

Archaea, Bacteria, and Viruses



PROKARYOTES, VIRUSES, AND THE STUDY OF PLANTS

PROKARYOTIC CELL STRUCTURE

- Many Prokaryotic Cells Have Simple Structures*
- Some Prokaryotic Cells Have Modified Extracellular and Intracellular Structures*
- Some Bacterial Cells Form Endospores*

LIFESTYLES OF SELECTED GROUPS OF PROKARYOTES

- Archaea Inhabit Harsh Environments*
- Bacteria Include Many diverse Species*
- Simple Crosses Yield Predictable Results*

PROKARYOTES THAT FORM SYMBIOTIC RELATIONSHIPS WITH PLANTS

- Rhizobium Forms a Mutualistic Association with Legumes*
- Bacteria Can Be Plant Parasites*

VIRUSES

- Viruses Are Infectious Genes*
- Virus Infections Stunt Plant Growth*

SUMMARY

BIOTECHNOLOGY: *Bacteria as Biocontrol Agents*

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Microbes and Global Warming*

BIOTECHNOLOGY: *Plant Breeding and the Green Revolution*

KEY CONCEPTS

1. All prokaryotic organisms can be divided into two domains: the Archaea and the Bacteria. Members of the Archaea dominate harsh environments such as hot springs, salt flats, and anaerobic mud flats, and they also are found in more equable habitats. Members of the Bacteria show great variation, to some degree in structure, but especially in metabolic capabilities, habitat, and life histories.
2. The cellular organization of the prokaryotes (Archaea and Bacteria) seems much less complex than that of eukaryotic cells. However, some prokaryotic cells develop complex, specialized structures such as flagella, thylakoid membranes, and spores.
3. Prokaryotes obtain energy for movement and metabolism and carbon for growth and reproduction from various sources. Chemotrophs get energy by oxidizing organic or inorganic compounds; phototrophs capture the energy of light (photosynthesis). Autotrophs obtain carbon from an inorganic source, typically by reducing CO₂; heterotrophs obtain carbon by metabolizing organic compounds.
4. Many bacteria have close, symbiotic associations with other organisms. Some associations are mutualistic: they benefit the bacterium and its host. The relationship between the nitrogen-fixing *Rhizobium* and legumes is one example. Some associations are parasitic: the bacterium harms the host. *Erwinia amylovora*, which causes fire blight in apples, is an example of a plant parasite.
5. Viruses are genes, wrapped in a coat of protein, that infect cells. They appropriate the biochemical machinery of the cells, using it to reproduce themselves and sometimes to kill the cells. Viral diseases of plants cause serious reductions in crop yield and quality.

19.1 PROKARYOTES, VIRUSES AND THE STUDY OF PLANTS

Prokaryotes is one term to describe all the organisms with cells that lack a nucleus. These organisms generally have a simpler cell structure than do plants, animals, or other **eukaryotes**. The terms *prokaryote* and *eukaryote* were introduced in the 1920s by Edouard Chatton, based on microscope observations. Eukaryotic cells had clear nuclei and other inclusions that were lacking in prokaryotic cells. (The words *eukaryote* and *nucleus* are related: *Karyon* is Greek, and *nucleus* is derived from the Latin *nuculeus*, both meaning "kernel.")

In the late 1970s, a microbiologist named Carl Woese proposed using the small subunit ribosomal RNA (rRNA) gene to create a universal tree of life. This gene is critical for a major cell function, protein synthesis, and it is therefore ubiquitous and constrained in its rate of evolution. The slow rate at which the gene evolves allows a comparison of even the most evolutionarily distant organisms.

Woese's tree had immediate and profound effects on our views of evolutionary history. The most important of Woese's findings was that the prokaryotes are not a

coherent group, as previously thought. Rather, they are composed of two separate groups, which he named the Eubacteria (*eu-* is derived from the Greek, meaning "true") and the Archaeobacteria (*archae-* is derived from the Greek, meaning "ancient"). Later, in recognition that this division was as basic as the division between prokaryotes and eukaryotes, biologists coined the grouping *domain*, and named the three domains **Archaea** (the Archaeobacteria), **Bacteria** (the Eubacteria), and **Eukarya** (the eukaryotes). Although Archaea and Bacteria differ in fundamental ways, in this textbook it is convenient to consider them together. The word bacteria with a lowercase *b* often is used as a common noun for all prokaryotes.

Most often, the prokaryotes are single-celled organisms, although many form colonies, and some form structures with a degree of morphological differentiation. As small and apparently simple as they are, they pervade the world and represent a large fraction of the earth's biomass. Although their structures are simple, their biochemical abilities often are complex and sometimes unique--that is, they possess enzymes and metabolic pathways not found in any eukaryotes. Some of these metabolic capabilities are absolutely essential for maintaining the physical and chemical characteristics of the earth in a state suitable for life. The group of prokaryotes is much too large a subject to be covered in any detail by a textbook on plants. Yet there are three important reasons why an individual who studies plants should also be familiar with prokaryotes:

1. Many of the biochemical compounds, enzymes, and metabolic pathways of plants also are found in prokaryotes. Photosynthesis, the uptake of mineral nutrients, and responses to environmental stresses (such as drought) occur in both prokaryotes and plants. The discoveries made in studying prokaryotes can be use to guide plant research.
2. The evolutionary ancestors of plants were prokaryotes. Not only did the eukaryotic cells probably evolve from one or more unknown prokaryotes, including an Archaea, but the large organelles in plant cells--the mitochondria and plastids--are probably related to two different types of Bacteria. Studying prokaryotes is necessary for understanding the origin of plants.
3. Plants form ecological associations with prokaryotes. Some of these associations are mutualistic symbioses (for instance, the nitrogen-fixing association between the bacterium *Rhizobium* and legumes). In some association, the prokaryote is a parasite on the plant. In either case, it is necessary to study the prokaryotes to understand how the plant responds to its environment.

Viruses are particles constructed of a nucleic acid genome (either RNA or DNA) and a protein coat. They are not prokaryotes. They are not even cells and cannot live independently. To reproduce, they must infect the cells of an organism, and they are parasites on the cells they infect. Viruses should be studied by plant biologists for many of the same reasons that prokaryotes should be studied. Many of the basic properties of genes and proteins can be investigated using viruses. The discoveries obtained by studying viruses can be used to guide plant research. Some viruses are plant parasites, and thus are important in the lives of many plants. The diseases that viruses cause, the

ways in which they are transmitted from plant to plant, and the methods plants used to combat viral diseases are all part of the life histories of plants.

19.2 PROKARYOTIC CELL STRUCTURE

Many Prokaryotic Cells Have Simple Structures

A prokaryotic cell appears in an electron micrograph to be simpler than a eukaryotic cell, because it lacks the internal membrane-enclosed organelles (compare Figs. 19.1 and 3.3). The prokaryotic cell is surrounded by a plasma membrane. This plasma membrane fulfills all the same roles that it does in plants (and sometimes more). It accumulates cell components (such as enzymes) in the cytoplasm; it excludes toxic compounds; it allows charge separation, which is necessary for energy generation; and it is sensitive to aspects of the environment, such as water potential or the presence of nutrients. Archaea and Bacteria differ in the chemical compositions of their plasma membranes. Bacterial plasma membrane lipids are similar to those of eukaryotes. Archaeal plant membrane lipids are unlike any others and are held together by stronger bonds, which is perhaps essential, given the severe environments in which many of them live.

Outside the plasma membrane, Archaea and Bacteria differ markedly. Bacterial cell surfaces fit into one of two categories, termed Gram-positive or Gram-negative, on the basis of a differential staining technique devised by the Dutch physician Gram (Fig. 19.2). **Gram-negative cells** have a thin cell wall that, like plant cell walls, functions to prevent cells from bursting in a hypotonic solution (a solution more dilute than the cytoplasm) and determines the

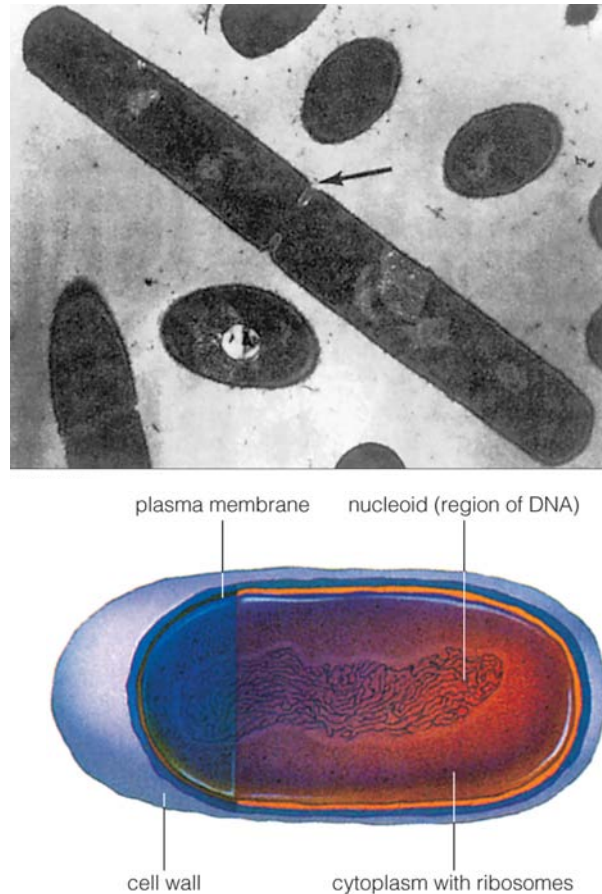


Figure 19.1. The prokaryotic cell. (a) A transmission electron micrograph of *Bacillus cereus* showing the light-colored nucleoid and darker cytoplasm. At the time the cell was prepared for microscopy, it had recently divided and a new cross-wall (*arrow*) was forming. (b) Organization of the major components of a prokaryotic cell.

shape of the cells. The various shapes are **cocci** (small, round cells), **bacilli** (rods), **vibrios** (bent or hooked rods), **spirilla** (helical forms), and stalked forms. Unlike plant cell walls, the Bacterial cell wall is composed of **peptidoglycan**, a combination of amino acids and sugars that surrounds the cell like a net. Outside of the cell wall is a second membrane composed of phospholipids, polysaccharide, and protein, termed the outer membrane or **lipopolysaccharide** layer. The area between the two membranes is called the **periplasmic space**, a compartment for certain cell functions that contains specific enzymes and other proteins, including those that sense the osmotic potential of the environment.

Gram-positive cells have a thick peptidoglycan cell wall. Although no Gram-positive cells have a second membrane, some have a waxy polysaccharide capsule that is analogous to an outer membrane. The capsule protects some Gram-positive human pathogens from being recognized by microbe-eating cells of the immune system, such as macrophages. One of the best-known families of antibiotics, which includes penicillin, acts by inhibiting the formation of the Bacterial cell wall and is particularly effective against Gram-positive cells. Bacteria treated with these antibiotics become osmotically sensitive and lyse in hypotonic solutions, including human body fluids.

Most Archaea have a paracrystalline surface layer (called an S layer), composed of protein or glycoprotein, that performs the same general functions as a Bacterial cell wall. Because the outer layer is protein, Archaeal cells often are sensitive to proteases (enzymes that degrade proteins) and surfactants. Alternatively, some Archaea have pseudo-peptidoglycan, which is similar to Bacterial peptidoglycan, or thick walls of polysaccharide. Archaea typically lack an outer membrane.

