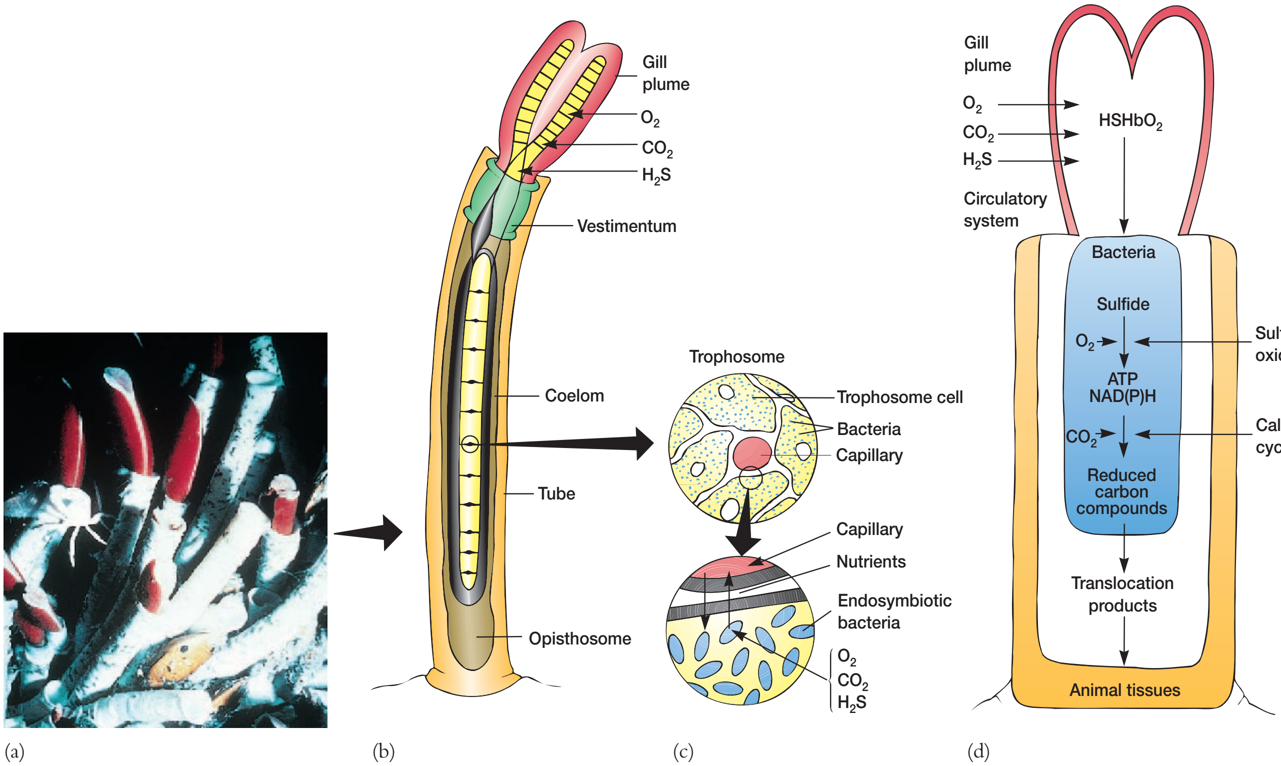


Figure 28.6 **The Tube Worm—Bacterial Relationship.** (**a**) A community of tube worms (*Riftia pachyptila*) at the Galápagos Rift hydrothermal vent site (depth 2,550 m). Each worm is more than a meter in length and has a 20 cm gill plume. (**b, c**) Schematic illustration of the anatomical and physiological organization of the tube worm. The animal is anchored inside its protective tube by the vestimentum. At its anterior end is a respiratory gill plume. Inside the trunk of the worm is a trophosome consisting primarily of endosymbiotic bacteria, associated cells, and blood vessels. At the posterior end of the animal is the opisthosome, which anchors the worm in its tube. (**d**) Oxygen, carbon dioxide, and hydrogen sulfide are absorbed through the gill plume and transported to the blood cells of the trophosome. Hydrogen sulfide is bound to the worm's hemoglobin ($HSHbO_2$) and carried to the endosymbiont bacteria. The bacteria oxidize the hydrogen sulfide and use some of the released energy to fix CO_2 in the Calvin cycle. Some fraction of the reduced carbon compounds synthesized by the endosymbiont is translocated to the animal's tissues.

concentrations around 250 μM and temperatures 10 to 20°C above the normal seawater temperature of 2.1°C.

The giant (>1 m in length), red, gutless tube worms (*Riftia* spp.) near these hydrothermal vents provide an example of a unique form of mutualism and animal nutrition in which chemolithotrophic bacterial endosymbionts are maintained within specialized cells of the tube worm host (**figure 28.6**). To date all attempts to culture these microorganisms have been unsuccessful.

The tube worm takes up hydrogen sulfide from the seawater and binds it to hemoglobin (the reason the worms are bright red). The hydrogen sulfide is then transported in this form to the bacteria, which use the sulfide-reducing power to fix carbon dioxide in the Calvin cycle (*see figure 10.4*). The CO_2 required for this cycle is transported to the bacteria in three ways: freely dissolved in the blood, bound to hemoglobin, and in the form of organic acids such as malate and succinate. These acids are decarboxylated to release CO_2 in the trophosome, the tissue containing bacterial symbionts. Using these mechanisms, the bacteria synthesize reduced organic material from inorganic substances. The organic material is then supplied to the tube worm through its circulatory system and serves as the main nutritional source for the tissue cells.

Methane-Based Mutualisms

Other unique food chains involve methane-fixing microorganisms as the first step in providing organic matter for consumers. Methanotrophs, bacteria capable of using methane, occur as intracellular symbionts of methane-vent mussels. In these mussels the thick fleshy gills are filled with bacteria. In addition, methanotrophic carnivorous sponges have been discovered in a mud volcano at a depth of 4,943 m in the Barbados Trench. Abundant methanotrophic symbionts were confirmed by the presence of enzymes related to methane oxidation in sponge tissues. These sponges are not satisfied to use bacteria to support themselves; they also trap swimming prey to give variety to their diet.

Microorganism-Insect Mutualisms

Mutualistic associations are common in the insects. This is related to the foods used by insects, which often include plant sap or animal fluids lacking in essential vitamins and amino acids. The required vitamins and amino acids are provided by bacterial symbionts in exchange for a secure physical habitat and ample nutrients. The aphid is an excellent example of this mutualistic relationship. This insect contains *Buchnera aphidicola* in its cytoplasm, and a mature insect contains literally millions of these bacteria in its body. The *Buchnera* provides its host with amino acids, particularly tryptophan, and if the insect is treated with antibiotics, it dies. *Wolbachia pipientis,* a rickettsia, is a cytoplasmic endosymbiont found in 15 to 20% of insect species and can control the reproduction of its host. This microbial association is thought to be a major factor in the evolution of sex and speciation in the parasitic wasps. *Wolbachia* also can cause cytoplasmic incompatibility in insects, parthenogenesis in butterflies, and the feminization of genetic males in isopods. What could be the advantage to the *Wolbachia*? By limiting sexual variability, the bacterium might benefit by creating a more stable asexual environment for its own longer-term maintenance. Our understanding of microbe-insect mutualisms, including the role of *Wolbachia* in insects, is constantly expanding with the increased use of molecular techniques.

1. What is a lichen? Discuss the benefits the phycobiont and mycobiont provide each other.
2. What is the critical characteristic of a mutualistic relationship?
3. How do tube worms obtain energy and organic compounds for their growth?
4. What is the source of the waters released in a deep hydrothermal vent, and how is it heated?
5. What are important roles of bacteria, such as *Buchnera* and *Wolbachia,* in insects?

The Rumen Ecosystem

Ruminants are a group of herbivorous animals that have a stomach divided into four compartments and chew a cud consisting of regurgitated, partially digested food. Examples include cattle, deer, elk, camels, buffalo, sheep, goats, and giraffes. This feeding method has evolved in animals that need to eat large amounts of food quickly, chewing being done later at a more comfortable or safer location. More importantly, by using microorganisms to degrade the thick cellulose walls of grass and other vegetation, ruminants digest vast amounts of otherwise unavailable forage. Because ruminants cannot synthesize cellulases, they have established a mutualistic relationship with anaerobic microorganisms that produce these enzymes. Cellulases hydrolyze the β $(1 \rightarrow 4)$ linkages between successive D-glucose residues of cellulose and release glucose, which is then fermented to organic acids such as acetate, butyrate, and propionate (*see figure 9.10*). These organic acids are the true energy source for the ruminant.

The upper portion of a ruminant's stomach expands to form a large pouch called the **rumen** (**figure 28.7**) and also a smaller honeycomblike reticulum. The bottom portion of the stomach consists of an antechamber called the omasum, with the "true" stomach (abomasum) behind it.

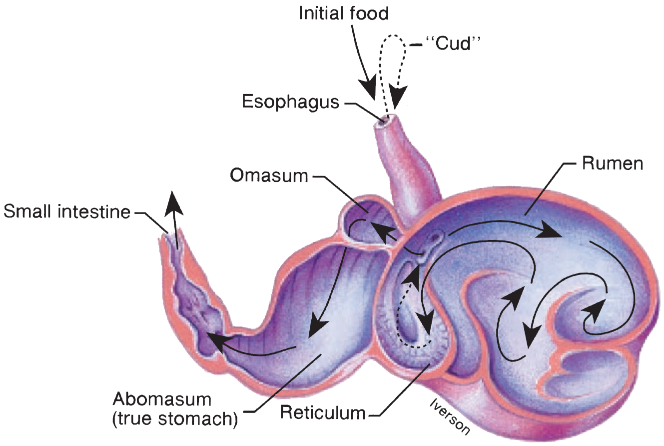
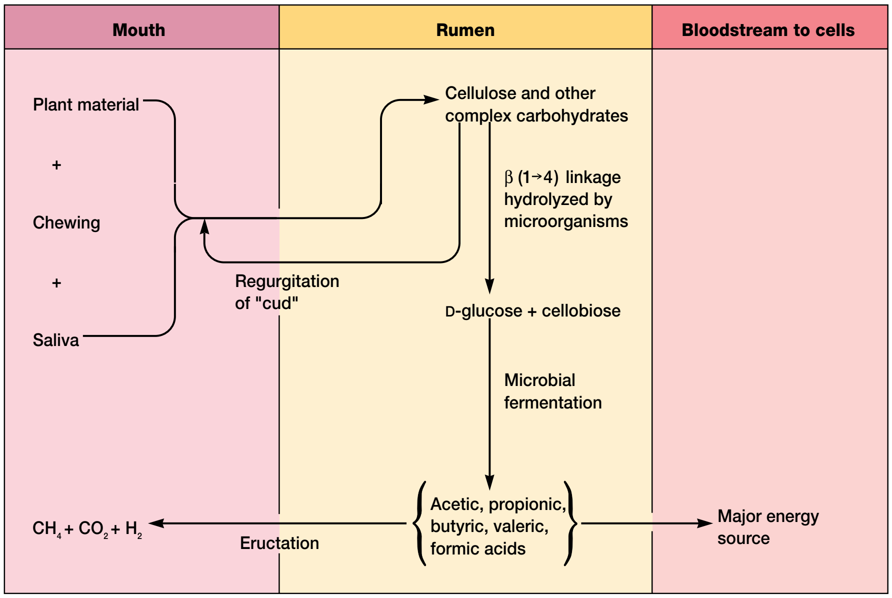


Figure 28.7 Ruminant Stomach. The stomach compartments of a cow. The microorganisms are active mainly in the rumen. Arrows indicate direction of food movement.

