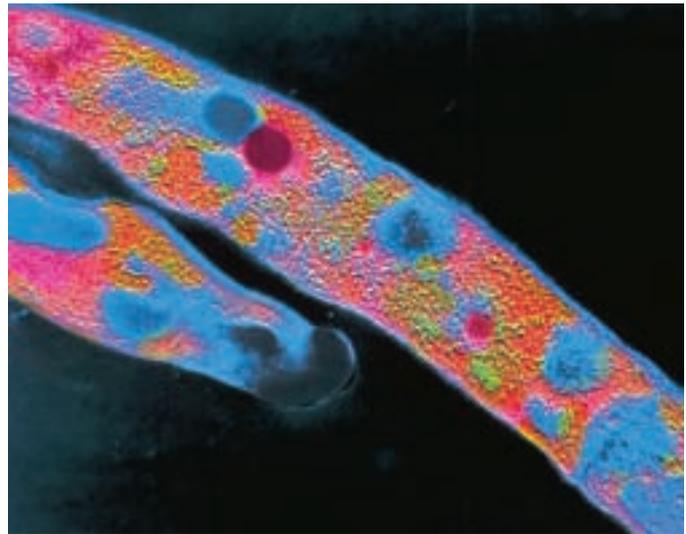


FIGURE 34.9
Mycobacterium tuberculosis. This color-enhanced image shows the rod-shaped bacterium responsible for tuberculosis in humans.

Dental Caries

One human disease we do not usually consider bacterial in origin arises in the film on our teeth. This film, or plaque, consists largely of bacterial cells surrounded by a polysaccharide matrix. Most of the bacteria in plaque are filaments of rod-shaped cells classified as various species of *Actinomyces*, which extend out perpendicular to the surface of the tooth. Many other bacterial species are also present in plaque. Tooth decay, or **dental caries**, is caused by the bacteria present in the plaque, which persists especially in places that are difficult to reach with a toothbrush. Diets that are high in sugars are especially harmful to teeth because lactic acid bacteria (especially *Streptococcus sanguis* and *S. mutans*) ferment the sugars to lactic acid, a substance that reduces the pH of the mouth, causing the local loss of calcium from the teeth. Frequent eating of sugary snacks or sucking on candy over a period of time keeps the pH level of the mouth low resulting in the steady degeneration of the tooth enamel. As the calcium is removed from the tooth, the remaining soft matrix of the tooth becomes vulnerable to attack by bacteria which begin to break down its proteins and tooth decay progresses rapidly. Fluoride makes the teeth more resistant to decay because it retards the loss of calcium. It was first realized that bacteria cause tooth decay when germ-free animals were raised. Their teeth do not decay even if they are fed sugary diets.