In the cytoplasm is a full set of genes and a complete apparatus for expressing them to make proteins. The genes are encoded in DNA, just as in eukaryotic cells. Typically, the

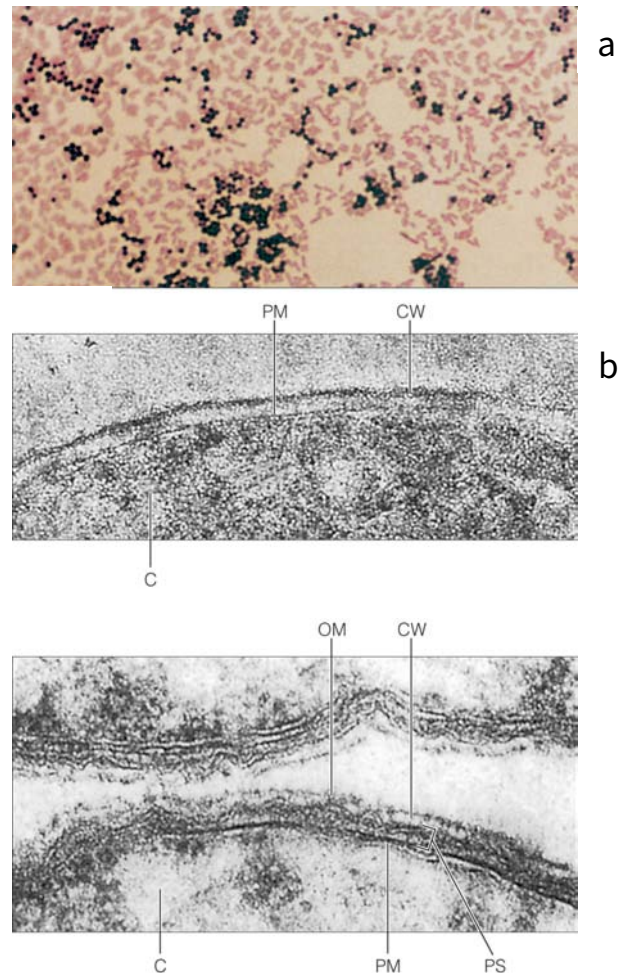


Figure 19.2. Some distinguishing features of Gram-positive and Gram-negative bacteria. (a) Light micrograph of stained Gram-positive cocci (purple spheres) and Gram-negative bacilli (pink rods). (b) Electron microscopic comparison of the plasma membrane and cell wall regions of Gram-positive (top) and Gram-negative (bottom) bacteria. C, cytoplasm; OM, outer membrane (lipopolysaccharide layer); PM, plasma membrane; PS-periplasmic space; CW, cell wall.

"housekeeping" genes (genes needed for the basic functions of life) are on a single circular chromosome. This chromosome may be very long (in circumference). In the best-studied bacterium, *Escherichia coli*, the chromosome is 1.4 mm in length and contains 4.6 million nucleotide pairs (Fig. 19.3), which is a large amount of DNA, considering that the *E. coli* cell is only about 1 μm in length and 0.5 μm in width. The chromosome is wound up in the cell and is localized in an area called the **nucleoid**. Unlike eukaryotes, the prokaryotic chromosome is not surrounded by a nuclear envelope, so there is no defined nucleus. It used to be thought that the Bacterial chromosome had no structure and was packed randomly into the cell. However, recent investigations have found that it is complexed with specific structural proteins that organize it into loops. The Archaeal chromosome is complexed with histone proteins, similar to the chromosomes of eukaryotes.

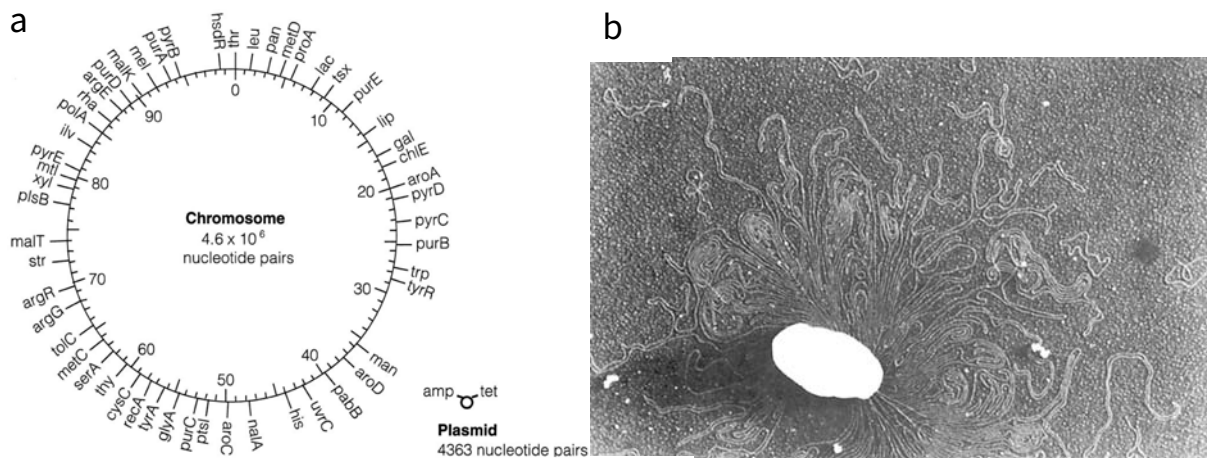
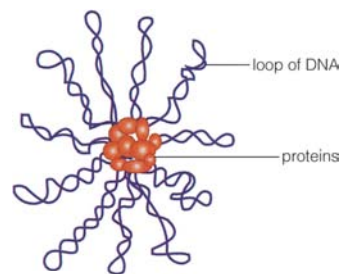


Figure 19.3. A prokaryotic chromosome. (a) This diagram of an *Escherichia coli* chromosome shows a fraction of the identified genes. The order of the genes was identified using F plasmids. The sequence of all 4.6×10^6 nucleotide pairs is known. There are 4,288 genes identified from the sequence. Next to the chromosome is a diagram of a plasmid, showing two genes that confer resistance to antibiotics. The plasmid is actually one-thousandth the size of the chromosome.



(b) An *E. coli* nucleoid spread out for electron microscopy, with diagram below.

Many prokaryotes have sets of accessory genes called **plasmids**, which are relatively small circles of DNA, about 2,000 to 200,000 nucleotide pairs in length. They often contain functionally related sets of genes. Some plasmids, for instance, have genes that confer a resistance to antibiotics. Some plasmids in parasitic bacteria have genes that make them pathogenic (disease-causing) in their hosts. The plasmids can be replicated (reproduced) independently of the chromosome. Sometimes they are replicated faster than the chromosome and the cell, so there are many copies in a cell. Sometimes, such as at higher temperatures, the plasmids are replicated more slowly, and daughter cells are formed that do not have a plasmid.

Some plasmids have genes for enzymes and structural proteins that transfer copies of the plasmid to Bacteria that do not have any. This is one method by which Bacteria acquire new genetic capabilities. Although most plasmids are transferred only among cells of one species, some can be transferred to many species of Bacteria. This is how it has been possible for resistance to antibiotics to spread so quickly to many pathogenic Bacteria in the past few years, a situation that threatens to neutralize many of our modern defenses against disease.

A special type of plasmid, the F plasmid, has the ability to incorporate itself into the main chromosome. The F plasmid contains genes for making a tube, called an F pilus, that connects its cell with one that lacks an F plasmid. An F pilus is a conduit for the transfer of plasmid or chromosomal DNA from a donor (the cell with the pilus) to a receiver cell (Fig. 19.4). When the F plasmid is part of the main chromosome and the chromosomal DNA is replicated, part of one copy of the chromosome can be transferred to the recipient cell through the F pilus. Once the new DNA is in the recipient cell, there is a possibility of an exchange of

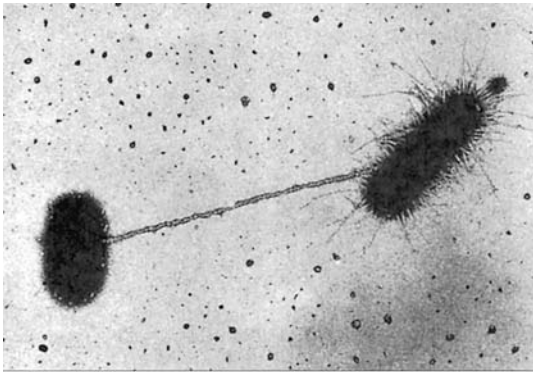


Figure 19.4. Conjugation between two *Escherichia coli* cells. The donor (F^+) cell is on the right; the recipient (F^-) cell is on the left. The long connecting arm is an F pilus. Note that the donor cell also has many smaller pili.

pieces of the new DNA with the recipient's original chromosome. The transfer, called **conjugation**, allows for a genetic recombination of chromosomal genes. Although it is entirely unlike meiosis, conjugation may play a similar role (promoting diversity) in the population genetics of prokaryotes.

The prokaryotic cell contains ribosomes with a general composition and structure similar to those of eukaryotes. The ribosomes have two subunits, each made of RNA and proteins, although prokaryotic ribosomes are smaller than eukaryotic ribosomes. In nucleotide sequence, the rRNAs of Archaea are more similar to the rRNAs of eukaryotes than are those of Bacteria, evidence that an Archaea was an ancestor of the original eukaryotes.

Prokaryotic cells reproduce by **binary fission**, meaning that the cell splits in two. Preceding this step, the DNA in the main chromosome replicates, so that there are two complete copies of the chromosome. It is thought that each copy of the chromosome may be attached to the plasma membrane and that the separation of the points of attachment (as the cell grows and the membrane enlarges) may pull the chromosome copies apart (Fig. 19.5). This process is analogous to the separation of chromosome in mitosis of eukaryotic cells, but it differs from mitosis because prokaryotes do not have microtubules, and thus they do not have a spindle apparatus for separating the chromosome copies. A new cross-wall (Fig. 19.1a) forms between the two chromosomes, so that each progeny cell

receives a copy. The other organelles, ribosomes, enzymes, and plasmids are probably divided randomly as the cross-wall forms. Although cell division in prokaryotes seems much simpler than it is in eukaryotes, this may be because of the small size of the cells. Only recently have researchers begun visualizing the intricate details of the division process.