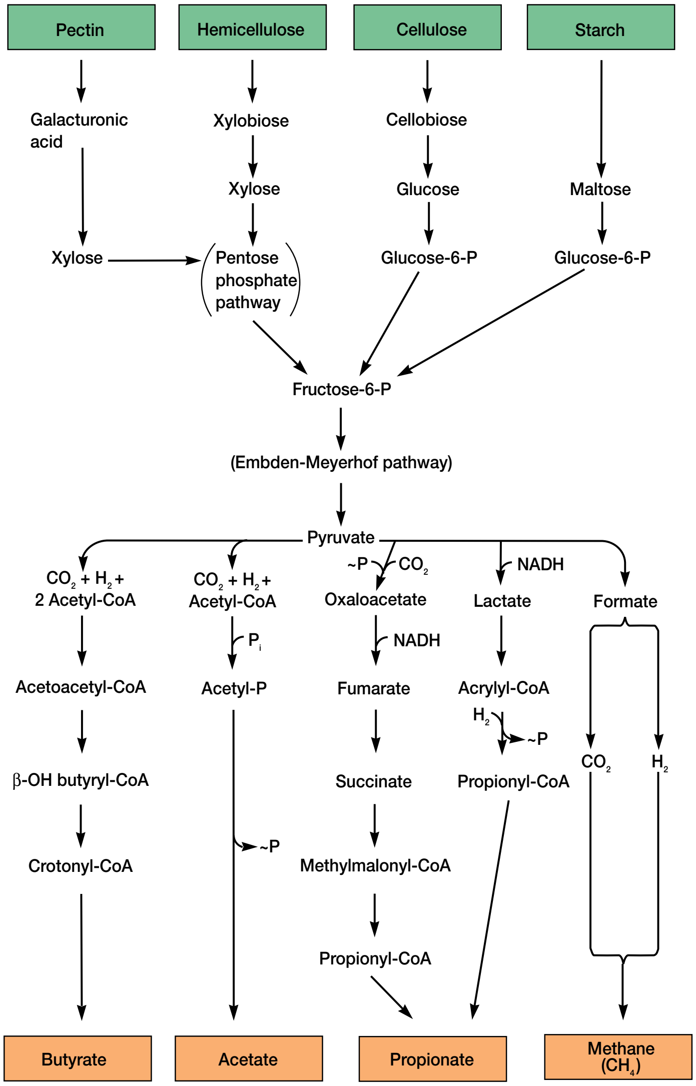
The insoluble polysaccharides and cellulose eaten by the ruminant are mixed with saliva and enter the rumen. Within the rumen, food is churned in a constant rotary motion and eventually reduced to a pulpy mass, which is partially digested and fermented by microorganisms. Later the food moves into the reticulum. It is then regurgitated as a "cud," which is thoroughly chewed for the first time. The food is mixed with saliva, reswallowed, and reenters the rumen while another cud is passed up to the mouth. As this process continues, the partially digested plant material becomes more liquid in nature. The liquid then begins to flow out of the reticulum and into the lower parts of the stomach: first the omasum and then the abomasum. It is in the abomasum that the food encounters the host's normal digestive enzymes and the digestive process continues in the regular mammalian way.

The rumen contains a large and diverse microbial community (about 10^{12} organisms per milliliter), including procaryotes, anaerobic fungi such as *Neocallimastix,* and ciliates and other protozoans. Food entering the rumen is quickly attacked by the cellulolytic anaerobic procaryotes, fungi, and protozoa. Although the masses of procaryotes and protozoa are approximately equal, the processing of rumen contents is carried out mainly by the procaryotes. Microorganisms break down the plant material, as illustrated in **figure 28.8.** Because the reduction potential in the rumen is -30 mV, all indigenous microorganisms engage in anaerobic metabolism. The bacteria ferment carbohydrates to fatty acids, carbon dioxide, and hydrogen. The archaea (methanogens) produce methane (CH_4) from acetate, CO_2, and H_2.

Dietary carbohydrates degraded in the rumen include soluble sugars, starch, pectin, hemicellulose, and cellulose. The largest percentage of each carbohydrate is fermented to volatile fatty acids (acetic, propionic, butyric, formic, and valeric), CO_2, H_2, and methane. Fatty acids produced by the rumen organisms are absorbed into the bloodstream and are oxidized by the animal as its



(a)



(b)

Figure 28.8 Rumen Biochemistry. (**a**) An overview of the biochemical-physiological processes occurring in various parts of a cow's digestive system. (**b**) More specific biochemical pathways involved in rumen fermentation of the major plant carbohydrates. The top boxes represent substrates and the bottom boxes some of the end products.

main source of energy. The CO_2 and methane, produced at a rate of 200 to 400 liters per day in a cow, are released by eructation [Latin *eructare,* to belch], a continuous, scarcely audible reflex process similar to belching. ATP produced during fermentation is used to support the growth of rumen microorganisms. These microorganisms in turn produce most of the vitamins needed by the ruminant. In the remaining two stomachs, the microorganisms, having performed their symbiotic task, are digested to yield amino acids, sugars, and other nutrients for ruminant use.

Syntrophism

Syntrophism [Greek *syn,* together, and *trophe,* nourishment] is an association in which the growth of one organism either depends on or is improved by growth factors, nutrients, or substrates provided by another organism growing nearby. Sometimes both organisms benefit. This type of mutualism is also known as cross-feeding or the satellite phenomenon.

A very important syntrophism occurs in anaerobic methanogenic ecosystems such as sludge digesters (*see section 29.6*), anaerobic freshwater aquatic sediments, and flooded soils. In these environments, fatty acids can be degraded to produce H_2 and methane by the interaction of two different bacterial groups. Methane production by methanogens depends on **interspecies hydrogen transfer.** A fermentative bacterium generates hydrogen gas, and the methanogen uses it quickly as a substrate for methane gas production.

Various fermentative bacteria produce low molecular weight fatty acids that can be degraded by anaerobic bacteria such as *Syntrophobacter* to produce H_2 as follows:

$$\text{Propionic acid} \rightarrow \text{acetate} + CO_2 + H_2$$

Syntrophobacter uses protons ($H^+ + H^+ \rightarrow H_2$) as terminal electron acceptors in ATP synthesis. The bacterium gains sufficient energy for growth only when the H_2 it generates is consumed. The products H_2 and CO_2 are used by methanogenic archaea (e.g., *Methanospirillum*) as follows:

$$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$$

By synthesizing methane, *Methanospirillum* maintains a low H_2 concentration in the immediate environment of both bacteria. Continuous removal of H_2 promotes further fatty acid fermentation and H_2 production. If the hydrogen is not consumed, it will inhibit *Syntrophobacter.* Because increased H_2 production and consumption stimulate the growth rates of *Syntrophobacter* and *Methanospirillum,* both participants in the relationship benefit.

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1. What structural features of the rumen make it suitable for a herbivorous type of diet? Why does a cow chew its cud?
2. What biochemical roles do the rumen microorganisms play in this type of symbiosis?
3. What is syntrophism? Is physical contact required for this relationship?
4. What is interspecies hydrogen transfer, and why can this be beneficial to both the producer and consumer of hydrogen?

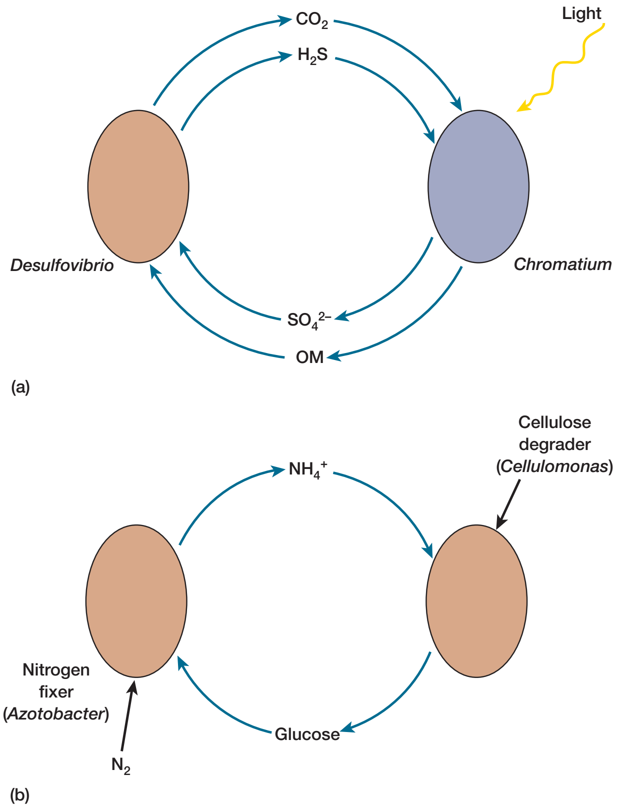


Figure 28.9 Examples of Protocooperative Symbiotic Processes. (**a**) The organic matter (OM) and sulfate required by *Desulfovibrio* are produced by the *Chromatium* in its photosynthesis-driven reduction of CO_2 to organic matter and oxidation of sulfide to sulfate. (**b**) *Azotobacter* uses glucose provided by a cellulose-degrading microorganism such as *Cellulomonas,* which uses the nitrogen fixed by *Azotobacter.*

Protocooperation

As noted in figure 28.1, **protocooperation** is a mutually beneficial relationship, similar to that which occurs in mutualism, but in protocooperation, this relationship is not obligatory. As noted in this figure, beneficial complementary resources are provided by each of the paired microorganisms. The organisms involved in this type of relationship can be separated, and if the resources provided by the complementary microorganism are supplied in the growth environment, each microorganism will function independently. Two examples of this type of relationship are the association of *Desulfovibrio* and *Chromatium* (**figure 28.9*a***), in which the carbon and sulfur cycles are linked, and the interaction of a nitrogen-fixing microorganism with a cellulolytic organism such as *Cellulomonas* (figure 28.9*b*). In the second example, the cellulose-degrading microorganism liberates glucose from the cellulose, which can be used by nitrogen-fixing microbes.

