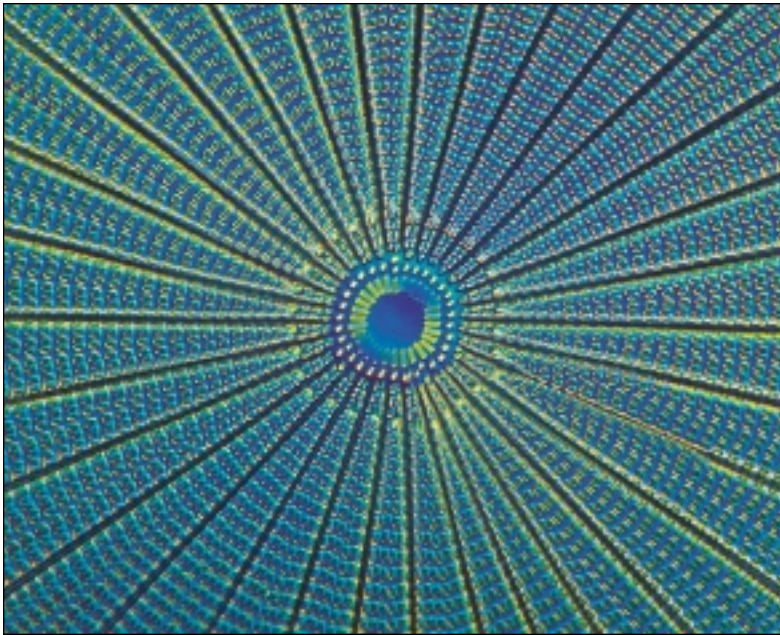


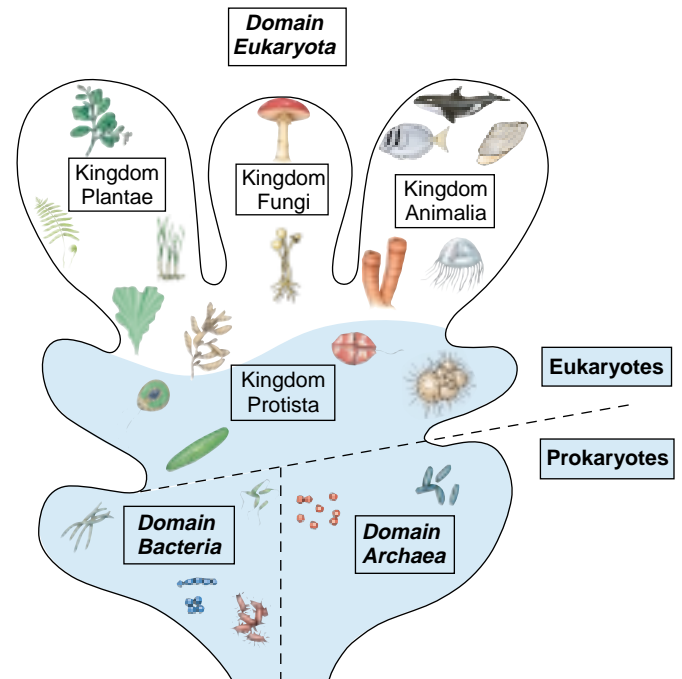
# The Microbial World

chapter

5



Marine diatom (*Arachnodiscus*).



This chapter, the first in our survey of life in the ocean, is devoted to marine microorganisms, which are easily the most abundant forms of marine life. Microorganisms live everywhere in the ocean, from the deepest trenches to the highest tide pools. The microbial world includes an incredibly diverse assortment of organisms, and new microorganisms are discovered regularly. Except for being small, the various groups of microorganisms discussed in this chapter have little in common. All three biological domains, the most basic divisions of life (see “The Tree

of Life,” p. 87), include microorganisms. The diversity of the microbial world can be bewildering even to biologists. Indeed, much of the scientific debate about how to group organisms into kingdoms within domains centers on microorganisms. One thing is for sure: The familiar concepts of “plants” and “animals” have been modified in classification schemes that consist of more than two kingdoms.

Though marine microorganisms include some of the smallest and structurally simplest organisms on earth, they have played critical roles in the evolu-

tion of life on our planet. Without them, the world we live in would be very different. Microorganisms are the most important **primary producers** in many marine environments, and directly or indirectly feed most marine animals. Some microorganisms make essential nutrients

**Primary Producers** Organisms that manufacture organic matter from CO<sub>2</sub>, usually by photosynthesis.

Chapter 4, p. 73

**Table 5.1****Chemical Compounds Used in the Characterization of Marine Photosynthetic Organisms**

	Photosynthetic Pigments	Major Storage Products	Major Cell-Wall Components
Bacteria ( <i>except Cyanobacteria</i> )	Bacteriochlorophyll <i>a, b, c, d, e</i>	Variety of types	Peptidoglycan containing muramic acid
Cyanobacteria	Chlorophyll <i>a</i>	Cyanophycean starch	Chains of amino sugars and amino acids
	Phycobilins (phycocyanin, phycoerythrin, and others)	Cyanophycin (protein)	
	Carotenoids		
Archaea	Bacteriorhodopsin	Variety of types	Variety of types, no muramic acid
Diatoms	Chlorophyll <i>a, c</i>	Chrysolaminarin	Silica
	Carotenoids	Oil	Pectin
Dinoflagellates	Chlorophyll <i>a, c</i>	Starch	Cellulose
	Carotenoids	Oil	
Green algae	Chlorophyll <i>a, b</i>	Starch	Cellulose
	Carotenoids		Carbonates in calcareous algae
Brown algae	Chlorophyll <i>a, c</i>	Laminarin	Cellulose
	Carotenoids (fucoxanthin, and others)	Oil	Alginates
Red algae	Chlorophyll <i>a</i>	Starch	Agar
	Phycobilins (phycocyanin, phycoerythrin)		Carrageenan
	Carotenoids		Cellulose
			Carbonates in coralline algae
Flowering plants	Chlorophyll <i>a, b</i>	Starch	Cellulose
	Carotenoids		

available to other primary producers, either for the first time or by recycling them. Others swim about in the water to ingest food very much like animals do, and play critical roles in marine food chains.

## PROKARYOTES

**Prokaryotes** are the smallest and structurally simplest organisms, and the oldest forms of life on earth. Nonetheless, they carry out nearly all the chemical processes performed by supposedly more complex organisms—most of which evolved in prokaryotes in the first place—as well as some that are unique to prokaryotes.