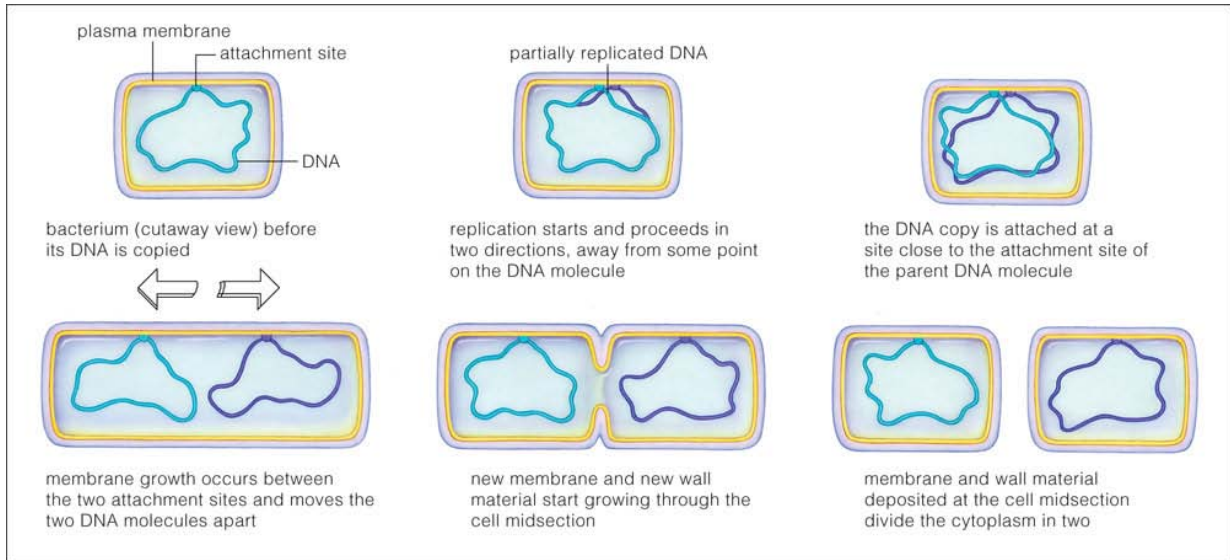


Figure 19.5. Bacterial reproduction by binary fission.

Notably lacking in the above description is any component of the eukaryotic endomembrane system: endoplasmic reticulum, Golgi apparatus, vesicles, or vacuole. Prokaryotes have no mitochondria or plastids and no known cytoskeleton (although genes related to the eukaryotic tubulin gene have recently been identified in both Archaea and Bacteria). It would be wrong, however, to think that there are no complex adaptations among the prokaryotes. The following sections describe some of the more common modifications to the basic prokaryotic cell structure.

Some Prokaryotic Cells Have Modified Extracellular and Intracellular Structures

Many Bacterial and some Archaeal cells swim using **flagella**, projections that propel the cell (Fig. 19.6). The prokaryotic flagellum is not related in any way to the eukaryotic flagellum. It is formed from many subunits of the protein flagellin, which line up to form a helical (corkscrew-shaped) filament. The filament rotates, propelled by a motor apparatus--the basal body--where it penetrates the plasma membrane. The rotation of the basal body is powered by a proton and electrical gradient produced across the plasma membrane. The rotating flagellum pulls the cell through the liquid medium. In certain Bacteria covered with many flagella, the motors can reverse direction. They generally do this when the cell senses an unsatisfactory change in the environment. Because the helical flagella are not as rigid under the reverse stress, they bend (flop), and the cell tumbles. After a short period, the motors reverse again, the flagella regain their original

conformation, and the cell starts swimming in a straight line. If once again the environment is unsatisfactory, the procedure is repeated, and this continues until the cell finds an improvement in its conditions (Fig. 19.7).

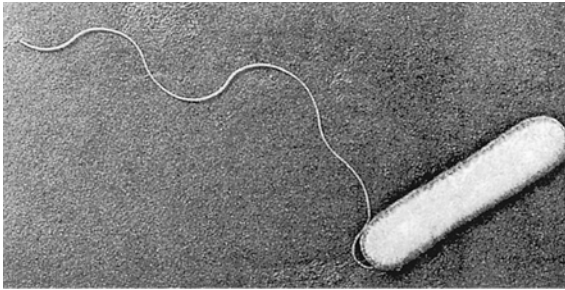


Figure 19.6. Bacterial flagella. (above) Bacterial cell with single flagellum. (below) Transmission electron micrograph of an isolated flagellum with interpretive diagram.

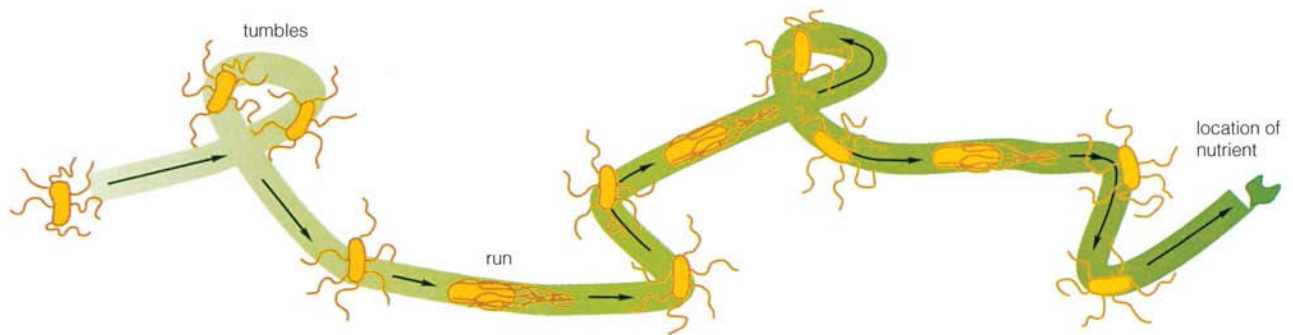
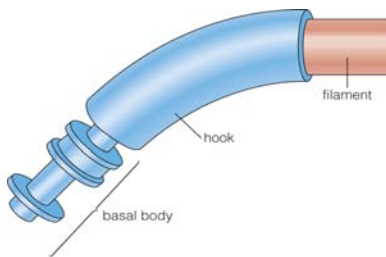


Figure 19.7. Bacteria control their flagella to seek nutrients and avoid stress or toxic compounds. With the flagella turn counterclockwise, the cell moves in a straight line (run); when the flagella turn clockwise, the cell tumbles. When conditions are getting better, the runs are longer.

Another extracellular organelle is the **pilus** (Latin, meaning "hair"), a thin, hollow, nonmotile projection from the cell. At the end are proteins that attach the cell to solid surfaces or to receptors on other cells. A pathogenic bacterium may recognize and bind to a host cell through a pilus.

Although prokaryotes usually are described as not having internal membranes, this is not true in all cases. Some cells have cisternae or thylakoid membranes, flattened bladders that enclose separate compartments within the cytoplasm (Fig. 19.8). These structures are related to the cell's energy metabolism. As in chloroplasts, the thylakoid membranes of prokaryotes function in the light reactions of photosynthesis. They separate two compartments with different pH values and electrical potentials, thereby enabling the cell to store the free energy generated by electron transport reactions across the membranes. Prokaryotes called **chemotrophs** derive energy from inorganic oxidation-reduction reactions, rather than from photosynthesis, and some of these also have cisternae for energy storage. The oxidation-reduction reactions presumably transport electrical charge and protons across the cisternal membranes; as in photosynthesis, the charge and proton gradients can be used to synthesize the high-energy compound adenosine triphosphate (ATP). But not all photosynthetic and chemotrophic prokaryotes have internal membranes. Some accomplish the same process by establishing their pH and electrical gradients across the plasma membrane.

Some Bacterial Cells Form Endospores

Under harsh environmental conditions, prokaryotic cells will die, but some species have developed ways of surviving by forming tough **endospores**. Typically, bacterial endospores are small, desiccated cells in a condition of suspended animation. Covered with a specialized, hardened cell wall, they contain a complete genome and sufficient enzymes and metabolites to germinate and re-establish growth when conditions improve. The combination of the hardened wall and the dry, inanimate state makes these spores resistant to many environmental insults, including boiling and the action of oxidizing agents (such as sodium hypochlorite, the active ingredient in household bleach) and antibiotic compounds.

The formation of endospores is a complex developmental process, involving the activation of specialized genes. In *Clostridium tetani*, an endospore forms within the vegetative (growing) cell (Fig. 19.9). The nucleoid and some ribosomes are surrounded by the spore wall, which in turn, is surrounded by the endospore coat. Because the nucleoid is isolated from it, the rest of the cell degenerates. In other Bacteria, endospores develop on specialized structures. In Actinobacteria, which are abundant in soil, a group of spores forms on a vertical stalk that raises the endospores above the substrate so they can be blown to new sites by air currents. Myxobacteria, another group of soil Bacteria, form sacs full of endospores that are released when the sac is hydrated (Fig. 19.10).

Every component of a prokaryotic cell plays a role in the cell's survival, growth, or dispersal. The next section describes the processes by which various prokaryotes find the energy to live, grow, and reproduce.

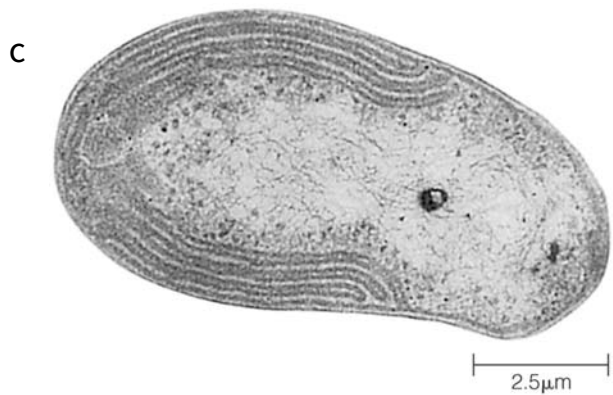
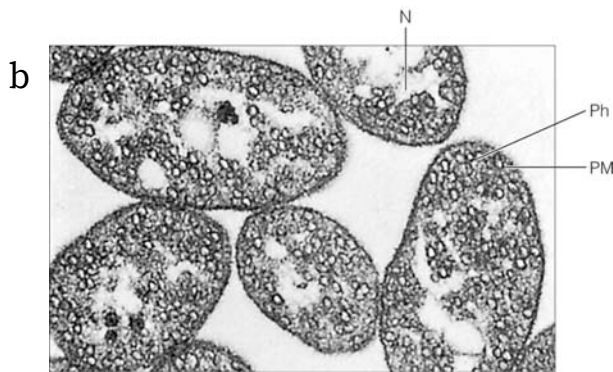
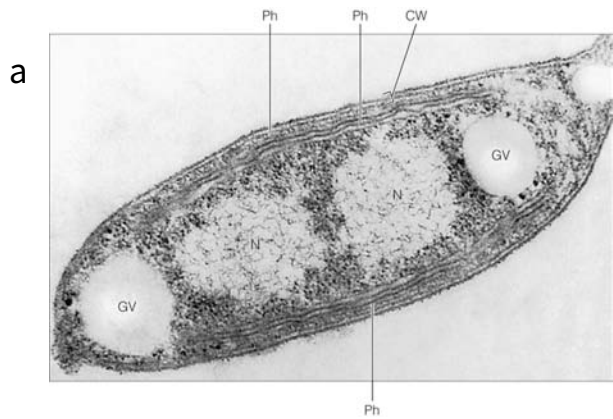


Figure 19.8. prokaryotes with internal membranes. (a,b) Photosynthetic bacteria, showing two different arrangements of thylakoid membranes. (c) A chemotroph with internal cisternae. CW, cell wall; GV, gas vesicle for flotation; N, nucleoid; Ph, photosynthetic thylakoids; PM, plasma membrane.

