Chapter 27

Prokaryotes

Key Concepts

27.1 Structural, functional, and genetic adaptations contribute to prokaryotic success

27.2 A great diversity of nutritional and metabolic adaptations have evolved in prokaryotes

27.3 Molecular systematics is illuminating prokaryotic phylogeny

27.4 Prokaryotes play crucial roles in the biosphere

27.5 Prokaryotes have both harmful and beneficial impacts on humans

Framework

This chapter presents the morphology, phylogeny, and ecology of prokaryotes. These generally single-celled organisms greatly outnumber and outweigh all eukaryotes combined and flourish in all habitats, including ones that are too harsh for any other forms of life. The collective impact of these microscopic organisms is huge.

Chapter Review

27.1 Structural, functional, and genetic adaptations contribute to prokaryotic success

Prokaryotic cells are usually 1–5 μm in diameter. The three most common cell shapes are spheres (cocci), rods (bacilli), and spirals.

Cell-Surface Structures Prokaryotic cell walls maintain cell shape and protect the cell from bursting in a hypotonic surrounding. Most prokaryotes plasmolyze in a hypertonic environment. The cell walls of bacteria (but not archaea) contain **peptidoglycan,** a matrix composed of modified-sugar polymers cross-linked by short polypeptides.

The **Gram stain** is an important tool for identifying bacteria as **gram-positive** (bacteria with walls containing a thicker layer of peptidoglycan) or **gram-negative** (bacteria with more complex walls including an outer lipopolysaccharide membrane).

Many prokaryotes secrete a sticky **capsule** outside the cell wall that serves as protection from attack by a host's immune system and as glue for adhering to a substrate or other prokaryotes. Some bacteria may also attach by means of surface hairlike appendages called **fimbriae** and **pili.** Fimbriae are shorter and more numerous, and pili may be specialized to hold bacteria together during conjugation.

Motility Many bacteria are equipped with flagella, either scattered over the cell surface or concentrated at one or both ends of the cell. These flagella differ from eukaryotic flagella in their lack of a plasma membrane cover, structure, and function. ATP-driven pumps and the diffusion of H^+ back into the cell power the basal apparatus, embedded in the cell wall, which turns a hook attached to the protein filament of the flagellum.

Many motile bacteria exhibit **taxis,** an oriented movement in response to chemical, light, magnetic, or other stimuli.

Internal and Genomic Organization Extensive internal compartmentalization is not found in prokaryotic cells, although some may have membranes, usually infoldings of the plasma membrane that function in respiration or photosynthesis.

The circular DNA chromosome is concentrated in a **nucleoid region.** It contains one one-thousandth as much DNA as a eukaryotic genome and has relatively little protein associated with it. Smaller rings of DNA, called **plasmids,** may carry genes for antibiotic resistance, metabolism of unusual nutrients, or other functions. They replicate independently and may be transferred between bacteria during conjugation.

The ribosomes of prokaryotes are smaller than eukaryotic ribosomes and differ in their protein and RNA content. Some antibiotics work by binding to prokaryotic ribosomes and blocking protein synthesis.

Reproduction and Adaptation With generation times from 20 minutes to 3 hours, prokaryotes have a huge reproductive potential. The growth of colonies usually stops due to the exhaustion of nutrients or the toxic accumulation of wastes. Some microorganisms release antibiotics, which inhibit the growth of competitors.

Some bacteria produce **endospores,** which are tough-walled dormant cells formed in response to harsh conditions. Endospores are so durable that microbiologists must use autoclaves to sterilize laboratory equipment and media.

Due to short generation times, favorable mutations are rapidly propagated, facilitating adaptive evolution to environmental changes. Scientists have studied such evolution in colonies of *E. coli* since 1988, documenting mutations and changes in gene expression through more than 20,000 generations. Horizontal gene transfer contributes to this rapid evolution.

■ INTERACTIVE QUESTION 27.1

Fill in the table in the next column with a brief description of the characteristics of prokaryotic cells.