Table 34.2 Important Human Bacterial Diseases

Disease	Pathogen	Vector/Reservoir	Epidemiology
Anthrax	<i>Bacillus anthracis</i>	Animals, including processed skins	Bacterial infection that can be transmitted through contact or ingested. Rare except in sporadic outbreaks. May be fatal.
Botulism	<i>Clostridium botulinum</i>	Improperly prepared food	Contracted through ingestion or contact with wound. Produces acute toxic poison; can be fatal.
Chlamydia	<i>Chlamydia trachomatis</i>	Humans, STD	Urogenital infections with possible spread to eyes and respiratory tract. Occurs worldwide; increasingly common over past 20 years.
Cholera	<i>Vibrio cholerae</i>	Human feces, plankton	Causes severe diarrhea that can lead to death by dehydration; 50% peak mortality if the disease goes untreated. A major killer in times of crowding and poor sanitation; over 100,000 died in Rwanda in 1994 during a cholera outbreak.
Dental caries	<i>Streptococcus</i>	Humans	A dense collection of this bacteria on the surface of teeth leads to secretion of acids that destroy minerals in tooth enamel—sugar alone will not cause caries.
Diphtheria	<i>Corynebacterium diphtheriae</i>	Humans	Acute inflammation and lesions of mucous membranes. Spread through contact with infected individual. Vaccine available.
Gonorrhea	<i>Neisseria gonorrhoeae</i>	Humans only	STD, on the increase worldwide. Usually not fatal.
Hansen's disease (leprosy)	<i>Mycobacterium leprae</i>	Humans, feral armadillos	Chronic infection of the skin; worldwide incidence about 10–12 million, especially in Southeast Asia. Spread through contact with infected individuals.
Lyme disease	<i>Borrelia burgdorferi</i>	Ticks, deer, small rodents	Spread through bite of infected tick. Lesion followed by malaise, fever, fatigue, pain, stiff neck, and headache.
Peptic ulcers	<i>Helicobacter pylori</i>	Humans	Originally thought to be caused by stress or diet, most peptic ulcers now appear to be caused by this bacterium; good news for ulcer sufferers as it can be treated with antibiotics.
Plague	<i>Yersinia pestis</i>	Fleas of wild rodents: rats and squirrels	Killed ¼ of the population of Europe in the 14th century; endemic in wild rodent populations of the western U.S. today.
Pneumonia	<i>Streptococcus, Mycoplasma, Chlamydia</i>	Humans	Acute infection of the lungs, often fatal without treatment
Tuberculosis	<i>Mycobacterium tuberculosis</i>	Humans	An acute bacterial infection of the lungs, lymph, and meninges. Its incidence is on the rise, complicated by the development of new strains of the bacteria that are resistant to antibiotics.
Typhoid fever	<i>Salmonella typhi</i>	Humans	A systemic bacterial disease of worldwide incidence. Less than 500 cases a year are reported in the U.S. The disease is spread through contaminated water or foods (such as improperly washed fruits and vegetables). Vaccines are available for travelers.
Typhus	<i>Rickettsia typhi</i>	Lice, rat fleas, humans	Historically a major killer in times of crowding and poor sanitation; transmitted from human to human through the bite of infected lice and fleas. Typhus has a peak untreated mortality rate of 70%.

Sexually Transmitted Diseases

A number of bacteria cause sexually transmitted diseases (STDs). Three are particularly important (figure 34.10).

Gonorrhea. **Gonorrhea** is one of the most prevalent communicable diseases in North America. Caused by the bacterium *Neisseria gonorrhoeae*, gonorrhea can be transmitted through sexual intercourse or any other sexual contacts in which body fluids are exchanged, such as oral or anal intercourse. Gonorrhea can infect the throat, urethra, cervix, or rectum and can spread to the eyes and internal organs, causing conjunctivitis (a severe infection of the eyes) and arthritic meningitis (an infection of the joints). Left untreated in women, gonorrhea can cause pelvic inflammatory disease (PID), a condition in which the fallopian tubes become scarred and blocked. PID can eventually lead to sterility. The incidence of gonorrhea has been on the decline, but it remains a serious threat.

Syphilis. **Syphilis**, a very destructive STD, was once prevalent but is now less common due to the advent of blood-screening procedures and antibiotics. Syphilis is caused by a spirochete bacterium, *Treponema pallidum*, that is transmitted during sexual intercourse or through direct contact with an open syphilis sore. The bacterium can also be transmitted from a mother to her fetus, often causing damage to the heart, eyes, and nervous system of the baby.

Once inside the body, the disease progresses in four distinct stages. The first, or primary stage, is characterized by the appearance of a small, painless, often unnoticed sore called a chancre. The chancre resembles a blister and occurs at the location where the bacterium entered the body about three weeks following exposure. This stage of the disease is highly infectious, and an infected person may unwittingly transmit the disease to others.

The second stage of syphilis is marked by a rash, a sore throat, and sores in the mouth. The bacteria can be transmitted at this stage through kissing or contact with an open sore.

The third stage of syphilis is symptomless. This stage may last for several years, and at this point, the person is no longer infectious but the bacteria are still present in the body, attacking the internal organs. The final stage of syphilis is the most debilitating, however, as the damage done by the bacteria in the third stage becomes evident. Sufferers at this stage of syphilis experience heart disease, mental deficiency, and nerve damage, which may include a loss of motor functions or blindness.