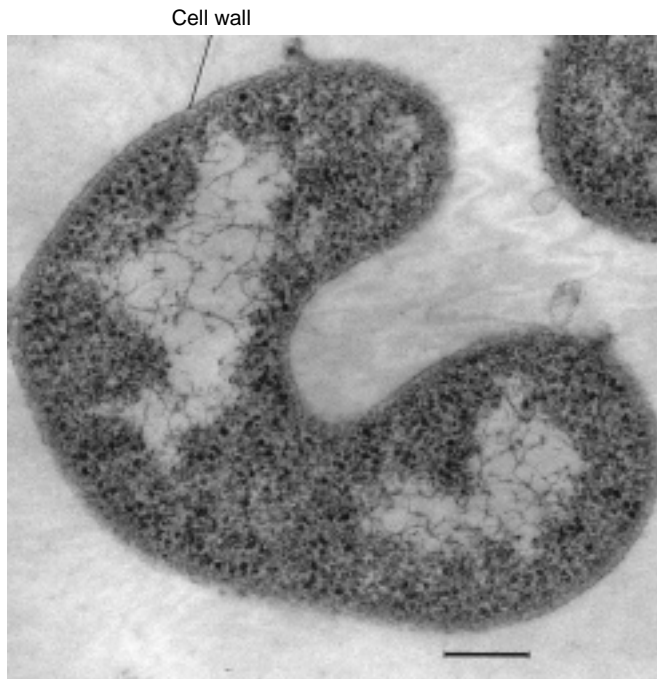
Prokaryotes cells are enclosed by a protective **cell wall**. The **plasma membrane**, or **cell membrane**, lies immediately inside the cell wall (see Fig. 4.7). In addition to lacking membrane-bound organelles, prokaryotes differ from eukaryotes in the circular shape of the DNA molecules that encode their genetic information, in the size of their ribosomes, and in a number of other ways.

Despite their similarities, the two prokaryotic domains, **Bacteria** and **Archaea**, also have important differences, including the chemistry of their cell walls (Table 5.1) and plasma membranes, and the cellular machinery that manufactures proteins. In fact, genetic analyses indicate that bacteria and archaea are as different from each other as they are from humans!

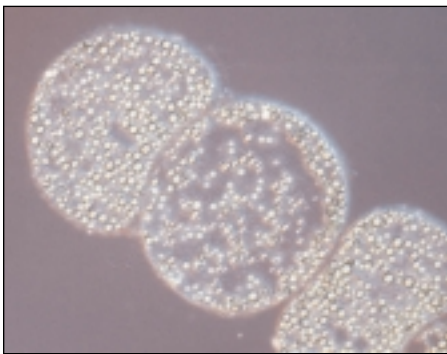
## Bacteria

**Bacteria** (domain **Bacteria**) appear to have branched out very early on the tree of life and are genetically distant from both archaea and eukaryotes. Because they are prokaryotes, bacteria (singular, **bacterium**), have remained structurally simple, but they have evolved a great range of metabolic abilities and chemical features. They are abundant in all parts of the ocean.

Bacterial cells have many shapes, including spheres, coils, rods, or rings (Fig. 5.1) depending on the species. The cells are very small (see Appendix A for relative size), much smaller than those of single-celled eukaryotes. About 250,000 average bacterial cells would fit on the period at the end of this sentence. There are



**FIGURE 5.1** A high-magnification photograph taken with an electron microscope showing *Cyclobacterium marinus*, a ring-forming marine bacterium. The bar represents 0.1 micron ( $\mu\text{m}$ ).



**FIGURE 5.2** Three cells of *Thiomargarita namibiensis*, the largest bacterium known so far. Cells can be 0.75 mm (0.03 in) wide. The round, white structures are sulfur granules.

exceptions, however, such as a sediment bacterium discovered off Namibia, southwest Africa, with cells in filaments as wide as 0.75 mm (0.03 in), large enough to be seen with the naked eye (Fig. 5.2)! Another giant bacterium (0.57 mm or 0.02 in long) is found inside the intestines of a coral reef fish.

The unique chemistry of bacterial cell walls (Table 5.1) makes them rigid

and strong. A stiff or gelatinous covering often surrounds the cell wall as additional protection or a means to attach to surfaces.

Bacteria can grow to extremely high numbers in favorable environments such as sediments or decomposing organic matter. In large numbers, marine bacteria are sometimes visible as iridescent or pink patches on the surface of stagnant pools in mudflats and salt marshes. Sometimes gigantic strands of cells can be seen as whitish hairs on rotting seaweed.

### Heterotrophic Bacteria

Most bacteria, like animals, are **heterotrophs** and obtain their energy from organic matter. Most of these bacteria are **decomposers**, which break down waste products and dead organic matter and release nutrients into the environment. These bacteria, the **decay bacteria**, are vital to life on earth because they ensure the recycling of essential nutrients. They are found everywhere in the marine environment—on almost all surfaces as well as in the water column. They are especially abundant in bottom sediments,

which are usually rich in organic matter. All organic matter is sooner or later decomposed, though in very deep, cold water the process is slower than elsewhere (see “Bacteria in the Deep Sea,” p. 374).

Decay and other types of bacteria play a crucial role because they constitute a major part of the organic matter that feeds countless bottom-dwelling animals. Even many organic particles in the water column are composed mostly of bacteria. Marine bacteria are also important in recycling dissolved organic matter in oceanic food webs (see “The Microbial Loop,” p. 343). Other marine bacteria are beneficial because they are involved in degrading oil and other toxic pollutants that find their way into the environment. The same process of decomposition is unfortunately involved in the spoilage of valuable fish and shellfish catches.

### Autotrophic Bacteria

**Autotrophic** bacteria make their own organic compounds and thus are primary producers. Some of them are **photosynthetic** (or **photoautotrophs**; see Fig. 4.7). They contain chlorophyll or other photosynthetic pigments (Table 5.1) and, like seaweeds and plants, tap light energy to manufacture organic compounds from  $\text{CO}_2$ . Photosynthetic bacteria are now known to account for much of the primary production in many open-ocean areas. The biochemistry of bacterial photosynthesis, however, is different from that of algae and

**Prokaryotes** Organisms with cells that do not have a nucleus or other organelles.

Chapter 4, p. 74; Figure 4.7

**Eukaryotes** Organisms with cells that contain a nucleus and other organelles that are enclosed by membranes.

Chapter 4, p. 74; Figure 4.8

**Heterotrophs** Organisms that cannot make their own food and must eat the organic matter produced by autotrophs. **Autotrophs** Organisms that can use energy (usually solar energy) to make organic matter.

Chapter 4, p. 72



## SYMBIOTIC BACTERIA—THE ESSENTIAL GUESTS

Some bacteria live in close, or **symbiotic**, associations with other marine organisms. Some symbiotic bacteria are **parasites** that may ultimately cause a disease. Others, on the other hand, benefit their hosts. These symbiotic bacteria began their association by increasing the chances of survival of the host and evolve to become essential—hosts cannot survive without them. In many cases the symbiotic bacteria are even sheltered in special tissues or organs that evolve in the host.