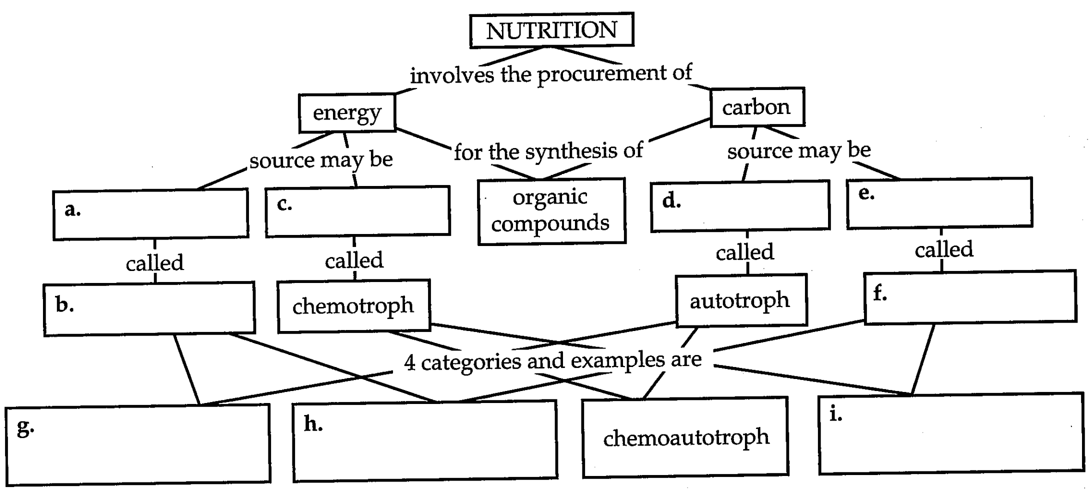
Property	Description
Cell shape	a.
Cell size	b.
Cell surface	c.
Motility	d.
Internal membranes	e.
Genome	f.
Reproduction and growth	g.

27.2 A great diversity of nutritional and metabolic adaptations have evolved in prokaryotes

Nutrition refers to how an organism obtains energy (photo- or chemotroph) and the carbon it uses for synthesizing organic compounds (auto- or heterotroph).

■ INTERACTIVE QUESTION 27.2

Complete the following concept map that summarizes the four categories of nutrition.



Thus, there are four major nutritional categories: (1) **photoautotrophs,** which use light energy and CO_2 to synthesize organic compounds; (2) **chemoautotrophs,** which obtain energy by oxidizing inorganic substances (such as H_2S, NH_3, or Fe^{2+}) and need only CO_2 as a carbon source; (3) **photoheterotrophs,** which use light energy but must obtain carbon in organic form; and (4) **chemoheterotrophs,** which use organic molecules as both an energy and a carbon source.

Metabolic Relationships to Oxygen **Obligate aerobes** need oxygen for cellular respiration; **facultative anaerobes** can use oxygen but also can grow in anaerobic conditions using fermentation; **obligate anaerobes** are poisoned by oxygen. Some obligate anaerobes use **anaerobic respiration** to break down nutrients, with inorganic molecules other than oxygen serving as the final electron acceptor.

Nitrogen Metabolism Nitrogen is an essential component of proteins and nucleic acids. Prokaryotes are able to metabolize various nitrogenous compounds. Some cyanobacteria and a few other prokaryotes obtain nitrogen through **nitrogen fixation,** converting atmospheric N_2 to ammonium.

Metabolic Cooperation The cyanobacterium *Anabaena* forms filaments in which most cells carry out photosynthesis, while a few cells called *heterocysts* perform nitrogen fixation. Members of the colony share nutrients through intercellular connections. **Biofilms** are surface-coating colonies characterized by intercellular signaling, proteins that adhere cells to each other and to the substrate, and channels in the colony for movement of nutrients and wastes.

27.3 Molecular systematics is illuminating prokaryotic phylogeny

While shape, staining characteristics, nutritional mode, and motility have been helpful characters for clinically identifying bacteria, they have not provided a phylogenetic classification.

Molecular Systematics Molecular comparisons of base sequences of SSU-rRNA indicate that domains Bacteria and Archaea diverged early in the history of life. A tentative phylogeny of taxa has been developed using molecular systematics. Continuing analysis of prokaryotic genomes shows that the genetic diversity of prokaryotes is huge and that horizontal gene transfer has been and continues to be significant in the evolution of prokaryotes.

Bacteria Bacteria show great diversity in their modes of nutrition and metabolism. Five major groups are described in the text.