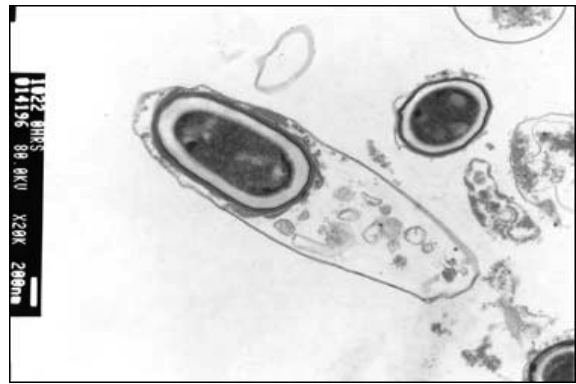


Figure 19.9. An endospore (oval region) inside *Clostridium*, an anaerobic bacterium.

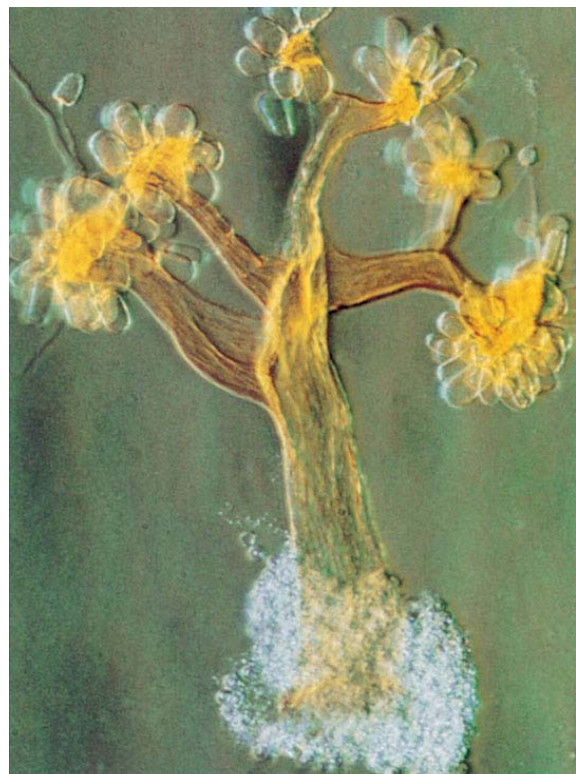


Figure 19.10. A "fruiting" form of the myxobacterium *Chondromyces crocatus*. The organism is a large (0.2 mm) colony with some specialized cells. The raised appendages are filled with spores.

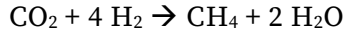
19.3 LIFESTYLES OF SELECTED GROUPS OF PROKARYOTES

A useful classification of prokaryotes is based on their nutritional requirements, particularly the ways they obtain carbon and energy. **Autotrophs** (*auto-*, "self"; *-troph*, "related to feeding") incorporate carbon into organic molecules from inorganic sources, typically by reducing CO₂ and HCO₃⁻. **Heterotrophs** (*hetero-*, "other") derive carbon from the breakdown of organic compounds. **Chemotrophs** (*chemo-*, "chemical") derive energy from catalyzing inorganic reactions. **Phototrophs** (*photo-* "light") derive energy by absorbing light photons. All four combinations--chemoautotrophs, chemoheterotrophs, photoautotrophs, and photoheterotrophs--are found in nature. These differences reflect basic genetic capabilities, and they have ecological implications because they may determine where a species lives and how it affects its environment. Table 19.1 lists selected prokaryotes and some of their characteristics.

Table 19.1 Selected Types of Prokaryotes			
Domain and Genus	Phylum	Comment	Physiological Type
Archaea			
<i>Methanococcus</i> , <i>Methanospirillum</i>	Euryarchaeota	Methanogenic $\text{CO}_2 + 4\text{H}_2 \rightarrow \text{CH}_4 + 2\text{H}_2\text{O}$	Chemoautotroph
<i>Halobacterium</i> , <i>Natronococcus</i>	Euryarchaeota	Extreme halophiles, grow in saturated salt solutions	Photoheterotroph
<i>Thermoplasma</i>	Euryarchaeota	Thermoacidophile, grows at pH 1–4 and 33–67°C	Chemoautotroph
<i>Pyrolobus</i>	Crenarchaeota	Extreme thermophile; grows up to 113°C	Chemoautotroph
Bacteria			
<i>Rhizobium</i>	Proteobacteria	N ₂ -fixing plant symbionts	Chemoheterotroph
<i>Frankia</i>	Actinobacteria	N ₂ -fixing plant symbionts	Chemoheterotroph
<i>Erwinia</i> , <i>Agrobacterium</i> , <i>Pseudomonas syringae</i>	Proteobacteria	Plant pathogens	Chemoheterotroph
<i>Rhodospseudomonas</i> , <i>Chromatium</i>	Proteobacteria	Anaerobic phototrophs; purple nonsulfur and purple sulfur groups	Photoautotroph or chemoheterotroph
<i>Chlorobium</i>	Chlorobi	Anaerobic phototrophs; green sulfur group	Photoautotroph
<i>Anabaena</i> , <i>Nostoc</i> , <i>Prochloron</i>	Cyanobacteria	Oxygen producers	Photoautotroph
<i>Desulfovibrio</i> , <i>Desulfomonas</i>	Proteobacteria	Sulfate-reducing bacteria	Chemoheterotroph
<i>Stigmatella</i> , <i>Chondromyces</i>	Proteobacteria	Myxobacteria; colonial spore formers	Chemoheterotroph
<i>Streptomyces</i>	Actinobacteria	Antibiotic producers	Chemoheterotroph
<i>Nitrosomonas</i> , <i>Nitrobacter</i> , <i>Methylomonas</i>	Proteobacteria	Nitrogen, methane oxidizers	Chemoautotroph
<i>Spirochaeta</i> , <i>Treponema</i>	Spirochaetes	Long, thin, spiral-shaped; some pathogenic	Chemoheterotroph
<i>Bacillus</i>	Firmicutes	Aerobic endospore formers	Chemoheterotroph
<i>Escherichia</i>	Proteobacteria	Enteric; model organism	Chemoheterotroph

Archaea Inhabit Harsh Environments

Many Archaea live in places that we would consider stressful--even deadly. For example, **methanogens** (methane-generating Archaea) derive energy from the following reaction:



CH_4 is methane, a component of natural gas. In reducing (oxygen-poor) environments, such as swamp mud and the rumens of cows, this reaction is a thermodynamically favored reaction; therefore, it can produce usable free energy. In our normal, oxygen-rich atmosphere, methane tends to be oxidized to CO_2 ; but without oxygen, and in the presence of H_2 , the formation of methane is favored. Therefore, methanogenic Archaea actually require anoxic environments to obtain the free energy they need. All methane on Earth, including natural gas, comes from this reaction, catalyzed by methanogenic Archaea. Methanogenic Archaea also incorporate CO_2 into bio-organic molecules; therefore, they are examples of chemoautotrophs.

Another group of Archaea, the **halophiles**, live in saturated salt solutions, such as soda lakes and drying salt flats (Fig. 19.11). Some halophiles have adapted so well to these conditions that they have (and need) little or no cell wall. If such a halophile is moved from its normal environment to distilled water, it will burst. A representative halophile, *Halobacterium halobium*, has a unique type of photosynthesis. A photoreceptor, bacteriorhodopsin, which is more similar to the mammalian eye photoreceptor than to any type of chlorophyll, is embedded in its plasma membrane. There is no associated electron transport system. When this photoreceptor absorbs light, it forces a proton from the cytoplasm to the outside of the cell, forming a pH and electrical gradient (Fig. 19.12). This gradient can be used to synthesize ATP by the same mechanism that occurs in mitochondria. The Archaeal cell derives useful chemical energy from light, but because there is no photosynthetic electron transport chain, it cannot make carbohydrates by reducing CO_2 . Thus, it is a photoheterotroph.

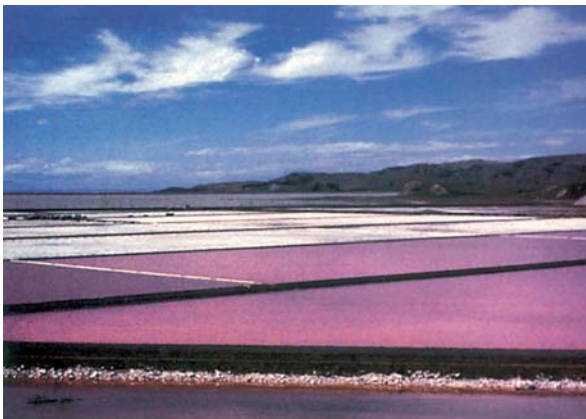


Figure 19.11. Evaporation ponds near Blenheim on the north coast of the south island of New Zealand. The red color is caused by *Halobacteria*, among other organisms, which thrive in salt-saturated water.

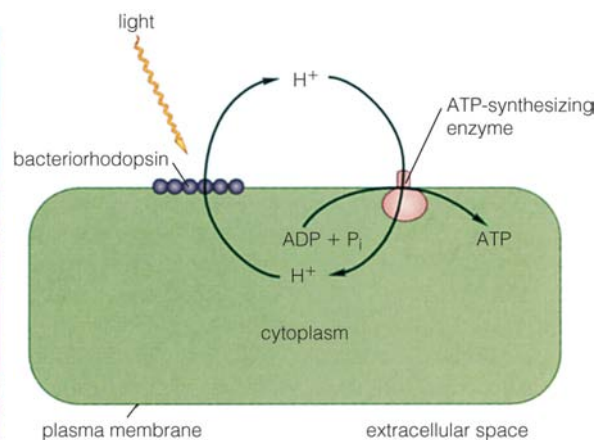


Figure 19.12. The mechanism of photosynthetic energy metabolism in *Halobacterium halobium*.

A third group of Archaea, the **thermoacidophiles**, live in hot, acid environments such as volcanic hot springs. For them, the optimum temperature is 70 to 75°C, with a maximum of 88°C; the optimum pH is 2 to 3 (minimum pH 0.9). One of the reasons that Archaea, and especially thermoacidophiles, are thought to be ancient is that these environments are expected to have prevailed on primitive Earth several billion years ago.

Recently, researchers have found Archaea in equable environments, such as forest soil. Therefore, they may be more widely distributed than is currently appreciated. The habitats and lifestyles of Archaea are a fascinating area of active research.

Bacteria Include Many Diverse Species

Bacteria as a group seem much more diverse than Archaea, especially in the various ways they derive energy from their environment (although this situation may change as more is learned about Archaea). Three lifestyles of Bacteria are described in the following sections.

CHEMOHETEROTROPHS Bacterial chemoheterotrophs live on the organic compounds of living or dead tissue or on the excretions of other organisms. In living organisms, these chemoheterotrophs may be harmful parasites, but many that live on skin or in the gut are beneficial because they compete for niches with potential pathogens. Gut chemoheterotrophs may be essential for nutrition—for example, they provide humans with vitamin K. In dead tissue and on excretions, chemoheterotrophs play the valuable ecological role of recycling carbon, nitrogen, and other elements that are locked in unused and otherwise unusable materials. Usually, energy is released for the use of the heterotrophs through oxidation of the organic compounds. Various species of Bacteria use different electron acceptors in these reactions, including oxygen, nitrate, nitrite, ferrous iron, and sulfate (Table 19.2).