An excellent example of a protocooperative biodegradative association is shown in **figure 28.10.** In this case 3-chlorobenzoate degradation depends on the functioning of microorganisms with complementary capabilities. If any one of the three microorgan-

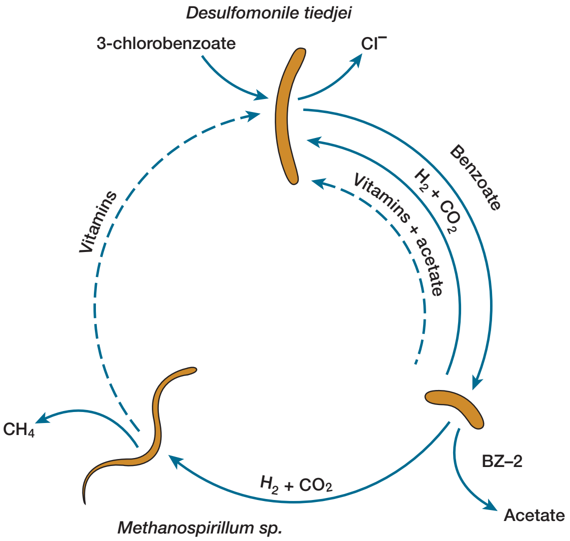
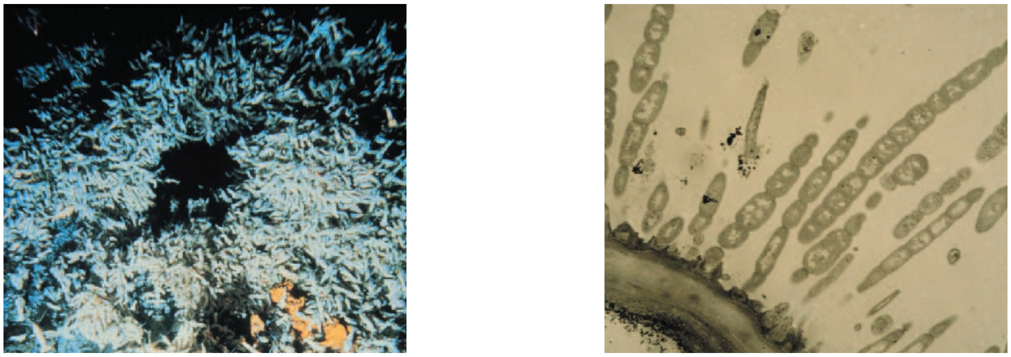


Figure 28.10 Associations in a Defined Three-Membered Protocooperative and Commensalistic Community That Can Degrade 3-Chlorobenzoate. If any member is missing, degradation will not take place. The solid arrows demonstrate nutrient flows, and the dashed lines represent hypothesized flows.

Figure 28.11 A Marine Worm-Bacterial Protocooperative Relationship. *Alvinella pompejana,* a 10 cm long worm, forms a protocooperative relationship with bacteria that grow as long threads on the worm's surface. These waters contain sulfur compounds that are used by the bacteria as electron acceptors in the presence of fumarate and pyruvate, and the worm uses the bacteria as a food source. The bacteria and *Alvinella* are found in tunnels near the black smoker–heated water fonts.



(a) (b)

Figure 28.12 A Marine Crustacean-Bacterial Protocooperative Relationship. (**a**) A picture of the marine shrimp *Rimicaris exoculata* clustering around a hydrothermal vent area, showing the massive development of these crustaceans in the area where chemolithotrophic bacteria grow using sulfide as an electron and energy source. The bacteria, which grow on the vent openings and also on the surface of the crustaceans, fix carbon from CO_2 in their autotrophic metabolism, and serve as the nutrient for the shrimp. (**b**) An electron micrograph of a thin section across the leg of the marine crustacean *Rimicaris exoculata,* showing the chemolithotrophic bacteria that cover the surface of the shrimp. The filamentous nature of these bacteria, upon which this commensalistic relationship is based, is evident in this thin section.

isms is not present and active, the degradation of the substrate will not occur.

In other protocooperative relations, sulfide-dependent autotrophic filamentous microorganisms fix carbon dioxide and synthesize organic matter that serves as a carbon and energy source for a heterotrophic organism. One of the most interesting such relationship is the Pompeii worm (*Alvinella pompejana*), named for the deep-sea submersible from Woods Hole, Massachusetts. This unusual organism is 10 cm in length and lives in tunnels near waters that approach 80°C in a deep area of the Pacific Ocean (**figure 28.11**). It uses as a nutrient source bacteria that appear to oxidize organic matter and reduce sulfur compounds. A deep-sea crustacean has been discovered that uses sulfur-oxidizing autotrophic bacteria as its food source. This shrimp, *Rimicaris exoculata* (**figure 28.12**)

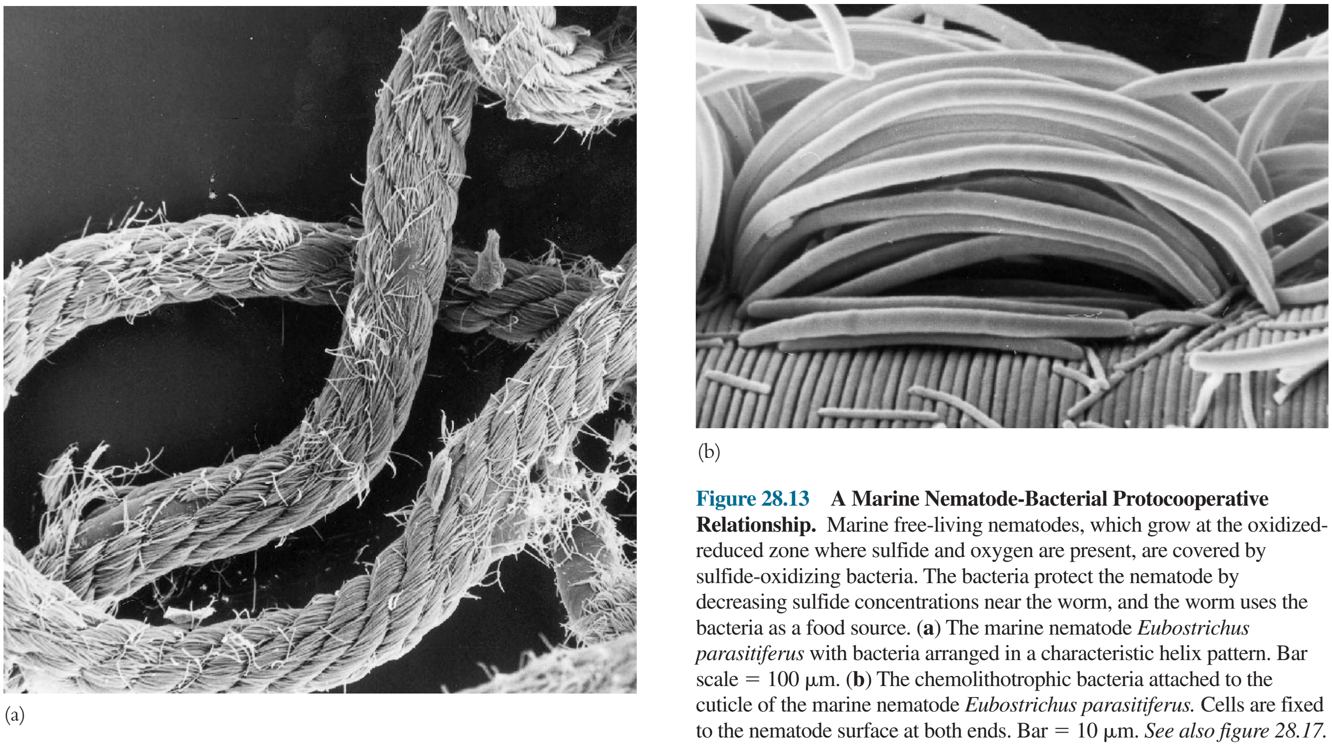


Figure 28.13 **A Marine Nematode-Bacterial Protocooperative Relationship.** Marine free-living nematodes, which grow at the oxidized-reduced zone where sulfide and oxygen are present, are covered by sulfide-oxidizing bacteria. The bacteria protect the nematode by decreasing sulfide concentrations near the worm, and the worm uses the bacteria as a food source. (**a**) The marine nematode *Eubostrichus parasitiferus* with bacteria arranged in a characteristic helix pattern. Bar scale = 100 µm. (**b**) The chemolithotrophic bacteria attached to the cuticle of the marine nematode *Eubostrichus parasitiferus.* Cells are fixed to the nematode surface at both ends. Bar = 10 µm. *See also figure 28.17.*

has filamentous sulfur-oxidizing bacteria growing on its surface. When these are dislodged the shrimp ingests them. This nominally "blind" shrimp can respond to the glow emitted by the black smoker, using a reflective organ on its back. The organ is sensitive to a light wavelength that is not detectable by humans.

Another interesting example of bacterial epigrowth is shown by nematodes, including *Eubostrichus parasitiferus,* that live at the interface between aerobic and anaerobic sulfide-containing marine sediments (**figure 28.13*a***). These animals are covered by sulfide-oxidizing bacteria that are present in intricate patterns (figure 28.13*b*). The bacteria not only decrease levels of toxic sulfide, which often surround the nematodes, but they also serve as a food supply.

In 1990, hydrothermal vents were discovered in a freshwater environment, at the bottom of Lake Baikal, the oldest (25 million years old) and deepest lake in the world. This lake is located in the far east of Russia (**figure 28.14*a***) and has the largest volume of any freshwater lake (not the largest area—which is Lake Superior). The bacterial growths, with long white strands, are in the center of the vent field where the highest temperatures are found (figure 28.14*b*). At the edge of the vent field, where the water temperature is lower, the bacterial mat ends, and sponges, gastropods, and other organisms, which use the sulfur-oxidizing bacteria as a food source, are present (figure 28.14*c*). Similar although less developed areas have been found in Yellowstone Lake, Wyoming.