Proteobacteria is a nutritionally diverse group of aerobic and anaerobic gram-negative bacteria. Its five subgroups are **Alpha Proteobacteria,** many of which are mutual symbionts or parasites of eukaryotes such as *Rhizobium* and *Agrobacterium;* **Beta Proteobacteria,** which include the important soil bacteria *Nitrosomonas;* **Gamma Proteobacteria,** which include photosynthetic sulfur bacteria and some serious pathogens and enterics (intestinal inhabitants such as *E. coli*); **Delta Proteobacteria,** including the colony-forming myxobacteria and the predacious bdellovibrio; and **Epsilon Proteobacteria,** the mostly pathogenic group that includes the stomach ulcer–causing *Helicobacter pylori.*

Chlamydias are obligate intracellular animal parasites. One of these gram-negative species is the most common cause of blindness and nongonococcal urethritis, a sexually transmitted disease.

Spirochetes are helical heterotrophs that move in a corkscrew fashion. Spirochetes cause syphilis and Lyme disease.

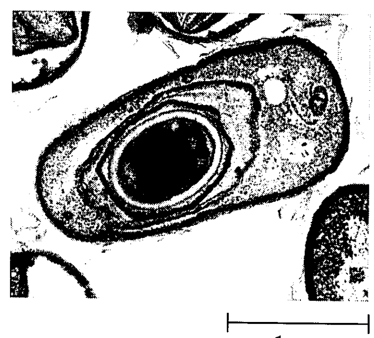
The **gram-positive bacteria** are a diverse group. The subgroup actinomycetes, colonial bacteria once mistaken for fungi, includes the species that cause tuberculosis and leprosy. Most actinomycetes are soil bacteria, some of which are cultured to produce antibiotics. There are diverse solitary species of gram-positive bacteria, including those responsible for anthrax and botulism, and the species of *Staphylococcus* and *Streptococcus.* Mycoplasmas, the smallest of all cells, are the only bacteria that lack cell walls.

The **cyanobacteria** have plantlike, oxygenic photosynthesis and are important producers in freshwater and marine ecosystems. Some filamentous cyanobacteria have cells specialized for nitrogen fixation.

■ INTERACTIVE QUESTION 27.3

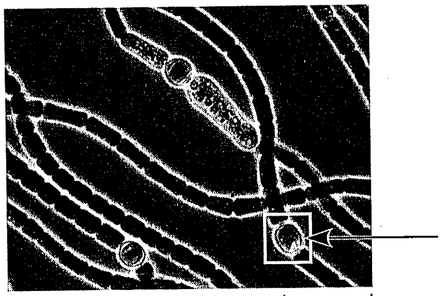
a. Identify the large structure inside this *Bacillus anthracis* cell. What is its significance?

Bacillus anthracis



b. Identify the major bacterial group to which this filamentous, photosynthetic species belongs. What is the function of the spherical cell indicated by the arrow?

Anabaena



5 µm

Archaea Archaea have some characteristics in common with bacteria, some with eukaryotes, and some unique characteristics. Many archaea are **extremophiles,** species that live in extreme habitats.

Extreme thermophiles may be found in hot sulfur springs and near deep-sea hydrothermal vents. The **extreme halophiles** (salt-lovers) live in extremely saline waters. **Methanogens** have a unique energy metabolism in which CO_2 is used to oxidize H_2, producing the waste product methane (CH_4). These strict anaerobes often live in swamps and marshes, are important decomposers in sewage treatment, and are gut inhabitants that contribute to the nutrition of cattle and other herbivores.

The methanogens and halophiles are placed into a clade called Euryarchaeota. Most thermophiles fit into the Crenarchaeota. Not all archaea are extremeophiles; numerous archaea have been found in more moderate habitats through genetic prospecting.

Prokaryote phylogeny continues to change as new groups are discovered. Examples include the oldest lineage, Korarchaeota, and the tiny Nanoarchaeota.

■ **INTERACTIVE QUESTION 27.4**

What is genetic prospecting? Why does it contribute to prokaryotic phylogeny?

27.4 Prokaryotes play crucial roles in the biosphere

Chemical Recycling Prokaryotes are indispensable in recycling chemical elements. As **decomposers,** they return carbon, nitrogen, and other elements to the environment for assimilation into new living forms.