In the absence of oxygen or another inorganic electron acceptor, some Bacteria derive energy from complex organic molecules by converting them to more stable states, a process called **fermentation**. For instance, carbohydrates—starch or sugars—can be broken up into smaller molecules of lactic, acetic, formic, or carbonic acid. Bacteria of the genus *Lactobacillus*, using these reactions, put the "sour" in sourdough bread.

The most intensively studied bacterium, *E. coli*, is a chemoheterotroph (Figs. 19.2 and 19.3). It belongs to the group Proteobacteria and the family Enterobacteriaceae, whose members live in the soil and in the intestines of animals. (They often are called enteric or coliform Bacteria, referring to the colon, the large intestine.) In intestines, they obtain their energy by metabolizing undigested foods; in the soil, they get it by metabolizing litter, excretions, dead microbes, and other sources of organic material. The presence of coliform Bacteria in water supplies is an indicator that the water is contaminated with sewage, which is a problem because human sewage carries pathogenic Bacteria and viruses. The particular coliform Bacteria that are detected in a water test may be perfectly safe—some are, after all, natural inhabitants of healthy animals—but some strains of *E. coli* produce toxins that cause severe infections.

Table 19.2 Oxidation–reduction Reactions Used by Chemotrophs to Obtain Energy and by Autotrophs to Incorporate Carbon into Organic Molecules

Bacteria/Genus Example or Type	Electron Donors	Electron Acceptors	Products
Chemoheterotrophs			
<i>Escherichia</i>	Organics	O ₂	CO ₂ , H ₂ O
<i>Escherichia</i>	Organics	NO ₃ ⁻	CO ₂ , NO ₂ ⁻
<i>Desulfovibrio</i>	Organics	SO ₄ ³⁻	CO ₂ , S ^o , H ₂ S
<i>Lactobacillus</i>	Carbohydrates	None	Lactic, acetic, formic, carbonic acids
Chemoautotrophs			
<i>Nitrosomonas</i>	NH ₃	O ₂ , CO ₂	NO ₂ ⁻ , carbohydrate
<i>Nitrobacter</i>	NO ₂ ⁻	O ₂ , CO ₂	NO ₃ ⁻ , carbohydrate
<i>Thiobacillus</i>	S ²⁻	O ₂ , CO ₂	SO ₄ ²⁻ , carbohydrate
<i>Thiobacillus denitrificans</i>	S	NO ₃ ⁻ , CO ₂	SO ₄ ²⁻ , N ₂ , carbohydrate
<i>Methylomonas</i>	CH ₄	O ₂	CO ₂ , H ₂ O
Photoautotrophs			
Green sulfur Bacteria	H ₂	CO ₂	Carbohydrate, H ₂ O
Green, purple sulfur Bacteria	H ₂ S	CO ₂	Carbohydrate, H ₂ O, S
Purple nonsulfur Bacteria	Reduced organics	CO ₂	Carbohydrate, H ₂ O, oxidized organics
Cyanobacteria, chloroxybacteria	H ₂ O	CO ₂	Carbohydrate, H ₂ O, O ₂

CHEMOAUTOTROPHS The accumulation of any compound, organic or inorganic, that is relatively reduced (electron-saturated) provides an organism in an oxygen atmosphere with the opportunity to obtain energy by catalyzing the transfer of electrons from the reduced compound to oxygen (or a relative oxidized substitute). Some of the electrons can be transferred to CO₂, reducing the carbon to the oxidation state of carbohydrate. Molecules of carbohydrate than can be used to synthesize the other compounds needed for growth and reproduction.

A group of chemoautotrophs, sometimes called **lithotrophs** (*litho*-, "rock"), specialize in the oxidation of inorganic compounds (Table 19.2). These Bacteria are especially important in recycling elements such as nitrogen and sulfur, so that these elements can be used by other organisms (Fig. 19.13).

The oxidation of sulfur by Bacteria also releases the elements that were chemically bound to it, which can help in the smelting of metals (see "BIOTECHNOLOGY: Bacteria and Biomining" at the end of the chapter). The oxidation of methane, produced by methanogenic Archaea, may be an important determinant of the earth's climate (see "PLANTS, PEOPLE, AND THE ENVIRONMENT" Microbes and Global Warming").

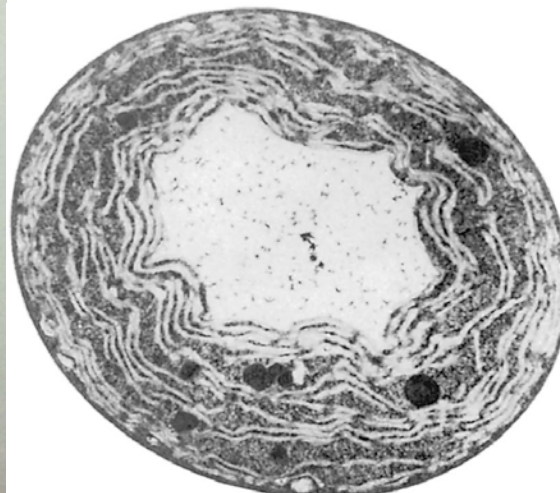


Figure 19.13. Algal and bacterial mats at Lassen Volcanic National Park in northern California. Some thermophilic prokaryotes derive energy from reduced sulfur compounds, easily detected by their smell, which are dissolved in the water.

PHOTOAUTOTROPHS Like plants, Bacterial photoautotrophs (Fig. 19.8a,b and 19.14) derive their energy from sunlight. They have light-absorbing pigments (bacteriochlorophyll or chlorophyll) that collect light energy, which excites electrons and promotes their transfer from one molecule to another. In other words, these organisms store light energy by transferring electrons from relative stable to relatively unstable chemical compounds. There are several types of photoautotrophic Bacteria. They all reduce carbon in CO_2 , but they differ in their cell structures, ecological habitats, and the substrates from which they derive electrons.



Figure 19.14. Phototrophic bacteria. (left) A light micrograph of a species of *Lyngbya*, a filamentous cyanobacterium. (below) An electron micrograph of *Prochloron*, a member of the chloroxybacteria, which has been found only as a symbiont in the gut of a tunicate (marine invertebrate).



Photosynthetic Bacteria include the green sulfur Bacteria (phylum Chlorobi), purple sulfur Bacteria and purple non-sulfur Bacteria (both in the phylum Proteobacteria), and the cyanobacteria (phylum Cyanobacteria)(Table 19.2). In each case, carbon is reduced

from an oxidized state, CO₂, to the more reduced state of carbohydrate. Also, an electron-rich compound loses electrons (and protons) and appears in its oxidized state.

The electron-rich compound may be H₂, H₂S, an organic compound such as H₃CCH₂OH (ethanol), or H₂O. The corresponding oxidized products would be nothing (from H₂), S, acetaldehyde, and O₂. Only cyanobacteria are able to oxidize water and produce O₂ like the plastids of plants. The green and purple sulfur Bacteria and the purple non-sulfur Bacteria are poisoned by oxygen and must grow under anaerobic conditions. The evolution of the capability to produce O₂ was a major innovation in photosynthetic metabolism. It is thought to be an important stage in the development of the earth as we now know it, because all the O₂ in the atmosphere was first formed by the ancestors of cyanobacteria.

There also are major differences among the Bacterial phototrophs in their photosynthetic pigments. The anaerobic phototrophs have bacteriochlorophyll, a pigment related to but different from chlorophyll. Cyanobacteria have chlorophyll *a* in their photosystems, but their major light-harvesting complexes contain proteins called *phycobilins* in a package called a *phycobilisome* attached to the surface of the thylakoid membranes. The phycobilin in cyanobacteria, phycocyanin, absorbs yellow-green light. This is why the cyanobacteria look relatively blue-green. A group within the cyanobacteria, sometimes called chloroxybacteria, have chlorophylls *a* and *b* in their light-harvesting complexes and no phycobilins.

PHOTOAUTOTROPHS AND ENDOSYMBIOSIS On the basis of the photosynthetic pigments of their present-day members, some primitive cyanobacteria and chloroxybacteria are thought to be evolutionary precursors of the plastids of photosynthetic eukaryotes. Researchers propose that Bacteria originally formed an **endosymbiotic relationship** with a eukaryotic precursor cell (*endo*-, "within"; *symbiotic*, "living together"). Over time, a substantial portion of the genetic material of the Bacteria was somehow transferred to the nucleus of the eukaryote, and this endosymbiont became an organelle, an actual part of the eukaryotic cell. Cyanobacteria and the eukaryotic Rhodophyta (red algae) have chlorophyll *a* and phycobilisomes; both also have phycocyanin, although members of the Rhodophyta also have a second phycobilin, phycoerythrin. Chloroxybacteria and Chlorophyta (green algae) have chlorophylls *a* and *b*, and both lack phycobilins.

Biologists consider that the similarities between the light-harvesting complexes of cyanobacteria and red algae and of chloroxybacteria and green algae provide strong evidence for the evolution of plastids through an endosymbiotic mechanism. The base sequences of genes for photosynthetic enzymes in Bacteria and photosynthetic eukaryotes also are very similar, and plastids have small subunit rRNA genes similar to those of cyanobacteria, providing further evidence for this mechanism. What is unknown--and a subject of controversy among biologists--is whether the loss of phycobilins and appearance of chlorophyll *b*, traits that distinguish chloroxybacteria from other cyanobacteria, occurred before or after the endosymbiotic event leading to green algae.

It is likely that the endosymbiotic mechanism applies to the formation of other organelles. Mitochondria probably arose from a Bacterium with the capability to use oxygen as an electron acceptor. The nucleus may have arisen from an endosymbiotic Archaea. Plastids of some algae (e.g., dinoflagellates and euglenids; see Chapter 21) have

structures suggesting that they arose from an already-formed plastid, a process known as secondary endosymbiosis, when a photosynthetic eukaryotic cell became an endosymbiote in another, non-photosynthetic cell.

This section has described the variety of ways by which various prokaryotes obtain their carbon and energy for growth and reproduction. Although obtaining nutrients is not the only significant activity of a cell, it is one of the more important ones. The chemical formulas just described especially demonstrate that prokaryotes play a major role in the interconversion of inorganic elements and compounds, many of which are nutrients on which plant metabolism depends. Thus, plants depend on prokaryotes for their existence on Earth. Plants sometimes form more intimate relationships with prokaryotes, as described in the following section.

19.4 PROKARYOTES THAT FORM SYMBIOTIC RELATIONSHIPS WITH PLANTS

Bacteria and plants can form **symbiotic relationships**, in which the Bacteria live on or within the plant. One kind of symbiosis, called *mutualism*, benefits both the Bacteria and the plant, but other kinds of symbiosis are damaging to the plant.

***Rhizobium* Forms a Mutualistic Association with Legumes**

As described in Chapter 11, nitrogen represents a special nutritional problem for a plant. The world's major store of nitrogen is N₂ in the atmosphere. Plants cannot use this N₂, but some Bacteria can. The infection of plants with such Bacteria can be beneficial and even sometimes essential for the plant.