All eukaryotic organisms, including humans, shelter bacteria without which life would be impossible. The chloroplasts and mitochondria of eukaryotic cells evolved from symbiotic bacteria (see “From Snack to Servant: How Complex Cells Arose,” p. 77). Indeed essential, these bacteria have become an integral part of all complex cells.

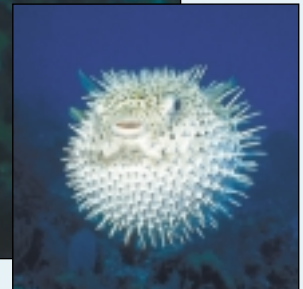
There are many cases of symbiotic bacteria among marine organisms. Symbiotic bacteria, for example, are involved in digesting the wood that is ingested by shipworms (*Teredo*), which happen to be bivalve molluscs, not worms. Like all wood-eating animals, shipworms lack cellulase, the enzymes needed to digest cellulose, the main component of wood. Wood is a surprisingly common habitat in many marine environments, and so everything from driftwood to boat bottoms is exploited by shipworms thanks to their symbiotic bacteria.

Symbiotic bacteria are also responsible for the light, or **bioluminescence**, that is produced by some fishes, squids, octopuses, and other animals of the deep (see “Bioluminescence,” p. 365). The bacteria are usually sheltered in special light-producing organs, or **photophores**. These deep-sea animals, which live in darkness, use light to communicate with other members of their species, lure prey, blend with the light that filters from the surface, and for other functions. Flashlight fishes (*Anomalops*), which live in shallow tropical waters, lodge their symbiotic bacteria in an organ beneath each eye. A shutter mechanism controls the emission of light so that the fish are provided with the ability of “blinking” at night! Groups of fish blink in synchrony, a behavior that is involved in attracting prey.

Chemosynthetic bacteria symbiotic with mussels, clams, and tube worms that live around deep-sea hydrothermal vents have a very particular role: manufacturing organic matter from CO<sub>2</sub> and the abundant hydrogen sulfide (H<sub>2</sub>S) from the vents. The symbiotic bacteria



A Japanese pufferfish, or *fugu* (*Takifugu niphobles*), and an inflated pufferfish (*Diodon histrix*).



live in a special organ, the feeding body, of the giant hydrothermal-vent tube worm *Riftia* (see Fig. 16.31).

Symbiotic bacteria are also involved in some unexpected ways. Pufferfishes are known to store a toxin that is deadly to any predators (or humans) who eat the fish. The fish, or *fugu*, is a delicacy in Japan. Licensed chefs must prepare the fish, otherwise the toxin (tetrodotoxin) will kill anyone feasting on fish that has been improperly prepared. Tetrodotoxin is a deadly neurotoxin (that is, it affects the nervous system). In fact, it is one of the most powerful poisons known, and there is no antidote! The deadly toxin is stored mostly in the liver and gonads of the fish, so the internal organs must be expertly removed. Mistakes do happen and numerous deaths (including the suicides of disgraced cooks) take place every year in Japan. Cooks may still be guilty, but not the puffers: The toxin is now known to be produced not by the fish but by symbiotic bacteria. No one knows yet how the fish is immune to the bacteria toxins.

Tetrodotoxin and very similar toxins have also been found in a variety of marine organisms such as flatworms, snails, crabs, sea stars, and several species of fishes. It has also been found in the blue-ring octopus, a notoriously toxic animal. We are not yet sure if in all of these animals the toxin is produced, as in *fugu*, by symbiotic bacteria or if it is accumulated from their food. Tetrodotoxin of an unknown source has also been found in dead sea urchins and is suspected as their cause of death.

The production of powerful toxins that are used by other organisms is just one example of the amazing abilities of bacteria—invisible to the eye but powerful giants when it comes to their role in the environment.

plants, and varies considerably among different groups of bacteria. Some bacteria, for example, have a kind of chlorophyll unique to prokaryotes and produce sulfur (S) instead of oxygen (O<sub>2</sub>).

Other bacterial autotrophs, called **chemosynthetic** or **chemoautotrophic**, derive energy not from light but from chemical compounds such as hydrogen (H<sub>2</sub>), ammonia (HN<sub>3</sub>), **hydrogen sulfide (H<sub>2</sub>S)**, and other sulfur or iron compounds. Many other ways of obtaining energy to manufacture organic matter are found among chemosynthetic bacteria.

*Bacteria are structurally simple microorganisms that are especially significant as decomposers, breaking down organic compounds into nutrients that can be used by other organisms. They are also an important food source and help degrade pollutants. Some species are autotrophic, and account for much of the oceanic primary production.*

## Cyanobacteria

**Cyanobacteria**, once known as blue-green algae, are a group of photosynthetic bacteria. In addition to having chlorophyll, most contain a bluish pigment called **phycocyanin** (Table 5.1). Most marine cyanobacteria also have a reddish pigment, **phycoerythrin**. The visible color of the organism depends on the relative amounts of the two pigments. When phycocyanin predominates, the bacteria appear blue-green, when phycoerythrin predominates they appear red. Photosynthesis takes place on folded membranes within the cell (as in Fig. 4.7) rather than in chloroplasts as in eukaryotic photosynthetic organisms such as seaweeds and plants. Unlike other photosynthetic bacteria, cyanobacteria do share with eukaryotic photosynthetic organisms a type of chlorophyll, chlorophyll *a* (Table 5.1), and liberate gaseous oxygen in photosynthesis. Most marine cyanobacteria are microscopic, though some form long filaments, strands, or thick mats visible to the naked eye.

Cyanobacteria were perhaps among the first photosynthetic organisms on earth. They are thought to have had an im-



**FIGURE 5.3** Stromatolites, calcareous mounds deposited by cyanobacteria are frequently found as fossils. These, however, are living stromatolites growing in shallow water in the Exuma Cays, Bahama Islands.

portant role in the accumulation of oxygen in our atmosphere. Fossil **stromatolites**, massive **calcareous** mounds formed by cyanobacteria, are known to date back some 3 billion years. Stromatolites are still being formed in tropical seas (Fig. 5.3).

Many species of cyanobacteria can tolerate wide ranges of salinity and temperature and are therefore found practically everywhere in the marine environment, including some unexpected places like the hair of polar bears! Some cyanobacteria, called **endolithic**, burrow into calcareous rocks and coral skeletons. Others form thick, dark crusts along the wave-splashed zone of rocky coasts. Some cyanobacteria exploit oxygen-poor sediments, which may include polluted sites. Planktonic species may rapidly multiply and change the color of the water. Even some of the so-called **red tides** (see “Red Tides and Harmful Algal Blooms,” p. 326) are caused by cyanobacteria that contain a red pigment. A few species are responsible for skin rashes on swimmers and divers.