Symbiotic Relationships **Symbiosis** is an ecological relationship involving direct contact between organisms of different species. If one organism is much larger than the other, it is called the **host** and the smaller is known as the **symbiont.** In **mutualism,** both symbiotic organisms benefit. Many of the 500–1,000 species of bacteria living in the human intestines are mutualists, digesting food and synthesizing important nutrients. In **commensalism,** one organism benefits while the other is neither harmed nor helped. In **parasitism,** a **parasite** benefits at the expense of the host.

■ **INTERACTIVE QUESTION 27.5**

Explain how cyanobacteria play an important role in chemical recycling.

27.5 Prokaryotes have both harmful and beneficial impacts of humans

Pathogenic Prokaryotes About one-half of all human diseases are caused by pathogenic prokaryotes. Pathogens most commonly cause disease by producing toxins. **Exotoxins,** are proteins secreted by prokaryotes that cause such diseases as botulism and cholera. **Endotoxins,** which are lipopolysaccharides released from the outer membrane of gram-negative bacteria that have died, cause such diseases as typhoid fever and *Salmonella* food poisoning.

Improved sanitation and the development of antibiotics have decreased the incidence of bacterial disease in developed countries. The evolution of antibiotic-resistant strains of pathogenic bacteria, however, poses a serious health threat. Horizontal gene transfer also spreads genes connected with virulence, as in the emergence of the dangerous *E. coli* strain, O157:H7. Pathogenic prokaryotes such as *Bacillus anthracis, C. botulinum,* and *Yersinia pestis,* which causes plague, are potential bioterrorism weapons.

Prokaryotes in Research and Technology **Bioremediation** is the use of organisms to remove environmental pollutants. Prokaryotes are used to treat sewage and clean up oil spills. They are used in the mining industry to recover metals from ores. Prokaryotes have been engineered to make vitamins, antibiotics, and other products.

Word Roots

-gen = produce (*methanogen:* microorganisms that obtain energy by using carbon dioxide to oxidize hydrogen, producing methane as a waste product)

-oid = like, form (*nucleoid:* a dense region of DNA in a prokaryotic cell)

an- = without, not; **aero-** = the air (*anaerobic:* lacking oxygen; referring to an organism, environment, or cellular process that lacks oxygen and may be poisoned by it)

anti- = against; **-biot** = life (*antibiotic:* a chemical that kills bacteria or inhibits their growth)

bi- = two (*binary fission:* the type of cell division by which prokaryotes reproduce; each dividing daughter cell receives a copy of the single parental chromosome)

chemo- = chemical; **hetero-** = different (*chemoheterotroph:* an organism that must consume organic molecules for both energy and carbon)

endo- = inner, within (*endotoxin:* a component of the outer membranes of certain gram-negative bacteria responsible for generalized symptoms of fever and ache)

exo- = outside (*exotoxin:* a toxic protein secreted by a bacterial cell that produces specific symptoms even in the absence of the bacterium)

halo- = salt; **-philos** = loving (*halophile:* microorganisms that live in unusually highly saline environments such as the Great Salt Lake or the Dead Sea)

mutu- = reciprocal (*mutualism:* a symbiotic relationship in which both the host and the symbiont benefit)

photo- = light; **auto-** = self; **-troph** = food, nourish (*photoautotroph:* an organism that harnesses light energy to drive the synthesis of organic compounds from carbon dioxide)

sym- = with, together; **-bios** = life (*symbiosis:* an ecological relationship between organisms of two different species that live together in direct contact)

thermo- = temperature (*thermophiles:* microorganisms that thrive in hot environments, often 60–80°C)

Structure Your Knowledge

1. What is the rationale for separating the archaea, the bacteria, and all the eukaryotes into three domains?
2. Describe four positive ways in which prokaryotes have an impact on our lives and on the world around us.

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Which of the following is *not* true of plasmids?
   a. They replicate independently of the main chromosome.
   b. They may carry genes for antibiotic resistance.
   c. They are essential for the existence of bacterial cells.
   d. They may be transferred between bacteria during conjugation.
   e. They may carry genes for special metabolic pathways.

2. Gram-positive bacteria
   a. have peptidoglycan in their cell walls, whereas gram-negative bacteria do not.
   b. have an outer membrane around their cell walls.
   c. have lipopolysaccharides in their cell walls and thus may be more pathogenic than gram-negative bacteria.
   d. are members of domain Archaea.
   e. have simpler, thick peptidoglycan cell walls.