Rhizobium is a chemoheterotrophic bacterium that lives in soil. Like several other prokaryotes, it synthesizes an enzyme called *nitrogenase*, which gives it the ability to *fix* nitrogen—that is, to convert N₂ to ammonium (NH₄⁺). Ammonium can be incorporated by the Bacteria and plants into the structures of amino acids and other nitrogen-containing organic compounds. Nitrogen fixation is an energy-using reaction: the formation of 2 NH₄⁺ ions from one N₂ molecule requires the addition of 8 high-energy electrons and the hydrolysis of 16 ATP. The bacteria get this energy by metabolizing other organic compounds, especially carbohydrates. Nitrogen fixation works best in a low-oxygen atmosphere, because oxygen inactivates the nitrogenase enzyme.

Rhizobium has developed an ability to form a close mutualistic association with legumes, plants of the family Fabaceae. Both partners in the association contribute, and both partners derive benefits. The plant contributes high-energy carbohydrate and a protected environment; the bacterium contributes nitrogenase and other enzymes. The benefit to both partners is the supply of fixed nitrogen. The association occurs in special organs called **root nodules** (see Fig. 7.20).

The establishment of the symbiotic association is a cooperative process in which each partner triggers steps in the other, including the induction of genes to make proteins that are used only in the active nodules. The sequence of events, as far as we now know it, is as follows:

1. The root secretes an attractive chemical.

2. The chemical induces *Rhizobium* Bacteria in the vicinity to swim toward the root. It also begins the induction of nitrogen fixation genes in the Bacteria.
3. The Bacteria enter at a root hair and move inward through an infection thread (a tube of plasma membrane), losing their cell wall and synthesizing nitrogen-fixing enzymes as they do so.
4. When the Bacteria reach the root cortex, they are released from the infection thread into several cells. The Bacteria without their cell walls are called *bacteroids*; they become surrounded by a special membrane, the peribacteroid membrane.
5. Chemicals secreted by the Bacteria (or bacteroids) during the formation of the infection thread later induce cell division in the root cortex and pericycle, forming the nodule. These chemical also induce the synthesis of specialized nodule proteins, including a type of hemoglobin (leghemoglobin) that buffers the oxygen concentration in the central part of the nodule, where the nitrogen is fixed.

A typical nodule in soybean has a core of bacteroid-infected cells surrounded by a cortex of parenchymal cells that contain extensive vascular bundles. The photosynthetically produced carbohydrate sucrose is transported to the nodule through the phloem (Fig. 19.15). The sucrose then diffuses or is actively transported to *Rhizobium* bacteroids in the core of the nodule. There, oxidative respiration of the carbohydrate provides the high-energy electrons and ATP necessary to reduce N_2 to NH_4^+ . The oxidative reaction not only provides energy but also reduces the concentration of O_2 , a necessary step because O_2 inactivates the nitrogenase enzyme. Leghemoglobin, present in the plant cells that host the bacteroids, also helps regulate or buffer the concentration of O_2 (Fig. 19.15).

The NH_4^+ produced by the bacteroids is used in the synthesis of a key amino acid, glutamine, which can donate nitrogen to other compounds. A substantial fraction of this amino acid is exported to the plant cells in the cortex of the nodule, which convert it into an easily transportable nitrogenous compound. This is secreted to the apoplast and transported up the xylem to the growing parts of the shoot.

Although best known, the *Rhizobium*-legume symbiosis is not the only Bacteria-plant symbiosis that fixes nitrogen. *Frankia*, a member of the Actinobacteria, can live within the cells of root nodules of alder trees and other plants. *Anabaena*, a cyanobacterium, forms a symbiotic association with the water fern, *Azolla*. *Nostoc*, another cyanobacterium, invades cavities in the gametophytes of hornworts (a type of bryophyte; see Chapter 22) and specialized roots of cycads (a type of gymnosperm; see Chapter 24). In each case, the Bacterial partner fixes nitrogen, and the reduced nitrogen compounds nourish both the Bacterium and the plant. Growing *Anabaena*-*Azolla* in rice paddies is a traditional method of fertilizing rice in Southeast Asia.

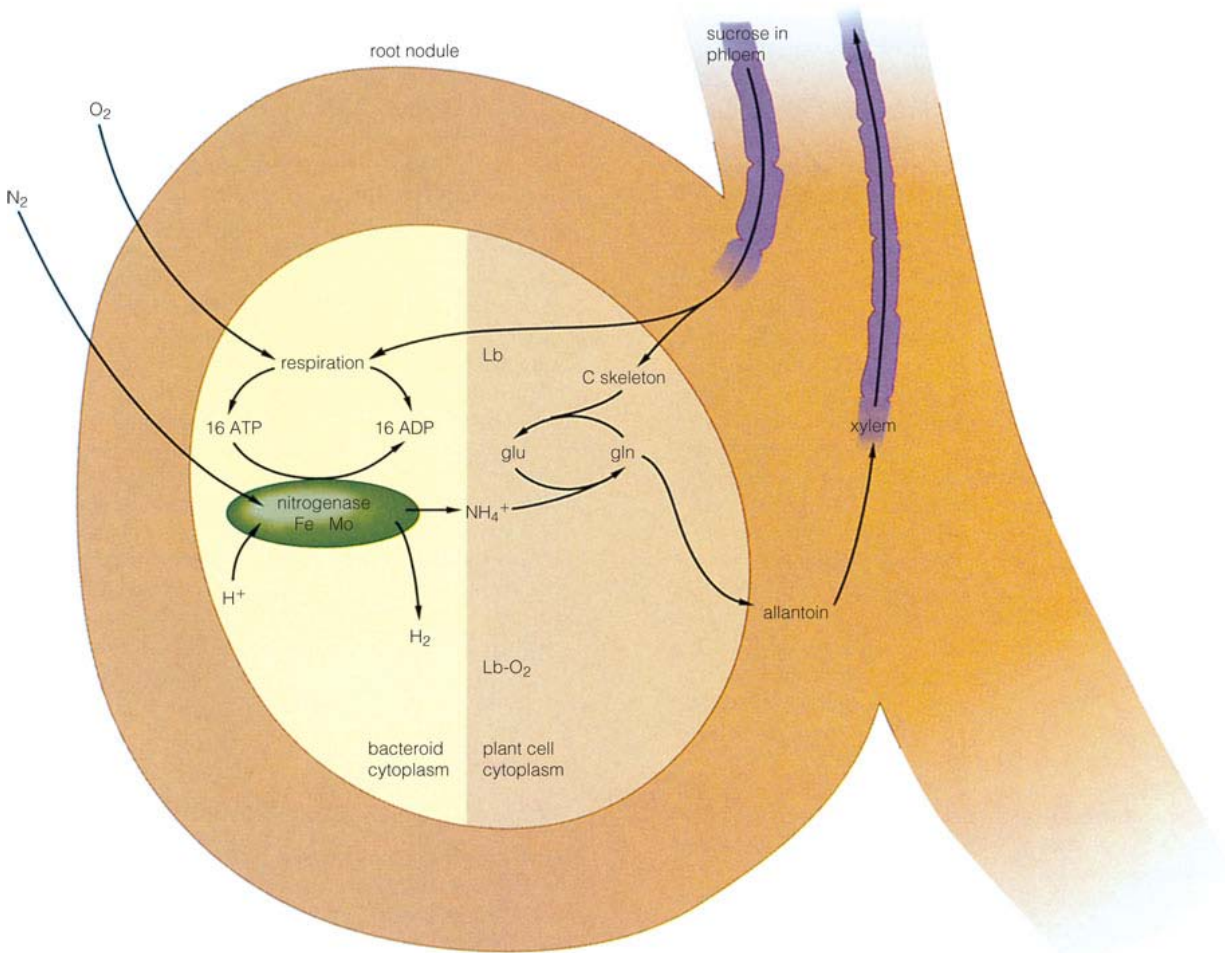


Figure 19.15. The synthesis of fixed nitrogen in a *Rhizobium*-legume nodule. Carbohydrate (sucrose) arrives through the phloem. Some of the carbohydrate is donated to the bacteroids for use in respiration; some is used to make carbon skeletons to which NH_4^+ can be attached. N_2 and O_2 arrive at the nodule through air spaces in the soil and diffuse into the core. O_2 is used quickly in bacterial respiration. This keeps the O_2 concentration low and protects the nitrogenase with its iron (Fe) and molybdenum (Mo) cofactors from inactivation by oxygen. Changes in the O_2 concentration are buffered by leghemoglobin (Lb), an oxygen-binding protein in plant cells. The nitrogen-rich amino acids, glutamate and glutamine, and/or allantoin carry nitrogen to the plant shoot in the xylem stream.

Bacteria Can Be Plant Parasites

Symbiotic associations are not always mutualistic. Those in which one organism benefits at the expense of the other are known as *parasitisms*. *Agrobacterium tumefaciens* is a Bacterial plant parasite, and there are many others, Two important examples are *Pseudomonas syringae* and *Erwinia amylovora*. Bacterial plant pathogens are divided into subgroups called pathovars, according to the plants they infect. Pathovars of *P. syringae* cause the wildfire disease of tobacco; blights of beans, peas, and soybeans; and diseases of

several other crops. Pathovars of *E. amylovora* cause fire blight of apple and pear. The name "wildfire" and "fire blight" suggest the speed at which a Bacterial infection can spread through a field of tobacco or a large apple tree.

Bacteria are carried to uninfected plants by water, insects, humans, or other animals. *E. amylovora*, for example, is carried from flower to flower in apple or pear orchards by bees, as they make their pollination rounds. The Bacteria can enter the plant tissues through natural openings: stomata, lenticels, hydathodes (the openings at the tips of leaves through which guttation water is extruded), and nectarhodes (the openings in flowers from which nectar comes). Once inside the plant, these heterotrophs multiply quickly, absorbing nutrients from the plant cells. Some Bacteria secrete enzymes that break down the plant cell walls, some produce chemical toxins, and some apparently cause their damage simply by absorbing nutrients and multiplying. The infected plant tissues often turn brown and die. A large portion of the plant may be involved. Some Bacterial pathogens can overwinter in the dead tissue, returning to infect new plant tissue at the next growing season.

Plants have some defenses against the infecting Bacteria. Sometimes, depending on the plant and the infecting agent, a plant will react by producing antibiotic compounds, including phytoalexins and hydrogen peroxide. This is called the **hypersensitivity response**. The antibiotics may directly kill some pathogenic cells, but hydrogen peroxide may also restrict the spread of infection by triggering the death of adjacent plant cells. In such a case, the infection may produce a spot of necrosis in a leaf, but it will not kill the whole leaf or the plant.

These descriptions of symbiotic associations between a plant and a Bacterium demonstrate the complexity of the relationships between members of the two kingdoms. They also show how important it is to consider the prokaryotes in the environment when describing the biology and ecology of plants.

Viruses, although they are not free-living and do not influence the physical environment, are parasites of plants and also form complex relationships with them. The next section describes some of these relationships.

19.5 VIRUSES

Viruses are subcellular parasites. They are said to be subcellular because they have neither the internal structures found in prokaryotic or eukaryotic cells nor the capacity to reproduce on their own. They are considered parasites because they invade cells and use their host's metabolism to produce more of their kind. Many biologists have debated the question of whether viruses are alive. Their inability to reproduce independently suggest that they cannot be considered truly alive, yet what functions they do possess are all based on physical and chemical principles basic to living organisms.