Chlamydia. Sometimes called the “silent STD,” chlamydia is caused by an unusual bacterium, *Chlamydia trachomatis*, that has both bacterial and viral characteristics. Like a bacterium, it is susceptible to antibiotics, and, like a virus, it depends on its host to replicate its genetic material; it is an obligate internal parasite. The bacterium is transmitted through vaginal, anal, or oral intercourse with an infected person.

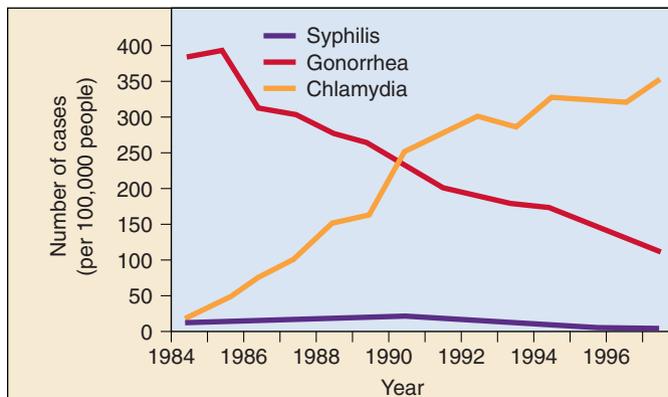


FIGURE 34.10
Trends in sexually transmitted diseases in the U.S.

Source: CDC, Atlanta, GA.

Chlamydia is called the “silent STD” because women usually experience no symptoms until after the infection has become established. In part because of this symptomless nature, the incidence of chlamydia has skyrocketed, increasing by more than sevenfold nationally since 1984. The effects of an established chlamydia infection on the female body are extremely serious. Chlamydia can cause pelvic inflammatory disease (PID), which can lead to sterility.

It has recently been established that infection of the reproductive tract by chlamydia can cause heart disease. *Chlamydia* produce a peptide similar to one produced by cardiac muscle. As the body’s immune system tries to fight off the infection, it recognizes this peptide. The similarity between the bacterial and cardiac peptides confuses the immune system and T cells attack cardiac muscle fibers, inadvertently causing inflammation of the heart and other problems.

Within the last few years, two types of tests for chlamydia have been developed that look for the presence of the bacteria in the discharge from men and women. The treatment for chlamydia is antibiotics, usually tetracycline (penicillin is not effective against chlamydia). Any woman who experiences the symptoms associated with this STD should be tested for the presence of the chlamydia bacterium; otherwise, her fertility may be at risk.

This discussion of STDs may give the impression that sexual activity is fraught with danger, and in a way, it is. It is folly not to take precautions to avoid STDs. The best way to do this is to know one’s sexual partners well enough to discuss the possible presence of an STD. Condom use can also prevent transmission of most of the diseases. Responsibility for protection lies with each individual.

Bacterial diseases have a major impact worldwide. Sexually transmitted diseases (STDs) are becoming increasingly widespread among Americans as sexual activity increases.

Importance of Bacteria

Bacteria were largely responsible for creating the properties of the atmosphere and the soil over billions of years. They are metabolically much more diverse than eukaryotes, which is why they are able to exist in such a wide range of habitats. The many autotrophic bacteria—either photosynthetic or chemoautotrophic—make major contributions to the carbon balance in terrestrial, freshwater, and marine habitats. Other heterotrophic bacteria play a key role in world ecology by breaking down organic compounds. One of the most important roles of bacteria in the global ecosystem relates to the fact that only a few genera of bacteria—and no other organisms—have the ability to fix atmospheric nitrogen and thus make it available for use by other organisms (see chapter 28).