3. Many prokaryotes secrete a sticky capsule outside the cell wall that
   a. allows them to glide along a slime thread.
   b. serves as protection from host defenses and glue for adherence.
   c. reacts with the Gram stain.
   d. is used for attaching cells during conjugation.
   e. is composed of peptidoglycan, polymers of modified sugars cross-linked by short polypeptides.

4. Chemoautotrophs
   a. are photosynthetic.
   b. use organic molecules for an energy and carbon source.
   c. oxidize inorganic substances for energy and use CO_2 as a carbon source.
   d. use light to generate ATP but need organic molecules for a carbon source.
   e. use light energy to extract electrons from H_2S.

5. A major source of genetic variation in prokaryotes is
   a. horizontal gene transfer.
   b. mutation.
   c. conjugation.
   d. plasmid exchange.
   e. all of the above.

6. A relationship in which one organism benefits and the host is neither harmed nor helped is called
   a. symbiosis.
   b. metabolic cooperation.
   c. mutualism.
   d. commensalism.
   e. parasitism.

7. Facultative anaerobes
   a. can survive with or without oxygen.
   b. are poisoned by oxygen.
   c. are anaerobic chemoautotrophs.
   d. are able to fix atmospheric nitrogen to make NH_4^+.
   e. include the methanogens that reduce CO_2 to CH_4.

8. Some prokaryotes have specialized membranes that
   a. contain ribosomes and function in protein synthesis.
   b. arose from endosymbiosis of smaller prokaryotes, creating mitochondria and chloroplasts.
   c. form from infoldings of the plasma membrane and may function in cellular respiration or photosynthesis.
   d. are produced by the endoplasmic reticulum, but differ in composition from eukaryotic membranes.
   e. enclose the nucleoid region and separate plasmids from the single prokaryotic chromosome.

9. Organizing prokaryotes into major clades within the domains Archaea and Bacteria has been based on
   a. fossil records of prokaryotes that have been recently discovered.
   b. molecular comparisons.
   c. the Gram stain and colony characteristics when grown on solid media.
   d. shape and motility.
   e. nutritional modes and ecology.

10. Some cyanobacteria are capable of nitrogen fixation. This process
    a. oxidizes nitrogen-containing compounds to produce ATP.
    b. allows these bacteria to live in anaerobic environments.
    c. removes soil nitrogen and returns N_2 gas to the atmosphere.
    d. converts N_2 to ammonium, making nitrogen available to plants for incorporation into proteins and nucleic acids.
    e. is an essential part of the nitrogen cycle that rescues nitrogen trapped in mineral deposits and makes it available to organisms for their nitrogen metabolism.

11. Archaea
    a. are believed to be more closely related to eukaryotes than to bacteria.
    b. have cell walls that lack peptidoglycan.
    c. are often found in harsh habitats, reminiscent of the environment of early Earth.
    d. include the methanogens, extreme halophiles, and extreme thermophiles, as well as groups found in more moderate habitats.
    e. are all of the above.

12. Which of the following groups is matched with an incorrect description?
    a. Proteobacteria—diverse gram-negative bacteria including pathogens such as *Salmonella* and *Helicobacter pylori*, as well as beneficial species such as *Rhizobium*
    b. Chlamydias—intracellular parasites, including a species that causes blindness and nongonococcal urethritis
    c. Spirochetes—helical heterotrophs, including pathogens causing syphilis and Lyme disease
    d. Gram-positive bacteria—diverse group that includes actinomycetes, mycoplasmas, and pathogens that cause anthrax, botulism, and tuberculosis
    e. Cyanobacteria—photosynthetic filamentous colonies; some solitary species use the pigment bacteriorhodopsin and inhabit saline waters

FILL IN THE BLANKS

_______________ 1. the name for spherical prokaryotes

_______________ 2. region in which the prokaryotic chromosome is found

_______________ 3. common laboratory technique that identifies two groups of bacteria

_______________ 4. surface appendages of prokaryotes used for adherence to substrate

_______________ 5. an oriented movement in response to light or chemical stimuli

_______________ 6. resistant cell that can survive harsh conditions

_______________ 7. surface-coating cooperative colonies of prokaryotes

_______________ 8. proteins that are secreted by pathogens and are potent poisons

_______________ 9. use of organisms to remove environmental pollutants

_______________ 10. type of respiration that uses molecules other than O_2 as final electron acceptor