Viruses Are Infectious Genes

All types of living organisms have viruses that infect them. You are undoubtedly acquainted with the effects of various human viruses: chicken pox, herpes, polio, and influenza are all caused by specific viruses, as is acquired immune deficiency syndrome

(AIDS). Insects and other animals, fungi, and bacteria all have their own types of viruses, and so do plants.

Viruses have simple structures, compared with cells. They contain a nucleic acid genome surrounded by a coat of protein. The coat sometimes includes lipids. Surprisingly, the genome may be either RNA or DNA, depending on the type of virus, and it may be single-stranded or double-stranded. Whatever its structure in the virus, the genome contains the information for making virus-specific proteins by using the same genetic code that operates in the infected cells. The coat may take different forms, It can be a rod, a polyhedron, or a more complex shape. Whatever its shape and composition, it protects the nucleic acid as it is transferred from one organism to the next and is sometimes instrumental in the infection process. Some viruses also contain one or more enzymes that play a role in the infection process, but outside a cell no virus has any metabolic activity (respiration or protein synthesis, for example). One might consider a virus to be an infectious gene.

Tobacco mosaic virus is a well-studied plant virus. It has a single-stranded RNA genome complexed with coat protein subunits, all wound into a helical rod (Fig. 19.16). When RNA and protein are separated chemically and applied separately to test plants, a plant that receives the RNA will develop a viral infection, whereas a plant that receives the protein will not. The experiment demonstrating this was among the early pieces of evidence that nucleic acids are hereditary material, carrying the instructions for reproduction of the entity from which they came.

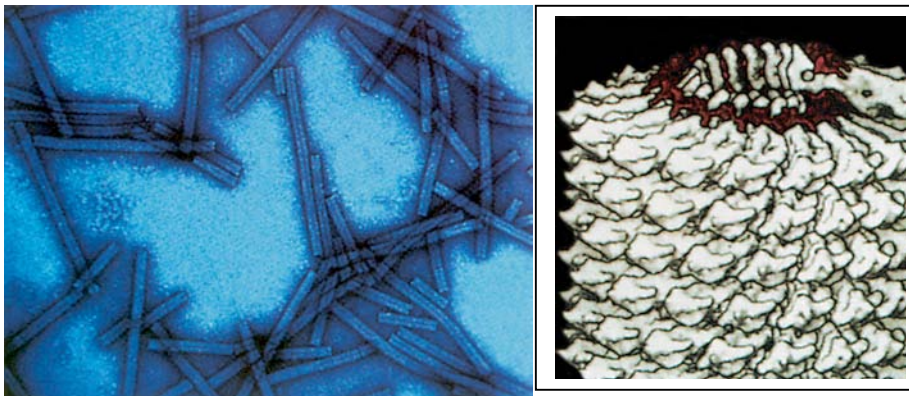


Figure 19.16. Tobacco mosaic virus. (left) Electron micrograph. (right) Interpretive diagram of the arrangement of nucleic acid (red) and coat protein (white).

Viral Infections Stunt Plant Growth

When the tobacco mosaic virus infects a cell of a tobacco, tomato, or other related plant, the coat protein is removed, and the viral RNA serves as a messenger RNA, forming complexes with the cell's ribosomes and using the cell's amino acids, transfer RNAs, and energy source to make viral proteins. The first protein formed is an enzyme, called an RNA-dependent RNA polymerase. This protein forms a complementary strand of RNA, that is, a single-stranded RNA with a base sequence complementary to that of the viral genome, using the viral genome as a template. This complementary RNA then serve as a template for the formation of new viral genomes. Later, another protein, the coat protein, will be synthesized. This protein will bind to and coat the new viral genomes, forming complete viral particles. The viral genome codes for at least one other protein, which promotes the transmission of the virus among plant cells.

Plant viruses, including tobacco mosaic virus, cannot infect plant cells without help. They are too large to pass through a normal primary cell wall, much less the barriers, such as epidermis or cork, that protect a plant from invasions. In nature, plant viral infections are almost always spread by insects, which pick up the viral particles as they chew or suck on infected plants and then transmit them to uninfected plants. Mites (arachnids, related to spiders), nematodes (roundworms), and fungi also can infect plants with viruses when they penetrate the cells.

In the laboratory, viral infections are induced by rubbing abrasive-treated leaves with a viral suspension. The abrasive (for example, Carborundum™) makes holes in the cell walls, through which the virus enters. Once in the cell and forming new viral particles, the virus may become systemic--that is, it may spread throughout the plant. Evidence indicates that viruses move through the plasmodesmata and phloem and that a viral protein is responsible for opening the plasmodesmata so that particles as large as a virus can pass through. A mutant virus has been found that cannot move systemically. A study of this mutant was instrumental in demonstrating that the sizes of the openings of plasmodesmata can be regulated. There also are mutant tobacco plants that do not allow tobacco mosaic virus to move systemically, but instead confine an infection to a local lesion, a small area of dying or dead cells. These plants have been used to study the hypersensitivity response, a reaction sometimes seen in plants with bacterial infections.

Generally, viral infections do not kill plants. Because further transmission of a virus that killed its host and made the host unappetizing to insects would be unlikely, natural selection may eliminate plant viruses that are excessively virulent. However, infected plants are usually stunted relative to uninfected plants, and the infection often, but not always, causes changes in the color or shape of the foliage (Fig. 19.17a). The mosaic of tobacco mosaic virus, the symptom of a systemic infection, is a pattern of dark and light green regions on a leaf. The necrotic local lesions of tobacco mosaic virus are small yellow or brown spots about 1 mm in diameter (Fig. 19.17b). Other viruses cause chlorosis (yellows), concentric white rings on a leaf (ringspot), transparent areas next to the leaf veins (vein clearing), or tumors (galls). Viral infections in flowers sometimes cause beautiful, multicolored patterns (color breaking). Variegated tulips are a famous example (Fig. 19.17c).

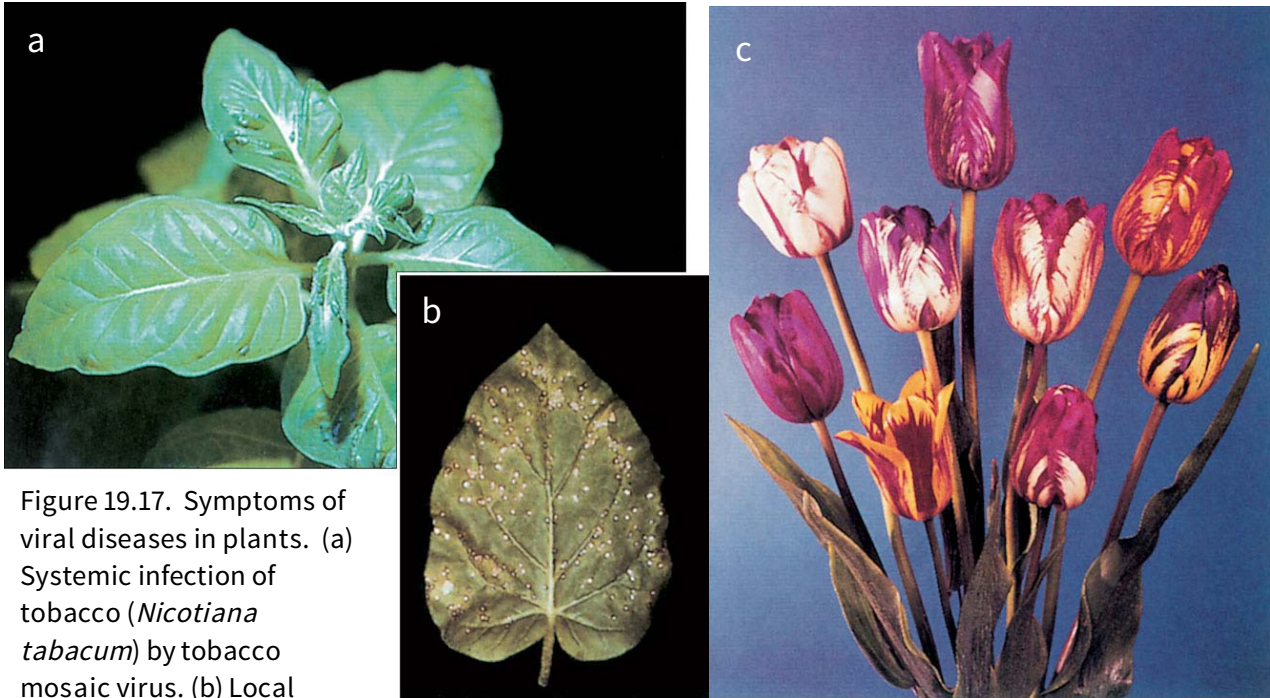


Figure 19.17. Symptoms of viral diseases in plants. (a) Systemic infection of tobacco (*Nicotiana tabacum*) by tobacco mosaic virus. (b) Local lesions in a tobacco leaf. (c) Variegation (color breaking) in tulips.

KEY TERMS

Archaea
 autotrophs
 bacilli
 Bacteria
 binary fission
 chemotrophs
 cocci
 conjugation
 endospores
 endosymbiotic relationship
 Eukarya
 eukaryotes
 fermentation
 flagella
 Gram-negative cells
 Gram-positive cells
 halophiles
 heterotrophs

hypersensitivity response
 lipopolysaccharide layer
 lithotrophs
 methanogens
 nodules
 nucleoid
 peptidoglycan
 periplasmic space
 phototrophs
 pilus
 plasmids
 prokaryotes
 root nodules
 spirilla
 symbiotic relationships
 thermoacidophiles
 vibrios

SUMMARY

1. The basic structure of a prokaryotic cell includes a cell wall and plasma membrane surrounding the cytoplasm and an undifferentiated nucleoid. Many prokaryotic cells have no other organelles recognizable by electron microscopy. Prokaryotes never have a complex endomembrane system, as eukaryotes do, but some contain internal membranes that provide sites for electron transport reactions and store electrochemical energy.
2. In prokaryotes, most genes are lined up on a single circular chromosome. Some specialized genes may be found on smaller DNA circles called plasmids. Plasmids can be transferred from cell to cell. The F plasmid, when incorporated into the chromosome, mediates the transfer of chromosomal genes from a donor cell to a recipient.
3. Some prokaryotes have complex modifications to their extracellular structures, such as an outer lipopolysaccharide membrane (in Gram-negative cells), one or more flagella for motility, and a pilus for attachment to other cells. Some prokaryotes form specialized spores for reproduction, dispersal, and resistance to harsh environmental conditions.
4. Prokaryotes can be divided into two major groups. Many Archaea live in hot, O₂-poor, or salt-rich environments. Bacteria are more diverse and specialized and often have more complex structures and metabolic capabilities.
5. Prokaryotes can be classified according to the ways in which they obtain carbon and energy. Chemoheterotrophs live on the organic compounds of living or dead tissue or on the excretions of other organisms. Chemoautotrophs get energy from the oxidation and reduction of inorganic compounds. Phototrophs derive their energy from light. Chemoheterotrophs and chemoautotrophs play major ecological roles by recycling the elements in organic and inorganic waste. Photoautotrophs contribute to this role; and, like plants, they also contribute to the input of carbon and energy into the organic components of an ecosystem.
6. Some prokaryotes form mutualistic associations with plants, cooperating in the fixation of N₂ to form NH₄⁺ and amino acids. The plants contribute carbohydrate as a source of energy and provide an oxygen-deficient environment. The prokaryotes contribute the enzyme nitrogenase.
7. Some prokaryotes are parasitic on plants, invading leaves and other organs through wounds, stomata, and hydathodes. Prokaryotic cells may multiply quickly in the intercellular spaces of a plant, secreting enzymes to break down cell walls and absorbing and metabolizing the cell contents.
8. Plant viruses are subcellular parasites, formed from a nucleic acid genome and a protein coat; they appropriate the plant cell's protein-synthesizing machinery, using it to reproduce huge numbers of themselves. Plant viruses are normally transmitted among plants by insects. Viral infection weakens a plant and causes various visible symptoms, but it does not generally kill the plant.