Many cyanobacteria are known to carry out **nitrogen fixation**, converting

gaseous nitrogen (N<sub>2</sub>) into other nitrogen compounds that can be used by other primary producers (see “Cycles of Essential Nutrients,” p. 227). Some cyanobacteria live on the surface of seaweeds and seagrasses. Photosynthetic organisms that live on other algae or plants are called **epiphytes**. Some cyanobacteria live *inside* algae and are called **endophytes**. Other cyanobacteria are known to lose their ability to photosynthesize, thus becoming heterotrophs.

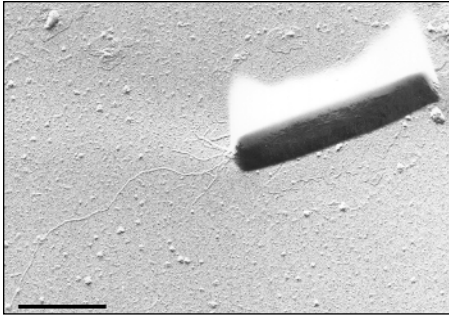
*Cyanobacteria are photosynthetic bacteria widely distributed in the marine environment.*

**Calcareous** Made of calcium carbonate (CaCO<sub>3</sub>).

*Chapter 2, p. 33*

**Plankton** Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.

*Chapter 10, p. 230; Figure 10.19*



**FIGURE 5.4** *Pyrobacterium aerophilum* is a rod-shaped marine archaeum that grows best at temperatures of 100°C. Each cell is about 0.5 microns ( $\mu\text{m}$ ) in diameter.

## Archaea

**Archaea** (domain **Archaea**), often called **archaeobacteria**, are the simplest, most primitive forms of life. Some look very similar to the oldest fossils ever found, cells estimated to be at least 3.8 billion years old. Like bacteria, their cells are small and may be spherical, spiral, or rod-shaped (Fig. 5.4). In fact, until recently archaea (singular, **archaeum**) were thought to be bacteria. It is now thought, however, that despite being prokaryotic, archaea are more closely related to eukaryotes than to bacteria.

Archaea may be heterotrophs or autotrophs and like bacteria exhibit a great variety of metabolic processes. One group, the methanogens is the only group of organisms that produces methane ( $\text{CH}_4$ ). They are important decomposers and extremely abundant in sediments, especially in organic-rich environments like salt marshes and mudflats. Some are nitrogen fixers. They are also important in breaking down organic matter in sewage treatment plants and landfills.

Other groups of archaea were discovered only recently, first in extreme environments on land such as hot sulfur springs, saline lakes, and highly acidic or alkaline environments. Marine archaea were subsequently found in extreme marine environments, such as in very deep water, where they survive at pressures of 300 to 800 atmospheres. Other archaea are associated with **hydrothermal vents** or coastal salt pans.

Because these groups of archaea were first known only from such extreme environments, they were thought to depend on them. Indeed, the term “extremophiles” (“lovers of extremes”) became almost synonymous with archaea. Some archaea, for example, cannot grow in temperatures less than 70° to 80°C (158° to 176°F), and one species can live at 113°C (235°F), the highest of any living organism known. Others depend on extremely acid, alkaline, or salty conditions. New techniques based on detecting **nucleic acid** sequences characteristic of archaea, however, have shown that they are exceedingly common in the water column and other marine environments (see “Tiny Cells, Big Surprises,” p. 99). Thus, the **hypothesis** that archaea are restricted to extreme environments was proven false.

*Archaea are prokaryotic microorganisms once thought to be bacteria, but are more closely related to eukaryotes. Most were thought to be restricted to extreme environments but are now known to be very common in the water column and elsewhere.*

## UNICELLULAR ALGAE

**Algae** (singular, **alga**) are a very diverse group of simple, mostly aquatic (that is, marine and freshwater), mostly photosynthetic organisms. They are eukaryotic, and as such their cells contain organelles enclosed by membranes. Photosynthesis takes place in **chloroplasts**—green, brown, or red organelles with layers of internal membranes that contain photosynthetic pigment (see Fig. 4.8*b*). The color of algae is a reflection of the pigments and their concentration. In contrast to the land plants with which we are familiar, algae lack flowers and have relatively simple reproductive structures. Their nonreproductive cells are also mostly simple and unspecialized. Algae lack true leaves, stems, and roots.

Biologists used to refer to algae as plants. Many of the unicellular algae, however, show animal-like characteristics. Some swim by moving their flagella. Distinguishing these free-swimming algae from some of the structurally sim-

pler animals becomes rather difficult, especially when there are species that carry out photosynthesis like plants, and very similar ones move and eat food particles like animals. Some are claimed by both botanists (plant biologists) and zoologists (animal biologists)! These unicellular organisms are grouped in a separate kingdom, **Protista**. Seaweeds, though multicellular, are algae that are generally placed in the kingdom Protista mostly because they lack the specialized tissues of plants. Seaweeds, together with other multicellular primary producers, the marine plants, are discussed in Chapter 6.

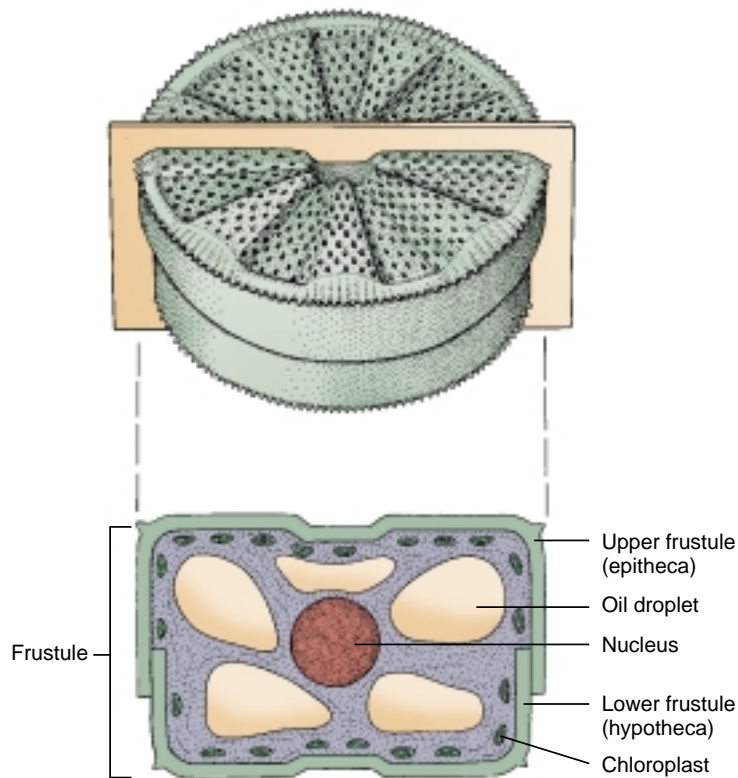
*Algae are protists. They are mostly aquatic primary producers that lack the specialized tissues of plants. They range in size and complexity from single cells to large multicellular seaweeds.*

## Diatoms

**Diatoms** (phylum **Bacillariophyta**) are unicellular, though many species aggregate into chains or star-like groups. Diatom cells are enclosed by cell walls made largely of **silica** ( $\text{SiO}_2$ ), a glass-like material (Table 5.1). This glassy shell, or **frustule**, consists of two tightly fitting halves often resembling a flat, round, or elongate box (Fig. 5.5). The frustule typically has intricate perforations and ornaments such as spines or ribs, making diatoms strikingly beautiful when seen under a microscope (see figure on page 91). The frustule allows light to pass through, so that the conspicuous golden-brown chloroplasts can capture light energy for photosynthesis. The minute perforations allow dissolved gases and nutrients to enter and exit. The sinking of open-ocean diatoms below the well-lit surface layer is often slowed by oil droplets in their cells and spines on the frustules. (see “Staying Afloat,” p. 333).