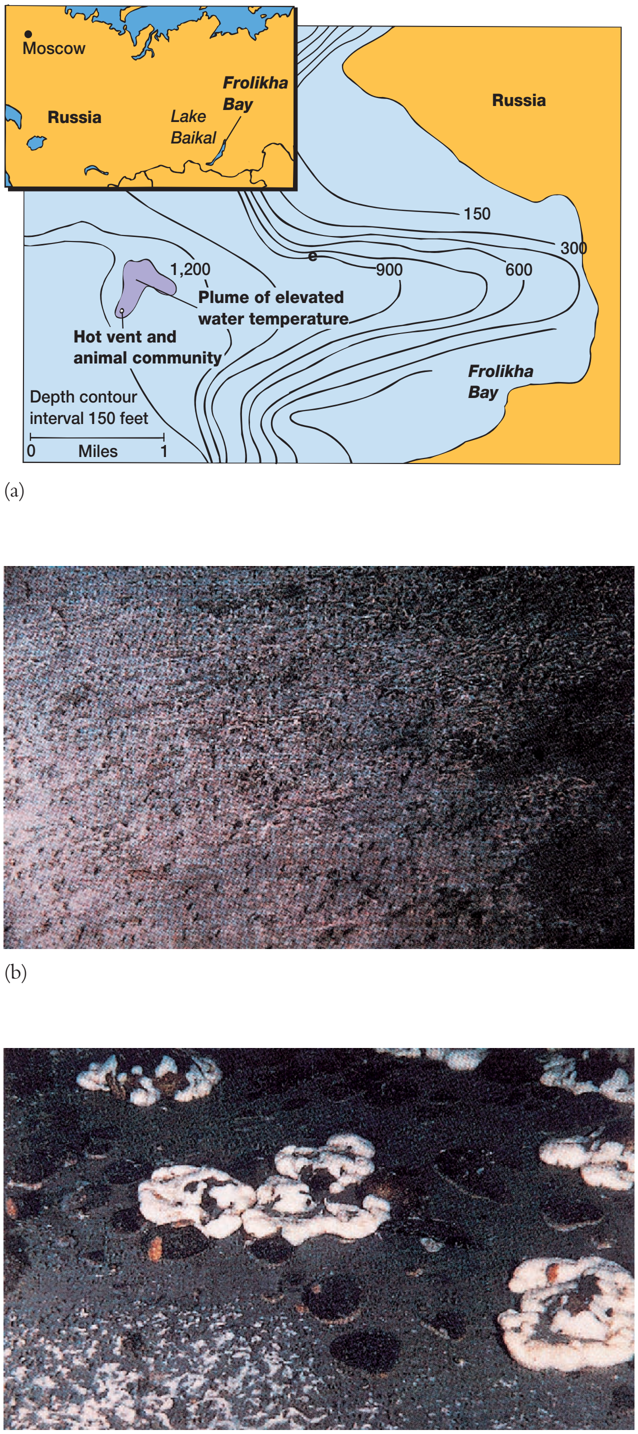
A hydrogen sulfide–based ecosystem has been discovered in southern Romania that is closer to the earth's surface. Caves in the area contain mats of microorganisms that fix carbon dioxide using hydrogen sulfide as the reductant. Forty-eight species of cave-adapted invertebrates are sustained by this chemoautotrophic base.

A form of protocooperation also occurs when a population of similar microorganisms monitors its own density, the process of quorum sensing, which was discussed in section 6.5. The microorganisms produce specific autoinducer compounds, and as the population increases and the concentration of these compounds reaches critical levels, specific genes are expressed. These responses are important for microorganisms that form associations with plants and animals, and particularly for human pathogens.

1. Why are *Alvinella, Rimicaris* and *Eubostrichus* good examples of protocooperative microorganism-animal interactions?
2. What important freshwater hydrothermal vent communities have been described?

Commensalism

Commensalism [Latin *com,* together, and *mensa,* table] is a relationship in which one symbiont, the **commensal,** benefits while the other (sometimes called the host) is neither harmed nor helped as shown in figure 28.1. This is a unidirectional process. Often both the host and the commensal "eat at the same table." The spatial proximity of the two partners permits the commensal to feed on substances captured or ingested by the host, and the commensal often obtains shelter by living either on or in the host. The commensal is not directly dependent on the host metabolically and causes it no particular harm. When the commensal is separated from its host experimentally, it can survive without being provided some factor or factors of host origin.



(c)

Figure 28.14 Hydrothermal Vent Ecosystems in Freshwater Environments. Lake Baikal (in Russia) has been found to have low temperature hydrothermal vents. (**a**) Location of Lake Baikal, site of the hydrothermal vent field. (**b**) Bacterial mat near the center of the vent field. (**c**) Bacterial filaments and sponges at the edge of the vent field. *(a) Source: Data from the National Geographic Society.*

Commensalistic relationships between microorganisms include situations in which the waste product of one microorganism is the substrate for another species. An example is nitrification, the oxidation of ammonium ion to nitrite by microorganisms such as *Nitrosomonas,* and the subsequent oxidation of the nitrite to nitrate by *Nitrobacter* and similar bacteria (*see pp. 193–94*). *Nitrobacter* benefits from its association with *Nitrosomonas* because it uses nitrite to obtain energy for growth.

Commensalistic associations also occur when one microbial group modifies the environment to make it more suited for another organism. For example, in the intestine the common, nonpathogenic strain of *Escherichia coli* lives in the human colon, but also grows quite well outside the host, and thus is a typical commensal. When oxygen is used up by the facultatively anaerobic *E. coli,* obligate anaerobes such as *Bacteroides* are able to grow in the colon. The anaerobes benefit from their association with the host and *E. coli,* but *E. coli* derives no obvious benefit from the anaerobes. In this case the commensal *E. coli* contributes to the welfare of other symbionts. Commensalism can involve other environmental modifications. The synthesis of acidic waste products during fermentation stimulate the proliferation of more acid-tolerant microorganisms, which are only a minor part of the microbial community at neutral pHs. A good example is the succession of microorganisms during milk spoilage. When biofilms are formed (section 28.4), the colonization of a newly exposed surface by one type of microorganism (an initial colonizer) makes it possible for other microorganisms to attach to the microbially modified surface.

Commensalism also is important in the colonization of the human body and the surfaces of other animals and plants. The microorganisms associated with an animal skin and body orifices can use volatile, soluble, and particulate organic compounds from the host as nutrients (*see section 31.2*). Under most conditions these microbes do not cause harm, other than possibly contributing to body odor. Sometimes when the host organism is stressed or the skin is punctured, these normally commensal microorganisms may become pathogenic. These interactions will be discussed in chapter 31.

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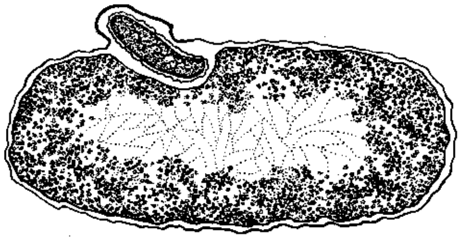
1. How does commensalism differ from protocooperation?
2. Why is nitrification a good example of a commensalistic process?
3. Why are commensalistic microorganisms important for humans? Where are these found in relation to the human body?

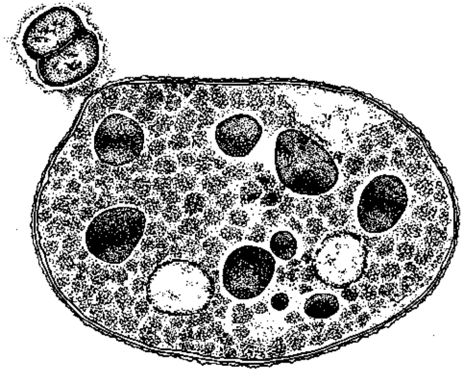
Predation

Predation is a widespread phenomenon where the predator engulfs or attacks the prey, as shown in figure 28.1. The prey can be larger or smaller than the predator, and this normally results in the death of the prey.

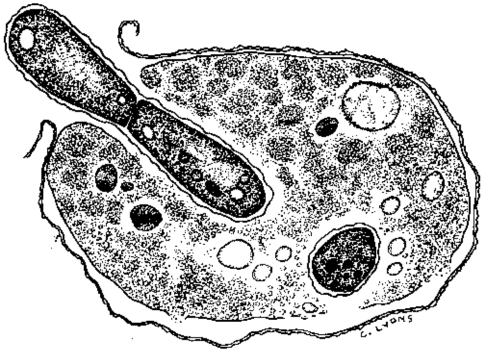
An interesting array of predatory bacteria are active in nature. Several of the best examples are shown in **figure 28.15,** including *Bdellovibrio, Vampirococcus,* and *Daptobacter.* Each of these has a unique mode of attack against a susceptible bacterium. *Bdellovibrio* penetrates the cell wall and multiplies between the wall and the



(a) *Bdellovibrio*



(b) *Vampirococcus*



(c) *Daptobacter*

Figure 28.15 Examples of Predatory Bacteria Found in Nature. (**a**) *Bdellovibrio,* a periplasmic predator that penetrates the cell wall and grows outside the plasma membrane, (**b**) *Vampirococcus* with its unique epibiotic mode of attacking a prey bacterium, and (**c**) *Daptobacter* showing its cytoplasmic location as it attacks a susceptible bacterium.

plasma membrane, a periplasmic mode of attack, followed by lysis of the prey and release of progeny (*see figure 22.33*). This bacterium has an interesting life cycle, which is discussed in section 22.4.

Nonlytic forms also are observed. *Vampirococcus* attaches to the surface of the prey (an epibiotic relationship) and then secretes enzymes to release the cell contents. *Daptobacter* penetrates a susceptible host and uses the cytoplasmic contents as a nutrient source.

Ciliates are excellent examples of predators that engulf their prey, and based on work with fluorescently marked prey bacteria, a single ciliate can ingest 60 to 70 prey bacteria per hour! Predation on bacteria is important in the aquatic environment and in sewage treatment where the ciliates remove suspended bacteria that have not settled.

A surprising finding is that predation has many beneficial effects, especially when one considers interactive populations of predators and prey, as summarized in **table 28.3.** Simple ingestion and assimilation of a prey bacterium can lead to increased rates of nutrient cycling, critical for the functioning of the **microbial loop** (*see section 29.1* and *figure 29.4*). In this process, organic matter produced through photosynthetic and chemotrophic activity is mineralized before it reaches the higher consumers, allowing the minerals to be made available to the primary producers, in a "loop." This is important in freshwater, marine, and terrestrial environments. Ingestion and short-term retention of bacteria also is critical for functioning of ciliates in the rumen, where methanogenic bacteria contribute to the health of the ciliates by decreasing toxic hydrogen levels through using H_2 to produce methane, which then is passed from the rumen.