Questions

1. From the list below, indicate the organelles (a) that are found in every prokaryotic cell, (b) that are found only some prokaryotic cells, and (c) that are found only in plant (or other eukaryotic) cells.

cell wall	ribosome	nucleoid
peptidoglycan	thylakoid	lipopolysaccharide
nuclar envelope	plasmid	flagellum
spore	endoplasmic reticulum	plasma membrane

2. Distinguish between prokaryotes and viruses. Which do you think appeared first in the evolution of life?

3. Provide a critical analysis for each of the following statements:

- The only way a bacterium can acquire new genetic information is by mutation.
- Conjugation in Bacteria is just like meiosis in plants and other eukaryotic cells.

4. Archaea are thought to represent an ancient live of organisms that may have existed on Earth for billions of years. Give one reason why they have bee able to resist competition from more highly evolved organisms.

5. For each of the reactions below, indicate whether the reaction would be catalyzed by a chemoheterotroph, chemoautotroph, or photoautotroph. Which of these reactions also would be catalyzed by a plant cell? (Note CH₂O represent carbohydrate. The reactions are not balanced.)

- $2 \text{H}_2\text{O} + \text{CO}_2 + \text{light} \rightarrow \text{H}_2\text{O} + \text{CH}_2\text{O} + \text{O}_2$
- $\text{organics} + \text{NO}_3^- \rightarrow \text{CO}_2 + \text{N}_2$
- $2 \text{NH}_3 + 3 \text{O}_2 \rightarrow 2 \text{NO}_2^- + 2 \text{H}_2\text{O}$
- carbohydrates \rightarrow lactic, acetic, formic, and carbonic acids
- $2 \text{H}_2\text{S} + \text{CO}_2 \rightarrow \text{H}_2\text{O} + \text{CH}_2\text{O} + 2\text{S}$

6. Describe the advantages to each partner of the mutualistic symbiotic association between *Rhizobium* bacteria and legume plants.

7. Legumes often are more successful than other plants in sandy soils that have little ability to retain anions, such as nitrate. Suggest one reason why this is true.

8. Distinguish between the methods by which the two plant parasites, *Erwinia amylovora* and *Agrobacterium tumefaciens* (see Chapter 17) derive nutrition by infecting plant cells.

9. A sample of tobacco mosaic virus is separated by chemical procedures into RNA and protein fractions. The leaf of one plant is rubbed with the protein solution. The leaf of another plant is rubbed with the solution of RNA. Which, if either, of these plants will be

infected? Will the infected plant produce viral protein, viral RNA, or whole viral particles (RNA plus protein)?

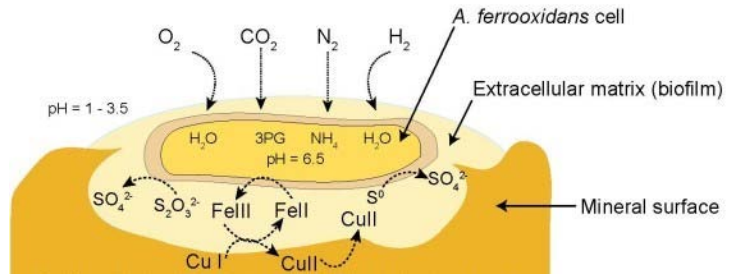
10. Explain the following statement: Agriculturalists have found that the most effective way to stop the spread of a plant viral disease is by the use of insecticides.

11. Find an example of biocontrol of a bacterial plant disease that is (or would be) useful in your region of the country.

BIOTECHNOLOGY: *Bacteria and Biomining*

Prokaryotes are impressive, both in the variety of chemical reactions they catalyze to obtain energy and in the scale at which they operate. Much of the earth's surface has been molded by the chemical activity of bacteria. Scientists believe that before the appearance of bacteria, virtually all the iron on Earth was present in a chemically reduced form; currently, most beds of iron ore are oxidized. Iron- and manganese-oxidizing bacteria have been isolated and studied.

The abilities of some species of bacteria to chemically modify various elements are now being used in the smelting of ores to extract copper, gold, and phosphate. Copper (Cu) often is found in rocks as an insoluble sulfide, CuS. Traditional energy-intensive smelting methods require that the rock be crushed and heated to extract the metal. A much easier and cheaper method is to soak



the ore in an acidic solution containing *Acidithiobacillus ferrooxidans*, a bacterium that obtains energy by oxidizing sulfide to sulfate. This bacterium functions happily under acidic conditions, which also promote the oxidation of reduced copper. The resulting copper sulfate is soluble and can be leached from the remaining insoluble rocks. The metal then is prepared from the copper sulfate solution. Currently, 25% of all copper produced in the world comes from this biomining technique.

The same bacterium can help extract gold from sulfide-containing ores. In low-quality ores, small particles of gold are trapped in an insoluble matrix of copper and iron sulfides. Oxidation of the sulfur and leaching of the remaining sulfates release the gold, which can be recovered by extraction with cyanide. Treating the ore with suspensions of *T. ferrooxidans* is cheaper than the traditional high-pressure, high-temperature method of oxidation, and it extracts a greater percentage of the gold.

Phosphate, needed as fertilizer in agriculture and in some industrial processes, is traditionally extracted from ore by using high temperatures or sulfuric acid. A new process dissolves the phosphates in organic acids, metabolic byproducts of the bacteria *Pseudomonas cepacia E-37* and *Erwinia herbicola*. This method is more environmentally friendly because the organic acids are themselves biodegradable through the actions of other bacteria.

A current research project is aimed at using films of the bacterium *Pseudomonas aeruginosa* to precipitate metallic flakes from solutions containing ions of gold, silver, or platinum.

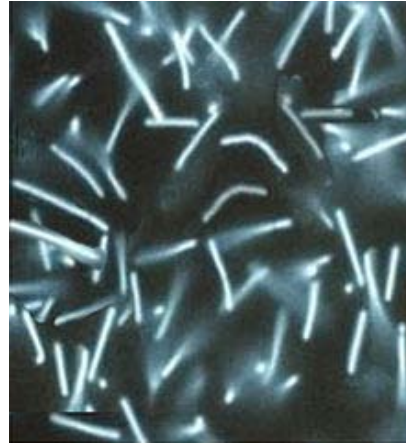
PLANTS, PEOPLE, AND THE ENVIRONMENT: *Microbes and Global Warming*

Methane formation plays an important role in human affairs, because it is a major component of natural gas. But methane is important for another reason. It is a greenhouse gas, 25 times more effective than CO₂ in trapping infrared radiation. An increase in the amount of methane in the atmosphere could result in seriously increased temperatures on the Earth's surface.

Geochemists estimate that the mud of the ocean floor contains 10 trillion tons of methane, and methanogenic Archaea below the surface of the ocean produce 300 million more tons of methane per year.

But little or none of this methane reaches the atmosphere. From studies of the muds in the Black Sea and Eel River canyon off California, scientists have found that Archaea, Bacteria, and symbiotic combinations of both use the methane as a carbon and energy source. However, the mud on the ocean bottom is anaerobic; therefore, the oxidation of the methane, needed to harvest its energy, requires another electron acceptor. The electron acceptor for this system is sulfate. The reduction of sulfate produces hydrogen sulfide, which may be useful as an energy source for other prokaryotes.

This is one example of prokaryotic symbiosis, and one that may have played a role in regulating the climate of Earth. Scientists suggest that in the ancient Earth, when the sun was not as bright, the presence of methane in the atmosphere warmed Earth to a temperature comfortable for life. As the sun's radiance increased, the evolution of methane-eating prokaryotes reduced this greenhouse gas and kept Earth's temperature equable.



Methanopyrus kandleri

BIOTECHNOLOGY: *Bacteria As Biocontrol Agents*



Alfalfa webworms killed by *Bacillus thuringiensis*.

Biological control (or biocontrol) involves the use of "natural enemies" to restrict the growth of pests, such as insects, molds, and weeds. It is a major component of the agricultural practice known as Integrated Pest Management, which seeks to limit the loss of crop value to pests through ecologically sound methods. Bacteria can play important roles in biocontrol strategies.

A good example of a bacterium used for biocontrol of insect pests is *Bacillus thuringiensis* (sometimes abbreviated *Bt*). *Bt* cells synthesize a protein that kills insect larvae. Once a larva has ingested the *Bt*, the protein is released and quickly binds to receptors in the gut. The larva stops eating, and the gut dissolves, releasing bacteria into the bloodstream. The larva dies from starvation and infection. Different strains of *Bt* produce different types of protein, so it is possible to control specific types of insects. For instance, there is a strain that kills wax moth larvae in beehives without harming the bees. *Bt* is used to protect cotton plants and forest trees, and it can be sprayed on fruits and vegetables. It has no harmful effect on humans, even in huge amounts. (In early tests, some subjects even ate *Bt* as a paste on crackers.)

Biocontrol of invasive plants--weeds--usually is accomplished with insects or fungi, not bacteria. However, there is at one commercial product that uses bacteria for pest control. An isolate of *Xanthomonas campestris*, a wilt-inducing bacterium, was isolated in Japan from *Poa annua* (annual bluegrass or wintergrass). Suspensions of the bacterial cells are registered in Japan as the bio-herbicide CAMPERICO® to control annual bluegrass in golf courses.

Pseudomonas syringae, the bacterium that causes wildfire disease in plants, forms the basis of an unusual commercial biocontrol agent. Strains of *P. syringae* that lack the ability to produce disease in plants have been isolated. When suspensions of these strains are sprayed on fruits, such as apples, pears, bananas, and oranges, they prevent mold fungi from infecting and destroying the fruits.

As global trade and travel increase, so does the incidence of biological invasions--pests from other parts of the world reproducing and spreading without limitation by the herbivores, predators, or pathogens of their native habitat. The strategy of biocontrol is to find organisms that restore the ecological balance. The same strategy can be a useful and economic management techniques in agriculture.

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Fig. 19.1. (a-d). Terence M. Murphy

Fig. 19.9. http://www.innovations-report.de/bilder_neu/49772_Botulinum.jpg

Fig. 19.10. Pioneer Hi-Bred International, Inc., copyright 1996.

Fig. 19.12. Adapted from information in Owngey, M. 1950. *American Journal of Botany* 37:487-499 with permission.

Fig. 19.13 <http://pubs.usgs.gov/fs/2002/fs101-02/>

Sidebar/Biomining Valdés J et al. *BMC Genomics* 9:597 (2008)

Sidebar/Global Warming Wikipedia "Methanogen"

Sidebar/Biocontrol W.S. Cranshaw Colorado State University Extension fact sheet 5.556