The characteristic color of diatoms is due to yellow and brown **carotenoid** pigments present in addition to two types of chlorophyll, *a* and *c* (Table 5.1). Diatoms are efficient photosynthetic factories, producing much-needed food (the food being the diatoms themselves), as well as oxygen for other forms of life. They are very important open-water primary producers in





**FIGURE 5.5** Diagrammatic representation of a diatom cell (also see Fig. 15.3).

temperate and polar regions (see “Epipelagic Food Webs,” p. 341). In fact, billions of diatom cells in the ocean account for a hefty share of the organic carbon and oxygen produced on planet earth.

Around half the estimated 12,000 living species of diatoms are marine. Most are planktonic, but many produce a stalk-like structure for attachment to rocks, nets, buoys, and other surfaces. The brownish scum sometimes seen on mudflats or glass aquaria often consists of millions of diatom cells. Some are able to slowly glide on surfaces. A few are colorless and, having no chlorophyll, live on the surfaces of seaweeds as heterotrophs.

• *Diatoms are unicellular organisms that live mostly as part of the plankton. A silica shell is their most distinctive feature. They are important open-water primary producers in cold waters.*

• Diatoms reproduce mostly by cell division, a type of **asexual reproduction**. The overlapping halves of the frustule separate, and each secretes a new, smaller

half (Fig. 5.6). Diatoms may also reproduce by **sexual reproduction**. Some cells develop eggs, others develop flagellated sperm (Fig. 5.6). Fertilization then results in the development of resistant stages known as **auxospores**.

Favorable environmental conditions, such as adequate nutrients and temperature, trigger periods of rapid reproduction called **blooms**. This is a general phenomenon that also occurs in other algae. During blooms, most diatoms get progressively smaller, partly because they use up the silica dissolved in the water and partly because the smaller frustule becomes the larger one in many of the new cells. Full size may be regained by the development of auxospores. The auxospores eventually give rise to larger cells that display the frustule characteristic of the species.

The glassy frustules of dead diatoms eventually settle to the bottom of the sea floor. Here they may form thick deposits of siliceous material that cover large portions of the ocean floor. Such sediments are known as **diatomaceous ooze**. Huge fossil

deposits of these sediments can now be found inland in various parts of the world. The siliceous material, or **diatomaceous earth**, is mined and used in products such as filters for swimming pools, for clarifying beer, as temperature and sound insulators, and as mild abrasives that may find their way into toothpaste.

## Dinoflagellates

The **dinoflagellates** (phylum **Dinoflagellata** or **Pyrrhophyta**) make up another large group of planktonic, unicellular organisms. Their most outstanding characteristic is the possession of two flagella, one wrapped around a groove along the middle of the cell (Fig. 5.7) and one trailing free. These flagella direct movement in practically any direction. Most dinoflagellates have a cell wall that is armored

**Ribosomes** Structures inside the cell, consisting of proteins and RNA, where proteins are manufactured.

*Chapter 4, p. 74; Figure 4.8*

**Hydrothermal Vents** Undersea hot springs associated with mid-ocean ridges and other geologically active environments.

*Chapter 2, p. 38*

**Nucleic Acids** DNA and RNA, complex molecules that store and transmit genetic information.

*Chapter 4, p. 70*

**Hypothesis** A statement about the world that might be true.

*Chapter 1, p. 13*

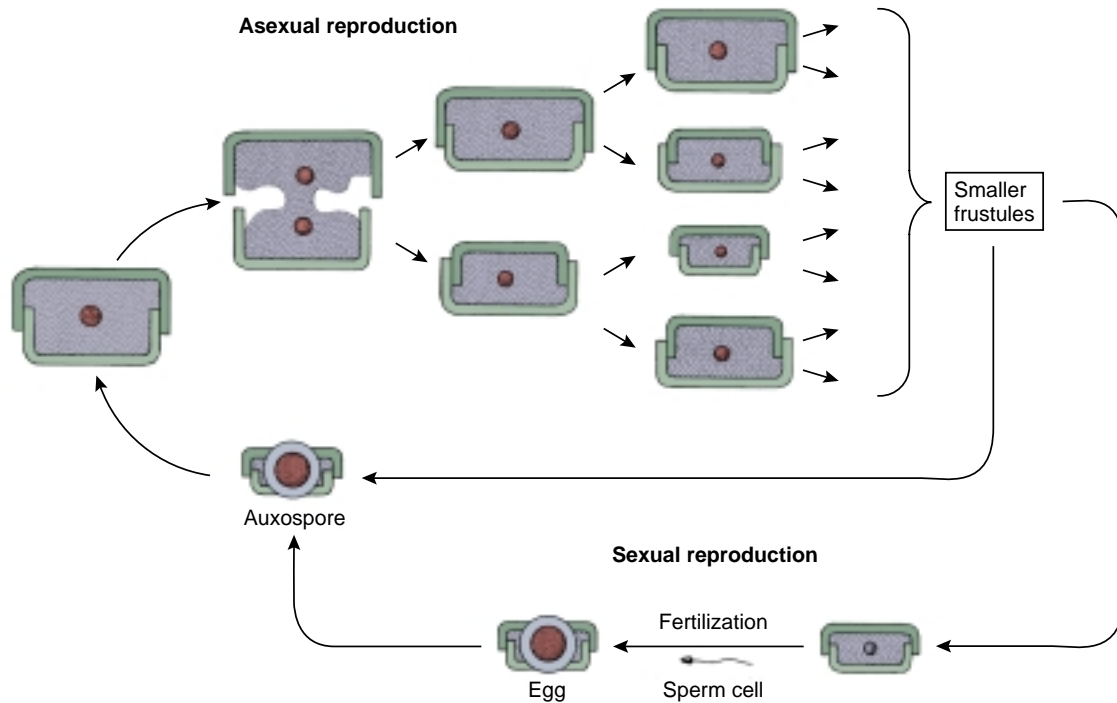
Types of reproduction:

**Asexual (or vegetative)** The production of new individuals by simple division (or other means) without involving *gametes*, so that the offspring are genetically identical to the parents.