Predation also can provide a protective, high-nutrient environment for particular prey. Ciliates ingest *Legionella* and protect this important pathogen from chlorine, which often is used in an attempt to control *Legionella* in cooling towers and air-conditioning units. The ciliate serves as a reservoir host. *Legionella pneumophila* also has been found to have a greater potential to invade macrophages and epithelial cells after predation, indicating that ingestion not only provides protection but also may make the bacterium a better pathogen. A similar phenomenon of survival in protozoa been observed for *Mycobac-*

Table 28.3 The Many Faces of Predation

Predation Result	Example
Digestion	The microbial loop. Soluble organic matter from primary producers is normally used by bacteria, which become a particulate food source for higher consumers. Flagellates and ciliates prey on these bacteria and digest them, making the nutrients they contain available again in mineral form for use in primary production, creating the microbial loop. In this way a large portion of the carbon fixed by the photosynthetic microbes is mineralized and recycled (thus the term microbial loop) and does not reach the higher trophic levels of the ecosystem (*see figure 29.4*). Predation also can reduce the density-dependent stress factors in prey populations, allowing more rapid growth and turnover of the prey than would occur if the predator were not active.
Retention	Bacteria retained within the predator serve a useful purpose, as in the transformation of toxic hydrogen produced by ciliates in the rumen to harmless methane. Also, trapping of chloroplasts (kleptochloroplasty) by protozoa provides the predator with photosynthate.
Protection and increased fitness	The intracellular survival of *Legionella* ingested by ciliates protects it from stresses such as heating and chlorination. Ingestion also results in increased pathogenicity when the prey is again released to the external environment, and this may be required for infection of humans. The predator serves as a reservoir host. Nanoplankton may be ingested by zooplankton and grow in the zooplankton digestive system. They are then released to the environment in a fitter state. Dissemination to new locations also occurs.

terium avium, a pathogen of worldwide concern. These protective aspects of predation have major implications for survival and control of disease-causing microorganisms in the biofilms present in water supplies and air-conditioning systems. In marine systems the ingestion of nanoplankton by zooplankton provides a nutrient-rich environment that allows nanoplankton reproduction in the digestive tract and promotes dissemination in the environment. A similar process occurs after bacteria are ingested by polychaetes (segmented worms found mostly in marine environments).

Fungi often show interesting predatory skills. Some fungi can trap protozoa by the use of sticky hyphae or knobs, sticky networks of hyphae, or constricting or nonconstricting rings. A classic example is *Arthrobotrys,* which traps nematodes by use of constricting rings. After the nematode is trapped, hyphae grow into the immobilized prey and the cytoplasm is used as a nutrient. Other fungi have conidia that, after ingestion by an unsuspecting prey, grow and attack the susceptible host from inside the intestinal tract. In this situation the fungus penetrates the host cells in a complex interactive process.

Thus predation, which usually has a fatal and final outcome for an individual prey organism, has a wide range of beneficial effects on prey populations, and is critical in the functioning of natural environments.

Parasitism

Parasitism is one of the most complex microbial interactions; the line between parasitism and predation is difficult to define (figure 28.1; *see also section 34.1*). This is a relationship in which one of a pair benefits from the other, and the host is usually harmed. This can involve nutrient acquisition and/or physical maintenance in or on the host. In parasitism there is a degree of coexistence of the parasite in association with the host. Depending on the equilibrium between the two organisms, this may shift and what might have been a stable parasitic relationship may then become a pathogenic one which can be defined as predation.

Some bacterial viruses can establish a lysogenic relationship with their hosts, and the viruses, in their prophage state, can confer positive new attributes on the host bacteria, as occurs with toxin production by *Corynebacterium diphtheriae* (*see sections 17.5 and 34.3*). Parasitic fungi include *Rhizophydium sphaerocarpum* with the alga *Spyrogyra.* Also, *Rhizoctonia solani* is a parasite of *Mucor* and *Pythium,* which is important in **biocontrol processes,** the use of one microorganism to control another. Human diseases caused by viruses, bacteria, fungi, and protozoa are discussed in chapters 38 through 40.

1. Define predation and parasitism. How are these similar and different?
2. How can a predator confer positive benefits on its prey? Think of the responses of individual organisms versus populations as you consider this question.
3. What are examples of parasites that are important in microbiology?

Amensalism

Amensalism (from the Latin for *not* at the same table) describes the negative effect that one organism has on another organism as shown in figure 28.1. This is a unidirectional process based on the release of a specific compound by one organism which has a negative effect on another organism. A classic example of amensalism is the production of antibiotics that can inhibit or kill a susceptible microorganism (**figure 28.16*a***). The attine ant-fungal mutualistic relationship is promoted by antibiotic-producing bacteria that are maintained in the fungal garden system (figure 28.16*b*). In this case a streptomycete produces an antibiotic that controls *Escovopsis,* a persistent parasitic fungus that can destroy the ant's fungal garden. This unique amensalistic process appears to have evolved 50 million years ago in South America.

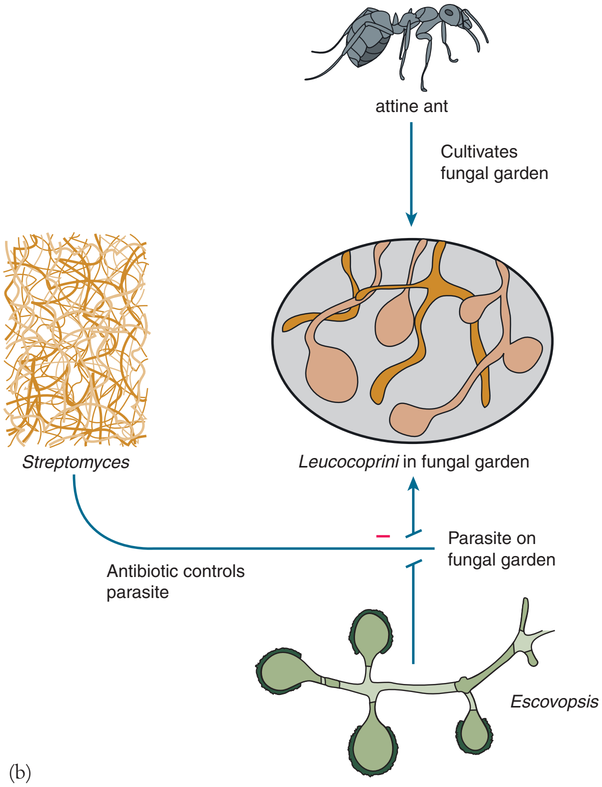
Other important amensalistic relationships involve microbial production of specific organic compounds that disrupt cell wall or plasma membrane integrity. These include the bacteriocins (*see p. 297, 712*). These substances are of increasing interest as food additives for controlling growth of undesired pathogens (*see section 41.3*). Antibacterial peptides can be released by the host and microorganisms in the intestine. These molecules, called cecropins in insects and defensins in mammals, recently have been recognized as effector molecules that play significant roles in innate immunity (*see p. 720*). In animals these molecules are released by phagocytes and intestinal cells, and are as powerful as tetracyclines. Finally, metabolic products, such as organic acids formed in fermentation, can produce amensalistic effects. These compounds inhibit growth by changing the environmental pH, for example, during natural milk spoilage (*see section 41.2*).

Competition

Competition arises when different microorganisms within a population or community try to acquire the same resource, whether this is a physical location or a particular limiting nutrient (figure 28.1). This principle of competition was studied by E. F. Gause, who in 1934 described this as the **competitive exclusion principle.** He found that if the two competing ciliates overlapped too much in terms of their resource use, one of the two protozoan populations was excluded. In chemostats (*see section 6.3*), we may see competition for a limiting nutrient among microorganisms with transport systems of differing affinity. This can lead to the exclusion of the slower-growing population under a particular set of conditions. If the dilution rate is changed, the previously slower-growing population may become dominant. Often two microbial populations that appear to be similar nevertheless coexist. In these cases there is a subtle difference in the characteristics of the microorganisms or their microenvironments that make this coexistence possible.

1. What is the origin of the term amensalism?
2. What are bacteriocins?
3. What is the competitive exclusion principle?

(a)



(b)

Figure 28.16 Amensalism: A Negative Microbe-Microbe Interaction. (**a**) Antibiotic production and inhibition of growth of a susceptible bacterium on an agar medium. (**b**) A schematic diagram describing the use of antibiotic-producing streptomycetes by ants to control fungal parasites in their fungal garden.

Symbioses in Complex Systems

It should be emphasized that the symbiotic interactions discussed in this section do not occur independently. Each time a microorganism interacts with other organisms and their environments, a series of feedback responses occurs in the larger biotic community that will impact other parts of ecosystems. As an illustration, the interactions between the nematode *Eubostrichus parasitiferus* and its protocooperative sulfide-oxidizing bacterium (p. 606) involves a series of symbiotic interactions, as shown in **figure 28.17.** In this case, the protocooperative interaction between the nematodes and the sulfide-oxidizing epibiont is influenced by the population size of the associated bacterium, and whether it is host-associated or free-living. This equilibrium between host-associated and free-

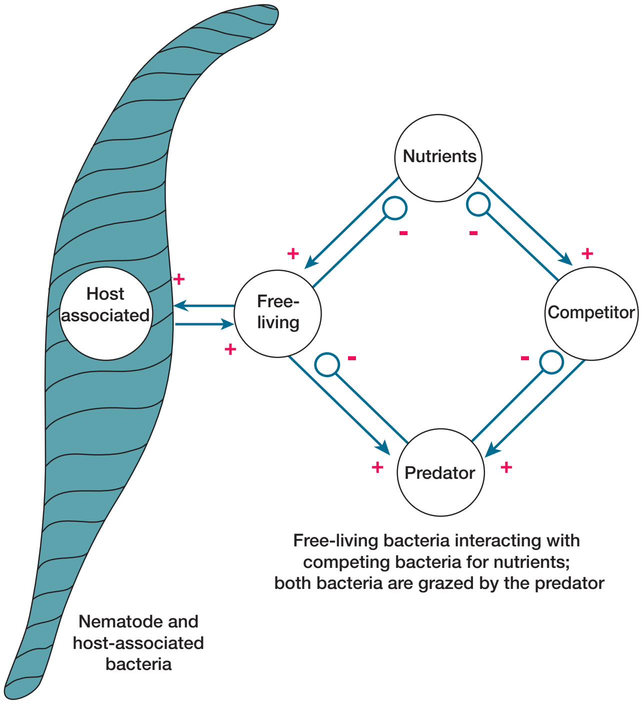


Figure 28.17 Complex Interactions in Microbial Ecology. Interactions between the marine nematode *Eubostrichus parasitiferus* and its host-associated and free-living protocooperative bacteria are influenced by levels of nutrients, as well as by other bacteria competing for these nutrients. Predators, in turn, use both the free-living protocooperative bacteria and the competing bacteria as food sources, leading to complex feedback responses in this dynamic ecosystem. Arrows show positive or enhancing interactions; lines with small circles indicate negative or damping interactions.