Bacteria are very important in many industrial processes. Bacteria are used in the production of acetic acid and vinegar, various amino acids and enzymes, and especially in the fermentation of lactose into lactic acid, which coagulates milk proteins and is used in the production of almost all cheeses, yogurt, and similar products. In the production of bread and other foods, the addition of certain strains of bacteria can lead to the enrichment of the final product with respect to its mix of amino acids, a key factor in its nutritive value. Many products traditionally manufactured using yeasts, such as ethanol, can also

be made using bacteria. The comparative economics of these processes will determine which group of organisms is used in the future. Many of the most widely used antibiotics, including streptomycin, aureomycin, erythromycin, and chloromycetin, are derived from bacteria. Most antibiotics seem to be substances used by bacteria to compete with one another and fungi in nature, allowing one species to exclude others from a favored habitat. Bacteria can also play a part in removing environmental pollutants (figure 34.11)

Bacteria and Genetic Engineering

Applying genetic engineering methods to produce improved strains of bacteria for commercial use, as discussed in chapter 19, holds enormous promise for the future. Bacteria are under intense investigation, for example, as non-polluting insect control agents. *Bacillus thuringiensis* attacks insects in nature, and improved, highly specific strains of *B. thuringiensis* have greatly increased its usefulness as a biological control agent. Bacteria have also been extraordinarily useful in our attempts to understand genetics and molecular biology.

Bacteria play a major role in modern medicine and agriculture, and have profound ecological impact.



FIGURE 34.11

Using bacteria to clean up oil spills. Bacteria can often be used to remove environmental pollutants, such as petroleum hydrocarbons and chlorinated compounds. In areas contaminated by the *Exxon Valdez* oil spill (rocks on the *left*), oil-degrading bacteria produced dramatic results (rocks on the *right*).

**Summary****Questions****Media Resources****34.1 Bacteria are the smallest and most numerous organisms.**

- Bacteria are the oldest and simplest organisms, but they are metabolically much more diverse than all other life-forms combined.
- Bacteria differ from eukaryotes in many ways, the most important of which concern the degree of internal organization within the cell.

1. Structural differences among bacteria are not great. How are different species of bacteria recognized?
2. In what seven ways do prokaryotes differ substantially from eukaryotes?



- Enhancement Chapter: Extremophilic Bacteria, Introduction and Section 1

34.2 Bacterial cell structure is more complex than commonly supposed.

- Most bacteria have cell walls that consist of a network of polysaccharide molecules connected by polypeptide cross-links.
- A bacterial cell does not possess specialized compartments or a membrane-bounded nucleus, but it may exhibit a nucleoid region where the bacterial DNA is located.

3. What is the structure of the bacterial cell wall? How does the cell wall differ between gram-positive and gram-negative bacteria? In general, which type of bacteria is more resistant to the action of most antibiotics? Why?



- Characteristics of Bacteria



- Enhancement Chapter: Extremophilic Bacteria, Section 2

34.3 Bacteria exhibit considerable diversity in both structure and metabolism.

- The two bacterial kingdoms, Archaeobacteria and Eubacteria, are made up of prokaryotes, with about 5000 species named so far.
- The Archaeobacteria differ markedly from Eubacteria and from eukaryotes in their ribosomal sequences and in other respects.
- Mutation and genetic recombination are important sources of variability in bacteria.
- Many bacteria are autotrophic and make major contributions to the world carbon balance. Others are heterotrophic and play a key role in world ecology by breaking down organic compounds.
- Some heterotrophic bacteria cause major diseases in plants and animals.

4. How do the Archaeobacteria differ from the Eubacteria? What unique metabolism do they exhibit?
5. Why does mutation play such an important role in creating genetic diversity in bacteria?
6. How do heterotrophic bacteria that are successful pathogens overcome the many defenses the human body uses to ward off disease?



- Bacteria Diversity



- Scientists on Science: Marine Biotechnology
- Enhancement Chapter: Extremophilic Bacteria, Section 3

34.4 Bacteria are responsible for many diseases but also make important contributions to ecosystems.

- Human diseases caused by heterotrophic bacteria include many fatal diseases that have had major impacts on human history, including tuberculosis, cholera, plague, and typhus.
- Bacteria play vital roles in cycling nutrients within ecosystems. Certain bacteria are the only organisms able to fix atmospheric nitrogen into organic molecules, a process on which all life depends.

7. What are STDs? How are they transmitted? Which STDs are caused by viruses and which are caused by bacteria? Why is the cause of chlamydia unusual?



- Student Research: Improving Antibiotics
- On Science Article: Antibiotic Resistance