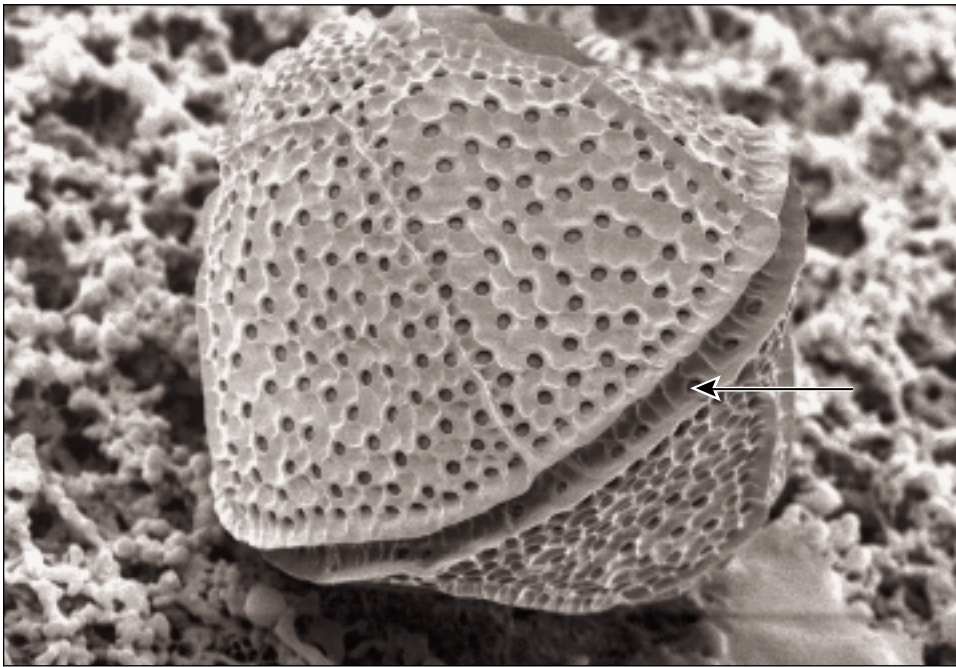
*Chapter 4, p. 82*

**Sexual** The production of new individuals by the formation of *gametes* (sperm and eggs), so that the offspring are genetically different from the parents.

*Chapter 4, p. 83*



**FIGURE 5.6** The usual method of reproduction in diatoms is by cell division. Most, but not all, frustules get smaller with time. Resistant cells called auxospores are produced two ways: directly from the expansion of a smaller frustule or by sexual reproduction when an egg is fertilized by a sperm cell, both of which are liberated from separate frustules.



**FIGURE 5.7** Dinoflagellates such as *Gonyaulax polyedra* have a cell wall, or theca, that consists of cellulose plates. The theca is marked by grooves for the flagella; only one groove is visible here (arrow). This species is bioluminescent and also responsible for red tides.

with plates made of **cellulose**, the characteristic component of the cell walls of seaweeds and land plants (Table 5.1). The plates may have spines, pores, or other ornaments.

Though most dinoflagellates photosynthesize, many can also ingest food particles. A few have a light-sensitive pigment spot that acts as a crude eye. It has been suggested that during their evolution dinoflagellates gained the ability to function as primary producers by capturing and using chloroplasts from other algae. Almost all known dinoflagellates, around 1,200 living species, are marine. Dinoflagellates are important planktonic primary producers, especially in warm water.

Dinoflagellates reproduce almost exclusively by simple cell division (see Fig. 4.18). They sometimes form blooms that color the water red, reddish-brown, yellow, or other unusual shades (see “Red Tides and Harmful Algal Blooms,” p. 326). Some of these dinoflagellates release toxic substances, and seafood collected during red tide periods may be poisonous. Other dinoflagellates are noted





## TINY CELLS, BIG SURPRISES

It is surprising how little biologists know about the lives of marine microbes. We know they are everywhere but we are not sure how many types there are, how common they are, and what exactly they are up to. The situation is rapidly changing as we apply new techniques and approaches studying the private lives of marine microorganisms that call the ocean home.

Information about marine microbes was traditionally gathered largely by growing them in artificial cultures inoculated with seawater samples. This information (what nutrients the microbes need to grow, the type of compounds they produce, and such) was gathered mostly from organisms collected in water samples and then grown under artificial conditions. Even worse, many organisms would not grow in the lab and their presence in the sample went undetected. At least some of this information was used by marine ecologists to deduce the role of microbes in the big ocean world—the role of decay bacteria in releasing nutrients, for example, and of bacteria that convert free nitrogen into nitrates or make dissolved organic matter (DOM) available to larger forms of life. Still, bacteria and other marine microbes remained vital but little-understood forms of life. Some groups of microbes remained undiscovered for a long time. Most archaea, for instance, have been known only since the 1970s. Certainly, other groups remain to be discovered.

The minute prokaryotic cells of bacteria and archaea and the smallest eukaryotic cells of some algae seem to be everywhere but are very difficult to collect and characterize by the microscopic examination of cells. Instead of culturing or filtering out these cells, fragments of nucleic acid (see “Nucleic Acids,” p. 70) are collected from the water and **sequenced**. The presence of organisms can be detected by identifying characteristic DNA or RNA sequences. Furthermore, the partial sequences can yield information about the unique characteristics of these microbes, even if whole cells or whole nucleic acid molecules are not collected.

The presence of RNA sequences characteristic of archaea in seawater and sediment samples has shown archaea to be abundant. In 2001 two groups of archaea were found to be extremely abundant in water samples collected from depths below the photic zone, that is, where light does not penetrate (see Chapter 16). The samples, collected from the Pacific Ocean south of Hawai‘i, showed that archaea were rare at the surface but sharply increased in abundance below depths of 250 m (720 ft). They were as common as bacteria below 1,000 m (3,280 ft). Judging from their numbers and the huge volume of the ocean in question, these archaea are among the ocean’s most abundant forms of life.

Similar techniques based on the detection of characteristic nucleic acid sequences have been used to identify previously unknown eukaryotic microorganisms. These eukaryotes are larger than prokaryotes but still minute (smaller than 2 to 3  $\mu\text{m}$ ), making them difficult to collect and study. This sharply contrasts other unicellular but larger eukaryotes in the phytoplankton, which are relatively easy to collect using plankton nets (see “The Plankton: A New Understanding,” p. 324). In 2001 two new groups related to dinoflagellates were discovered at depths of 250 to 3,000 m (720 to 9,840 ft) near Antarctica. Similar but unique groups of eukaryotic microorganisms (including yet another new group related to dinoflagellates) were reported at the same time by another team working at depths of 75 m (246 ft) in the tropical Pacific. The fact that these microorganisms collected in relatively shallow water (where light still penetrates) are photosynthetic adds a new dimension to the discovery. They represent a previously unknown source of primary production in typically unproductive tropical waters. Other groups of minute algae have been discovered in recent years, including three groups that are related to dinoflagellates. It will not be surprising if additional groups are discovered in the future.

for the production of light, or bioluminescence (see “The Bay of Fire,” on page 100). Though bioluminescence has also been observed in some bacteria and many types of animals, dinoflagellates are generally responsible for the diffuse bioluminescence sometimes seen on the sea surface. This effect is of course seen only at night. It is especially bright if the water is disturbed by a boat or when a wave crashes on the shore.