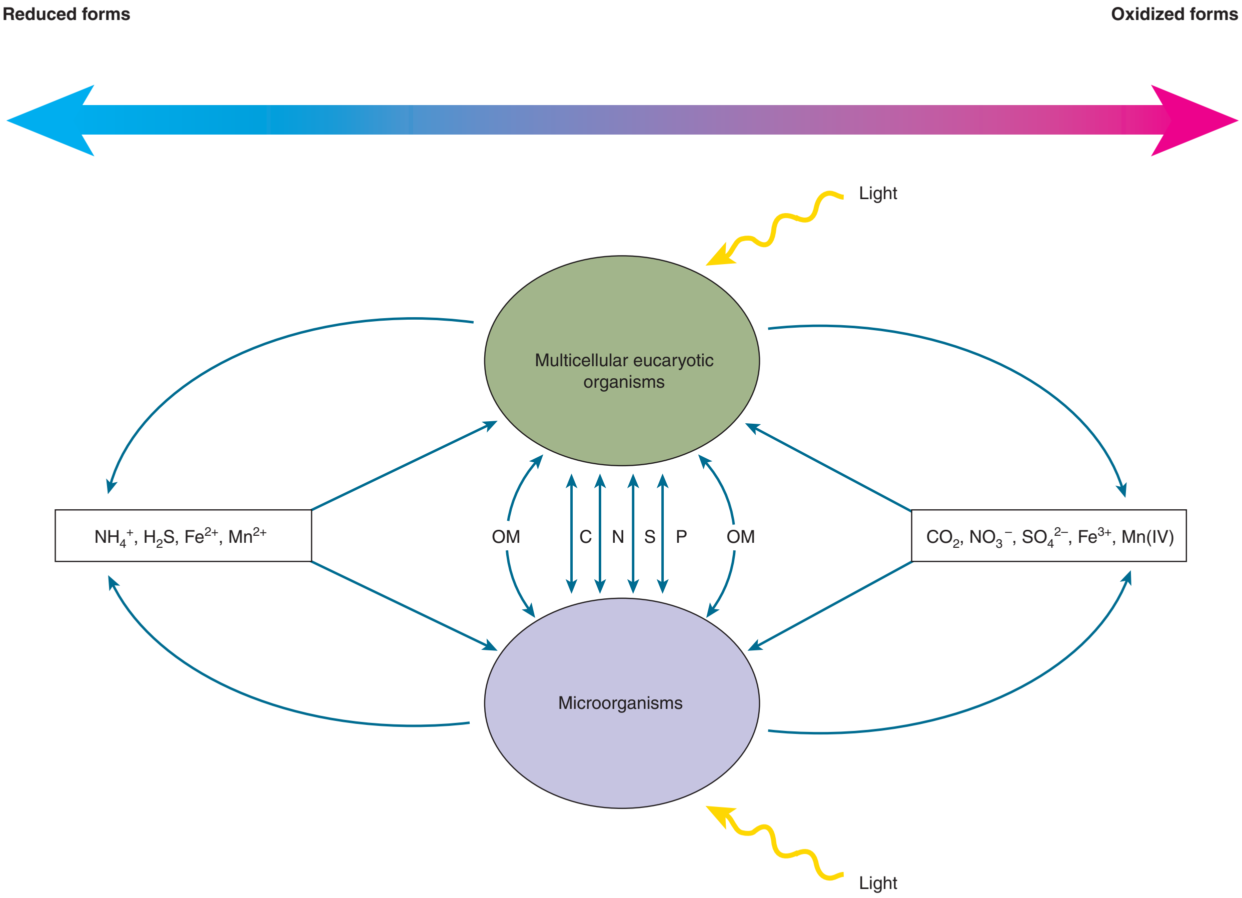


Figure 28.18 **Macrobiogeochemistry: A Cosmic View of Mineral Cycling in Microorganisms, Higher Organisms, and the Abiotic Chemical World.** All biogeochemical cycles are linked, with energy being obtained from light and pairs of reduced and oxidized compounds. Only major flows are shown. See individual cycles for details of energetic-linked relationships. The forms that move between the microorganisms and multicellular organisms can vary. The broad concept is that all cycles are linked. The biotic components include both living forms and those that have died/senesced and which are being processed. Flows from lithogenic sources are important for phosphorus. Methane transformations are only microbial (see discussion of the carbon cycle). Organic matter (OM).

living bacteria is controlled by a series of feedback processes that involve competition for sulfide with other bacteria, and predation on the epibiont and on the competing bacteria. Thus the equilibrium observed at any time is the result of a series of interactions, involving protocooperation, predation, and competition.

28.3 Nutrient Cycling Interactions

Microorganisms, in the course of their growth and metabolism, interact with each other in the cycling of nutrients, including carbon, sulfur, nitrogen, phosphorus, iron, and manganese. This nutrient cycling, called **biogeochemical cycling** when applied to the environment, involves both biological and chemical processes. Nutrients are transformed and cycled, often by oxidation-reduction reactions (*see section 8.5*) that can change the chemical and physical characteristics of the nutrients. All of the biogeochemical cycles are linked (**figure 28.18**), and the metabolism-related transformations of these nutrients have global-level impacts.

The major reduced and oxidized forms of the most important elements are noted in **table 28.4,** together with their valence states. Significant gaseous components occur in the carbon and nitrogen cycles and, to a lesser extent, in the sulfur cycles. Thus a soil, aquatic, or marine microorganism often can fix gaseous forms of carbon and nitrogen compounds. In the "sedimentary" cycles, such as that for iron, there is no gaseous component.

Carbon Cycle

Carbon can be present in reduced forms, such as methane (CH_4) and organic matter, and in more oxidized forms, such as carbon monoxide (CO) and carbon dioxide (CO_2). The major pools

Table 28.4 The Major Forms of Carbon, Nitrogen, Sulfur, and Iron Important in Biogeochemical Cycling

		Major Forms and Valences				
Cycle	**Significant Gaseous Component Present?**	**Reduced Forms**	**Intermediate Oxidation State Forms**			**Oxidized Forms**
C	Yes	CH_4 (–4)	CO (+2)			CO_2 (+4)
N	Yes	NH_4^+, organic N (–3)	N_2 (0)	N_2O (+1)	NO_2^- (+3)	NO_3^- (+5)
S	Yes	H_2S, SH groups in organic matter (–2)	S^0 (0)	$S_2O_3^{2-}$ (+2)	SO_3^{2-} (+4)	SO_4^{2-} (+6)
Fe	No	Fe^{2+} (+2)				Fe^{3+} (+3)

Note: The carbon, nitrogen, and sulfur cycles have significant gaseous components, and these are described as gaseous nutrient cycles. The iron cycle does not have a gaseous component, and this is described as a sedimentary nutrient cycle. Major reduced, intermediate oxidation state, and oxidized forms are noted, together with valences.

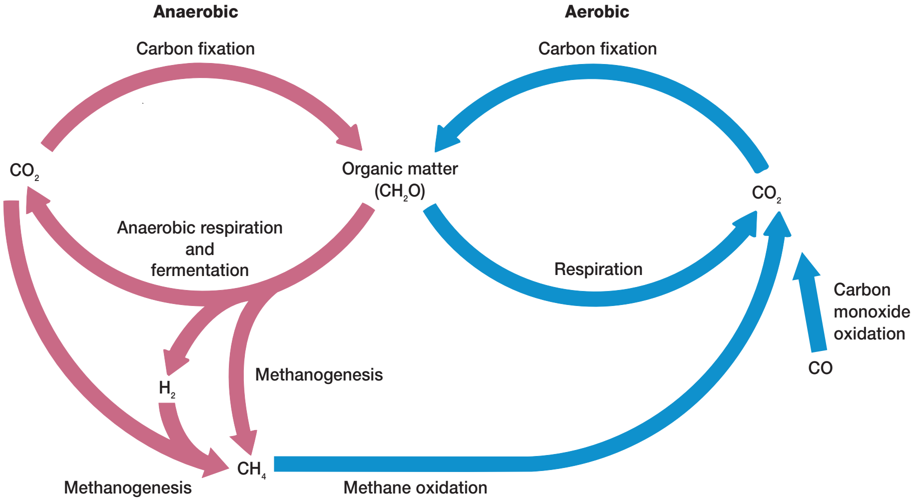


Figure 28.19 The Basic Carbon Cycle in the Environment. Carbon fixation can occur through the activities of photoautotrophic and chemoautotrophic microorganisms. Methane can be produced from inorganic substrates ($CO_2 + H_2$) or from organic matter. Carbon monoxide (CO)—produced by sources such as automobiles and industry—is returned to the carbon cycle by CO-oxidizing bacteria. Aerobic processes are noted with blue arrows, and anaerobic processes are shown with red arrows. Reverse methanogenesis will be discussed in chapter 29.

present in an integrated basic carbon cycle are shown in **figure 28.19.** Reductants (e.g., hydrogen, which is a strong reductant) and oxidants (e.g., O_2) influence the course of biological and chemical reactions involving carbon. Hydrogen can be produced during organic matter degradation especially under anaerobic conditions when fermentation occurs. If hydrogen and methane are generated, they can move upward from anaerobic to aerobic areas. This creates an opportunity for aerobic hydrogen and methane oxidizers to function.

Methane levels in the atmosphere have been increasing approximately 1% per year, from 0.7 to 1.6 to 1.7 ppm (volume) in the last 300 years. This methane is derived from a variety of sources. If an aerobic water column is above the anaerobic zone where the methanogens are located, the methane can be oxidized before it reaches the atmosphere. In many situations, such as in rice paddies without an overlying aerobic water zone, the methane will be released directly to the atmosphere, thus contributing to global atmospheric methane increases. Rice paddies, ruminants, coal mines, sewage treatment plants, landfills, and marshes are important sources of methane. Anaerobic microorganisms such as *Methanobrevibacter* in the guts of termites also can contribute to methane production.

Physiology of aerobic hydrogen and methane utilizers (pp. 193, 502–3)

Table 28.5 Complex Organic Substrate Characteristics That Influence Decomposition and Degradability

			Elements Present in Large Quantity					*Degradation*	
Substrate	**Basic Subunit**	**Linkages (if Critical)**	**C**	**H**	**O**	**N**	**P**	**With O_2**	**Without O_2**
Starch	Glucose	α(1→ 4) α(1→ 6)	+	+	+	–	–	+	+
Cellulose	Glucose	β(1→ 4)	+	+	+	–	–	+	+
Hemicellulose	C6 and C5 monsaccharides	β(1→ 4), β(1→ 3), β(1→ 6)	+	+	+	–	–	+	+
Lignin	Phenylpropane	C–C, C–O bonds	+	+	+	–	–	+	–
Chitin	*N*-acetylglucosamine	β(1→ 4)	+	+	+	+	–	+	+
Protein	Amino acids	Peptide bonds	+	+	+	+	–	+	+
Hydrocarbon	Aliphatic, cyclic, aromatic		+	+	–	–	–	+	+–
Lipids	Glycerol, fatty acids; some contain phosphate and nitrogen	Esters	+	+	+	+	+	+	+
Microbial biomass		Varied	+	+	+	+	+	+	+
Nucleic acids	Purine and pyrimidine bases, sugars, phosphate	Phosphodiester and *N*-glycosidic bonds	+	+	+	+	+	+	+

Carbon fixation occurs through the activities of cyanobacteria and green algae, photosynthetic bacteria (e.g., *Chromatium* and *Chlorobium*), and aerobic chemolithoautotrophs.

In the carbon cycle depicted in figure 28.19, no distinction is made between different types of organic matter that are formed and degraded. This is a marked oversimplification because organic matter varies widely in physical characteristics and in the biochemistry of its synthesis and degradation. Organic matter varies in terms of elemental composition, structure of basic repeating units, linkages between repeating units, and physical and chemical characteristics.

The formation of organic matter is discussed in chapters 10 through 12. The degradation of this organic matter, once formed, is influenced by a series of factors. These include (1) nutrients present in the environment; (2) abiotic conditions (pH, oxidation-reduction potential, O_2, osmotic conditions), and (3) the microbial community present.

The major complex organic substrates used by microorganisms are summarized in **table 28.5.** Of these, only previously grown microbial biomass contains all of the nutrients required for microbial growth. Chitin, protein, microbial biomass, and nucleic acids contain nitrogen in large amounts. If these substrates are used for growth, the excess nitrogen and other minerals that are not used in the formation of new microbial biomass will be released to the environment, in the process of **mineralization.** This is the process in which organic matter is decomposed to release simpler, inorganic compounds (e.g., CO_2, NH_4^+, CH_4, H_2).

The other complex substrates in table 28.5 contain only carbon, hydrogen, and oxygen. If microorganisms are to grow by using these substrates, they must acquire the remaining nutrients they need for biomass synthesis from the environment; in the process of **immobilization.**

The oxygen relationships for the use of these substrates also are of interest, because most of them can be degraded easily with or without oxygen present. The exceptions are hydrocarbons and lignin. Hydrocarbons are unique in that microbial degradation, especially of straight-chained and branched forms, involves the initial addition of molecular O_2. Recently, anaerobic degradation of hydrocarbons with sulfate or nitrate as oxidants has been observed. With sulfate present, organisms of the genus *Desulfovibrio* are active. This occurs only slowly and with microbial communities that have been exposed to these compounds for extended periods. Such degradation may have resulted in the sulfides that are present in "sour gases" associated with petroleum.

Lignin, an important structural component in mature plant materials, is a complex amorphous polymer based on a phenylpropane building block, linked by carbon-carbon and carbon-ether bonds. It makes up approximately 1/3 of the weight of wood. This is a special case in which biodegradability is dependent on O_2 availability. There often is no significant degradation because most filamentous fungi that degrade native lignin in situ can function only under aerobic conditions where oxidases can act by the release of active oxygen species. Lignin's lack of biodegradability under anaerobic conditions results in accumulation of lignified materials, including the formation of peat bogs and muck soils. This absence of lignin degradation under anaerobic conditions also is important in construction. Large masonry structures often are built on swampy sites by driving in wood pilings below the water table and placing the building footings on the pilings. As long as the foundations remain water-saturated and anaerobic, the structure is stable. If the water table drops, however, the pilings will begin to rot and the structure will be threatened. Similarly, the cleanup of harbors can lead to decomposition of costly docks built with wooden pilings due to increased aerobic degradation of wood by filamentous fungi. Rumen function provides a final example of the relationship between

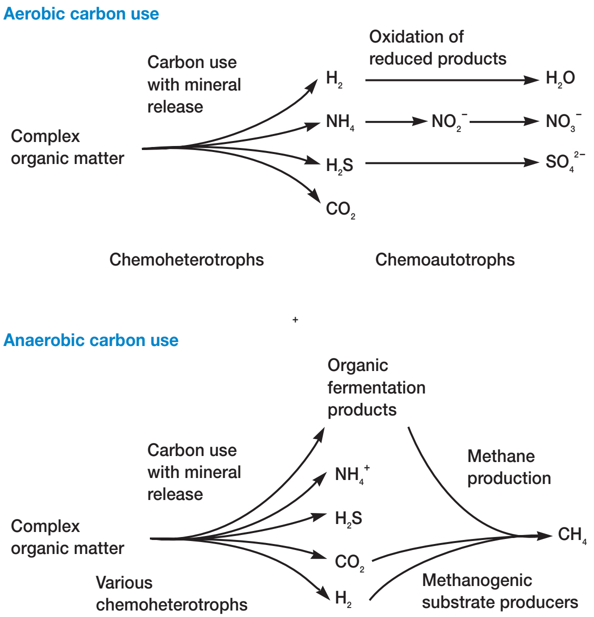


Figure 28.20 **The Influence of Oxygen on Organic Matter Decomposition.** Microorganisms form different products when breaking down complex organic matter aerobically than they do under anaerobic conditions. Under aerobic conditions oxidized products accumulate, while reduced products accumulate anaerobically. These reactions also illustrate commensalistic transformations of a substrate, where the waste products of one group of microorganisms can be used by a second type of microorganism.

lignin degradation and oxygen. The rumen (pp. 602–4), being almost free of oxygen, does not allow significant degradation of lignin present in animal feeds. The use of sugars and carbohydrates in the rumen leaves an inactive residue that can improve soils more effectively than the original feeds.

Patterns of microbial degradation are important in many habitats. They contribute to the accumulation of petroleum products, the formation of bogs, and the preservation of valuable historical objects.

The presence or absence of oxygen also affects the final products that accumulate when organic substrates have been processed by microorganisms and mineralized either under aerobic or anaerobic conditions. Under aerobic conditions, oxidized products such as nitrate, sulfate, and carbon dioxide (**figure 28.20**) will result from microbial degradation of complex organic matter. In comparison, under anaerobic conditions reduced end products tend to accumulate, including ammonium ion, sulfide, and methane.

These oxidized and reduced forms, if they remain in the aerobic or anaerobic environments where they were formed, will usually only serve as nutrients. If mixing occurs, oxidized species might be moved to a more reduced zone or reduced species might be moved to a more oxidized zone. Under such circumstances, additional energetic possibilities (linking of oxidants and reductants) will be created, leading to succession and further nutrient cycling as these mixed oxidants and reductants are exploited by the microbial community.

1. What is biogeochemical cycling?
2. Which organic polymers discussed in this section do and do not contain nitrogen?
3. What is unique about lignin and its degradation?
4. Define mineralization and immobilization and give examples.
5. What C, N, and S forms will accumulate after anaerobic degradation of organic matter?

Sulfur Cycle

Microorganisms contribute greatly to the sulfur cycle, a simplified version of which is shown in **figure 28.21.** Photosynthetic microorganisms transform sulfur by using sulfide as an electron source, allowing *Thiobacillus* and similar chemolithoautotrophic genera to function (*see pp. 193–94 and 496–98*). In contrast, when sulfate diffuses into reduced habitats, it provides an opportunity for different groups of microorganisms to carry out **sulfate reduction.** For example, when a usable organic reductant is present, *Desulfovibrio* uses sulfate as an oxidant (*see pp. 190 and 507–10*). This use of sulfate as an external electron acceptor to form sulfide, which accumulates in the environment, is an example of a **dissimilatory reduction** process and anaerobic respiration. In comparison, the reduction of sulfate for use in amino acid and protein biosynthesis is described as an **assimilatory reduction** process (*see section 10.4*). Other microorganisms have been found to carry out dissimilatory elemental sulfur reduction. These include *Desulfuromonas* (*see pp. 507–10*), thermophilic archaea (*see chapter 20*), and also cyanobacteria in hypersaline sediments. Sulfite is another critical intermediate that can be reduced to sulfide by a wide variety of microorganisms, including *Alteromonas* and *Clostridium,* as well as *Desulfovibrio* and *Desulfotomaculum. Desulfovibrio* is usually considered as an obligate anaerobe. Recent research, however, has shown that this interesting organism also respires using oxygen, when it is present at a dissolved oxygen level of 0.04%.

In addition to the very important photolithotrophic sulfur oxidizers such as *Chromatium* and *Chlorobium,* which function under strict anaerobic conditions in deep water columns, a large and varied group of bacteria carry out **aerobic anoxygenic photosynthesis.** These aerobic anoxygenic phototrophs use bacteriochlorophyll *a* and carotenoid pigments and are found in marine and freshwater environments; they are often components of microbial mat communities. Important genera include *Erythromonas, Roseococcus, Porphyrobacter,* and *Roseobacter.*

"Minor" compounds in the sulfur cycle play major roles in biology. An excellent example is dimethylsulfoniopropionate (DMSP), which is used by bacterioplankton (floating bacteria) as a sulfur source for protein synthesis, and which is transformed to dimethylsulfide (DMS), a volatile sulfur form that can affect atmospheric processes.