A variety of marine animals contain in their tissues round, golden-brown photosynthetic cells known as **zooxanthellae**. These cells are actually dinoflagellates adapted to live in close association with an animal host. Though hosts range from sponges and sea anemones to giant clams, it is perhaps in reef-building corals where

zooxanthellae are most significant (see Fig. 14.7). They fix carbon dioxide by photosynthesis, release organic matter used by the coral, and help in the formation of the coral skeleton (see “Coral Nutrition,” p. 301).

A few highly modified dinoflagellates are parasites of seaweeds and some marine animals. Like zooxanthellae, these highly specialized forms reveal their true nature by having life cycles that include free-swimming stages resembling typical dinoflagellates.

One such dinoflagellate is *Pfiesteria*, sometimes called the “phantom dinoflagellate” because they spend most of their lives as harmless resting stages, or cysts, in the sediments. Coastal pollution in the

form of excessive nutrients can trigger blooms of *Pfiesteria*, which release powerful poisonous substances that stun fishes. *Pfiesteria* and other *Pfiesteria*-like microorganisms have been linked to deadly open sores on the fishes. These parasites are also known to be harmful to crabs, oysters, and clams, and have been implicated with sores and symptoms such as temporary memory loss in humans.

**Cellulose** Complex carbohydrate characteristic of plants and other primary producers.

Chapter 4, p. 70



## THE BAY OF FIRE

Imagine entering a quiet tropical bay at night. There are no lights on shore, and on a moonless night the spectacle is unforgettable. As the propeller of your boat churns the black water, an intense blue-green light is left behind, like an eerie trail of cool fire. Outside the bay you see a few sparks of light as you approach, but inside the bay things are very different. Long streaks of light shoot like fireworks beneath the boat. They are created by fleeing fish. A swim in the bay is even more spectacular. Your dive into the water is accompanied by a blinding flood of light, and sparks scatter out as you wave your arms.

Such light effects result from an unusual concentration of bioluminescent dinoflagellates, a natural and permanent phenomenon in a few select locations such as *Bahía Fosforescente*, or Phosphorescent Bay, in southwestern Puerto Rico.

Bioluminescent Bay might be a more apt name because the light is produced by living organisms. The bay's most important source of bioluminescence is *Pyrodinium bahamense*, a unicellular, photosynthetic dinoflagellate about 40 microns ( $\mu\text{m}$ ) (0.004 cm or 0.0015 in) in diameter. As many as 720,000 individuals are found in a gallon of water, many more than outside the bay. The bay is small, about 90 acres, and fan-shaped, and it does not exceed 4.5 m (15 ft) in depth. The main reason that the dinoflagellates are concentrated here is that the bay is connected to the open sea by a narrow, shallow channel. As water containing the dinoflagellates flows into the bay, evaporation in the shallow water causes the surface water to sink because of the increase in salinity, and therefore density. Evaporation is enhanced by the dry and sunny days. The *Pyrodinium* stays near the surface and is therefore not carried out as the denser water flows out along the bottom of the shallow entrance. The tidal range here is only about a foot at the most, so water exchange with the outside is limited. The bay thus acts as a trap that keeps the dinoflagellates from leaving.



*Bahía Fosforescente* in Puerto Rico.

Of all the planktonic organisms that enter the bay, why is *Pyrodinium* favored? A key factor seems to be the thick mangrove trees bordering the bay. They grow along the muddy shores, together with all kinds of organisms living attached to their roots. Mangrove leaves fall into the water, where intense bacterial decomposition increases the organic nutrient levels in the water. Some nutrients essential to the growth of *Pyrodinium*, perhaps vitamins, may be released by bacteria or other microorganisms.

*Bahía Fosforescente* is protected to keep the critical natural balance intact, but bioluminescence has noticeably decreased during recent years. The same phenomenon in a bay in the Bahamas disappeared when its narrow entrance was dredged to allow larger boats, with larger loads of tourists, to pass through.

•  
*Dinoflagellates are unicellular organisms that have two unequal flagella. They are mostly marine and are particularly common in the tropics. Some are noted for their emission of light; others are closely associated with marine animals, especially reef corals.*

•

### Other Unicellular Algae

Three additional groups of primary producers may be abundant in some areas. **Silicoflagellates** (phylum **Chrysophyta**) are characterized by a star-shaped internal skeleton made of silica (Fig. 5.8) and a single flagellum. **Coccolithophorids** (phylum **Haptophyta**) are flagellated, spherical cells covered with button-like

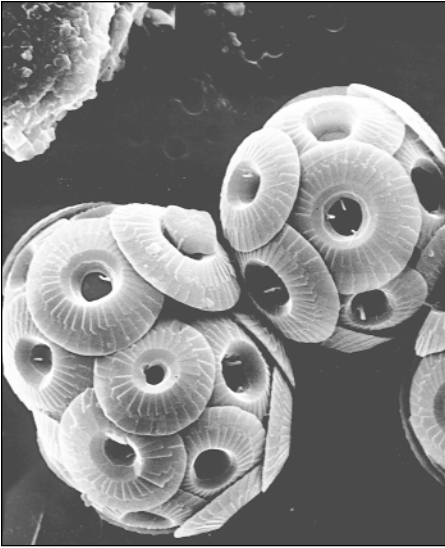
structures called **coccoliths** that are made of calcium carbonate (Fig. 5.9). Coccolith may be found in sediments as fossils. **Cryptomonads** (phylum **Cryptophyta**) have two flagella and lack a skeleton. Members of these three groups are so small that hundreds could fit into a large diatom or dinoflagellate cell.

## PROTOZOANS: THE ANIMAL-LIKE PROTISTS

**Protozoans** are structurally simple and very diverse organisms that are traditionally considered to be animal-like. Most biologists agree that protozoans (meaning



**FIGURE 5.8** Skeleton of *Dictyocha speculum*, a silicoflagellate.



**FIGURE 5.9** Cocolithophorids, like *Umbilicosphaera sibogae* from Australia, are tiny single-celled phytoplankton that can be very important primary producers in the open ocean. The plates that cover the cell are made of calcium carbonate.

“the first animals”) are actually composed of several groups of unrelated origins. Like animals, they ingest food (that is, they are heterotrophs) and are eukaryotic. Some protozoans, however, contain chlorophyll and photosynthesize. Although a few form colonies, most are single-celled, unlike true animals, and only visible under a microscope.