When pH and oxidation-reduction conditions are favorable, several key transformations in the sulfur cycle also occur as the

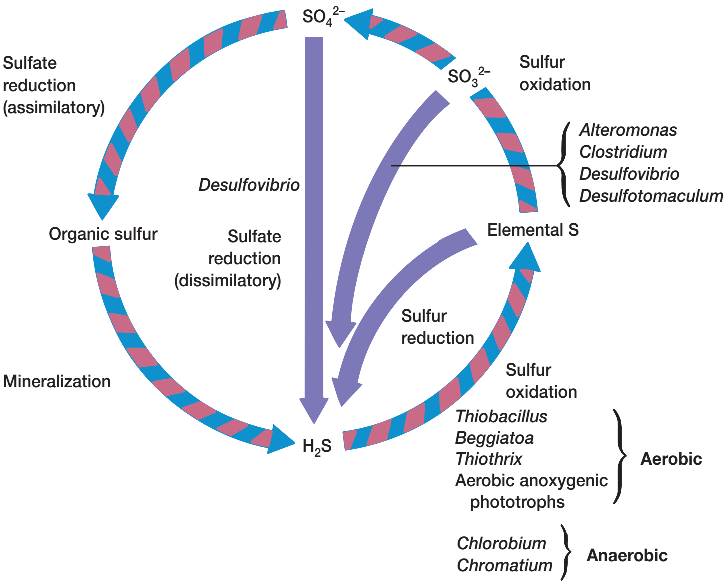


Figure 28.21 **The Basic Sulfur Cycle.** Photosynthetic and chemosynthetic microorganisms contribute to the environmental sulfur cycle. Sulfate and sulfite reductions carried out by *Desulfovibrio* and related microorganisms, noted with purple arrows, are dissimilatory processes. Sulfate reduction also can occur in assimilatory reactions, resulting in organic sulfur forms. Elemental sulfur reduction to sulfide is carried out by *Desulfuromonas,* thermophilic archaea, or cyanobacteria in hypersaline sediments. Sulfur oxidation can be carried out by a wide range of aerobic chemotrophs and by aerobic and anaerobic phototrophs.

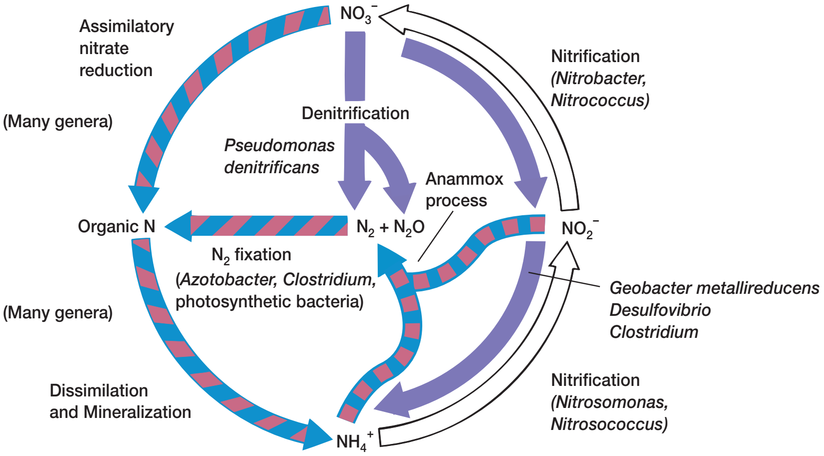


Figure 28.22 **The Basic Nitrogen Cycle.** Flows that occur predominantly under aerobic conditions are noted with open arrows. Anaerobic processes are noted with solid bold arrows. Processes occurring under both aerobic and anaerobic conditions are marked with cross-barred arrows. The anammox reaction of NO_2^- and NH_4^+ to yield N_2 is shown. Important genera contributing to the nitrogen cycle are given as examples.

result of chemical reactions in the absence of microorganisms. An important example of such an abiotic process is the oxidation of sulfide to elemental sulfur. This takes place rapidly at a neutral pH, with a half-life of approximately 10 minutes for sulfide at room temperature.

Nitrogen Cycle

Several important aspects of the basic nitrogen cycle will be discussed: the processes of nitrification, denitrification, and nitrogen fixation (**figure 28.22**). It should be emphasized that this is a "basic" nitrogen cycle. Although not mentioned in the figure, the heterotrophs can carry out nitrification, and some of these heterotrophs combine nitrification with anaerobic denitrification, thus oxidizing ammonium ion to N_2O and N_2 with depressed oxygen levels. The occurrence of anoxic ammonium ion oxidation (anammox is the term used for the commercial process) means that nitrification is not only an aerobic process. Thus as we learn more about the biogeochemical cycles, including that of nitrogen, the simple cycles of earlier textbooks are no longer accurate representations of biogeochemical processes.

Nitrification is the aerobic process of ammonium ion (NH_4^+) oxidation to nitrite (NO_2^-) and subsequent nitrite oxidation to nitrate (NO_3^-). Bacteria of the genera *Nitrosomonas* and *Nitrosococcus,* for example, play important roles in the first step, and *Nitrobacter* and related chemolithoautotrophic bacteria carry out the second step. Recently *Nitrosomonas eutropha* has been found to oxidize ammonium ion anaerobically to nitrite and nitric oxide (NO) using nitrogen dioxide (NO_2) as an oxidant in a denitrification-related reaction. In addition, **heterotrophic nitrification** by bacteria and fungi contributes significantly to these processes in more acidic environments. Nitrification and nitrifiers (p. 193)

The process of **denitrification** requires a different set of environmental conditions. This dissimilatory process, in which nitrate is used as an oxidant in anaerobic respiration, usually involves heterotrophs such as *Pseudomonas denitrificans.* The major products of denitrification include nitrogen gas (N_2) and nitrous oxide (N_2O), although nitrite (NO_2^-) also can accumulate. Nitrite is of environmental concern because it can contribute to the formation of carcinogenic nitrosamines. Finally, nitrate can be transformed to ammonia in dissimilatory reduction by a variety of bacteria, including *Geobacter metallireducens, Desulfovibrio* spp., and *Clostridium.* Denitrification and anaerobic respiration (pp. 190–91)

Nitrogen assimilation occurs when inorganic nitrogen is used as a nutrient and incorporated into new microbial biomass. Ammonium ion, because it is already reduced, can be directly incorporated without major energy costs. However, when nitrate is assimilated, it must be reduced with a significant energy expenditure. In this process nitrite may accumulate as a transient intermediate. The biochemistry of nitrogen assimilation (pp. 210–14)

Nitrogen fixation can be carried out by aerobic or anaerobic procaryotes and does not occur in eucaryotes. Under aerobic conditions a wide range of free-living microbial genera (*Azotobacter, Azospirillum*) contribute to this process. Under anaerobic conditions the most important free-living nitrogen fixers are members of the genus *Clostridium.* Nitrogen fixation by cyanobacteria such as *Anabaena* and *Oscillatoria* can lead to the enrichment of aquatic environments with nitrogen. These nutrient-enrichment processes are discussed in chapter 29. In addition, nitrogen fixation can occur through the activities of bacteria that develop symbiotic associations with plants. These associations include *Rhizobium* and *Bradyrhizobium* with legumes, *Frankia* in association with many woody shrubs, and *Anabaena,* with *Azolla,* a water fern important in rice cultivation. The establishment of the *Rhizobium*-legume association (pp. 675–78)

The nitrogen-fixation process involves a sequence of reduction steps that require major energy expenditures. Ammonia, the product of nitrogen reduction, is immediately incorporated into organic matter as an amine. Reductive processes are extremely sensitive to O_2 and must occur under anaerobic conditions even in aerobic microorganisms. Protection of the nitrogen-fixing enzyme is achieved by means of a variety of mechanisms, including physical barriers, as occurs with heterocysts in some cyanobacteria (*see section 21.3*), O_2 scavenging molecules, and high rates of metabolic activity. The biochemistry of nitrogen fixation (pp. 212–14)

As shown in figure 28.22, microorganisms have been isolated that can couple the anaerobic oxidation of NH_4^+ with the reduction of NO_2^-, to produce gaseous nitrogen, in what has been termed the **anammox process** (*an*oxic *amm*onia *ox*idation). This may provide a means by which nitrogen can be removed from sewage plant effluents to decrease nitrogen flow to sensitive freshwater and marine ecosystems. It has been suggested that chemolithotrophic members of the planctomycetes (*see section 21.4*) play a role in this process.

1. What are the major oxidized and reduced forms of sulfur and nitrogen?
2. Diagram a simple sulfur cycle.
3. Why is dimethylsulfide (DMS), considered to be a "minor" part of the sulfur cycle, of such environmental importance?
4. What is aerobic anoxygenic photosynthesis?
5. What are nitrification, denitrification, nitrogen fixation, and the anammox process?

Iron Cycle

The iron cycle (figure 28.23) includes several different genera that carry out iron oxidations, transforming ferrous ion (Fe^{2+}) to ferric ion (Fe^{3+}). *Thiobacillus ferrooxidans* carries out this process under acidic conditions, *Gallionella* is active under neutral pH conditions, and *Sulfolobus* functions under acidic, thermophilic conditions. Much of the earlier literature suggested that additional genera could oxidize iron, including *Sphaerotilus* and *Leptothrix.* These two genera are still termed "iron bacteria" by many nonmicrobiologists. Confusion about the role of these genera resulted from the occurrence of the chemical oxidation of ferrous ion to ferric ion (forming insoluble iron precipitates) at neutral pH values, where microorganisms also grow on organic substrates. These microorganisms are now classified as chemoheterotrophs.

Recently microbes have been found that oxidize Fe^{2+} using nitrate as an electron acceptor. This process occurs in aquatic sediments with depressed levels of oxygen and may be another route by which large zones of oxidized iron have accumulated in environments with lower oxygen levels.

Iron reduction occurs under anaerobic conditions resulting in the accumulation of ferrous ion. Although many microorganisms can reduce small amounts of iron during their metabolism, most iron reduction is carried out by specialized iron-respiring microorganisms such as *Geobacter metallireducens, Geobacter sulfurreducens, Ferribacterium limneticum,* and *Shewanella putrefaciens,* which can obtain energy for growth on organic matter using ferric iron as an oxidant.

In addition to these relatively simple reductions to ferrous ion, some magnetotactic bacteria such as *Aquaspirillum magnetotacticum* (*see section 3.3*) transform extracellular iron to the mixed valence iron oxide mineral magnetite (Fe_3O_4) and construct intracellular magnetic compasses. Furthermore, dissimilatory iron-reducing bacteria accumulate magnetite as an extracellular product.

Magnetite has been detected in sediments, where it is present in particles similar to those found in bacteria, indicating a longer-term contribution of bacteria to iron cycling processes. Genes for magnetite synthesis have been cloned into other organisms, creating new magnetically sensitive microorganisms. Magnetotactic bacteria are now described as **magneto-aerotactic bacteria,** due to their using magnetic fields to migrate to the position in a bog or swamp where the oxygen level is best suited for their functioning. In the last decade new microorganisms have been discovered that use ferrous ion as an electron donor in anoxygenic photosynthesis. Thus, with production of ferric ion in lighted