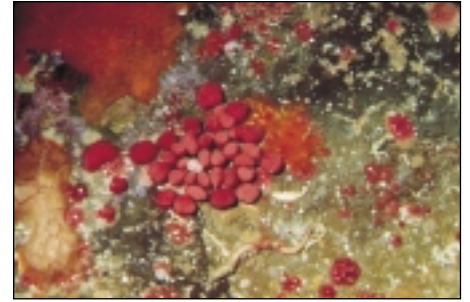
Having a single cell is about the only thing that all protozoans, which show an enormous diversity in structure, function, and lifestyle, have in common. There is little agreement as to how to classify the estimated 50,000 species of protozoans, but for now biologists group them in the kingdom Protista with unicellular algae and seaweeds.

*Protozoans are the most animal-like of the protists. They are eukaryotic and unicellular. They are heterotrophic and ingest food like true animals.*

The minute size and apparent simplicity of protozoans disguise a complex nature. Each cell might be described as a “super cell” because it can perform many



(a)



(b)

**FIGURE 5.10** Foraminiferans. (a) Foraminiferans typically have calcareous shells that consist of a spiral arrangement of chambers. The thin, long strands are the pseudopodia used to capture food. (b) *Homotrema rubrum* is a foraminiferan that forms bright red calcareous growths several millimeters in diameter at the base of corals in the tropics. It is so common in Bermuda that their skeletons are responsible for the island’s famous pink beaches.

of the same functions carried out by the multitude of cells in the structurally more complex organisms. They inhabit water everywhere, living not only in marine and freshwater environments, but even inside other organisms. Many kinds of marine protozoans can be readily collected from sediments rich in organic debris, the surface of seaweeds, the guts of animals, and plankton samples.

### Foraminiferans

The **foraminiferans**, (phylum **Foraminifera**), better known as **forams**, are marine protozoans that usually have a shell, or **test**, made of **calcium carbonate (CaCO<sub>3</sub>)**. The test is usually microscopic and may have several chambers (Fig. 5.10a) that increase in size as the foram grows. **Pseudopodia**—extensions of the jelly-like contents of the cell, or **cytoplasm**—are thin, long, and retractable in forams. The pseudopodia protrude through pores in the shell and form a network used to trap diatoms and other organisms suspended in the water (see Fig. 15.5). Food is then moved into the interior of the cell as if on a conveyor belt.

Most forams live on the bottom, either free or attached. Attached forams may develop into conspicuous growths as much as 5 cm (2 in) in diameter (Fig. 5.10b). Each growth consists of a single cell that forms a shell, though

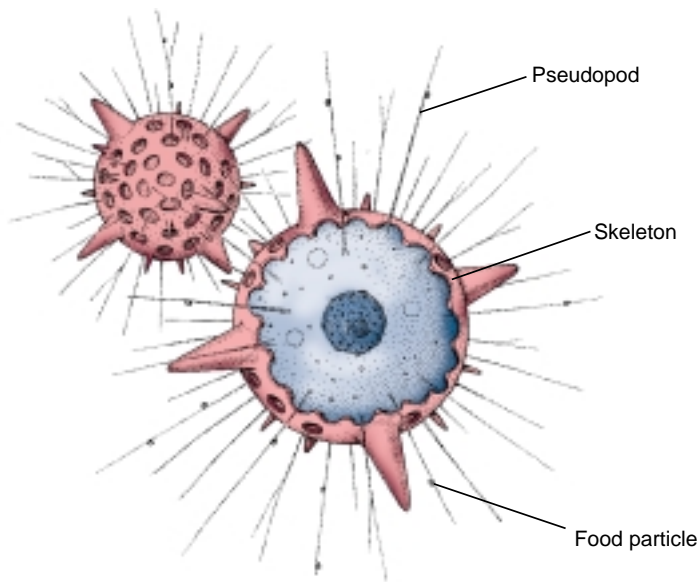
some may be covered with sand grains or other materials instead. The shells of bottom-living forams can be important contributors of calcareous material on coral reefs and sandy beaches. Only a few species are planktonic, but these can be very abundant. Their shells are smaller and thinner than those that live on the bottom and may have delicate spines that aid in flotation. The shells of planktonic forams eventually sink to the bottom in such high numbers that large stretches of the ocean floor are covered by **foraminiferan ooze**, a type of calcareous ooze. Many limestone and chalk beds around the world, like the white cliffs of Dover in England, are products of foram sediments that were uplifted from the ocean floor.

*Forams are protozoans characterized by a shell usually made of calcium carbonate. Most live on the bottom. The shells of planktonic species are important components of marine sediments.*

**Biogenous Sediments** Sediments made of the skeletons and shells of marine organisms; *calcareous ooze* is made of calcium carbonate and *siliceous ooze* of silica.

Chapter 2, p. 33





**FIGURE 5.11** A typical radiolarian cell consists of a dense central portion surrounded by a less dense zone that is involved in the capture of food particles and in buoyancy.

Most species of forams are known only as microfossils. The distribution of these microfossils in sediments is very important to geologists. Shells of warm-water species are slightly larger and more porous than those from colder water. Past water temperatures can be estimated from the distribution of certain marker species. Their distribution is also valuable in the search for oil because it is used to determine the age of sediments.

### Radiolarians

**Radiolarians** (phylum **Polycystina**) are planktonic marine protozoans that secrete elaborate and delicate shells made of glass (silica) and other materials. Typical shells are spherical with radiating spines (Fig. 5.11), though the structure varies. Thin, needle-like pseudopodia capture food, as in forams.

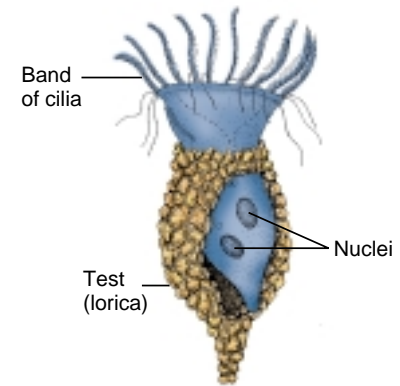
Most radiolarians are microscopic, but some form bizarre, sausage-shaped colonies that reach 3 m (9 ft) in length, making them true giants among protozoans. Radiolarians inhabit open water throughout the oceans. When abundant, the remains of their shells settle to the

bottom and form a siliceous ooze known as **radiolarian ooze**. This ooze is more extensive in deep water because radiolarian shells are more resistant to dissolving under pressure than those of forams.

•  
*The shells of radiolarians are made primarily of silica (glass). These shells form siliceous sediments that cover large areas of the ocean floor.*

### Ciliates

**Ciliates** (phylum **Ciliophora**) are protozoans that have many hair-like **cilia** that are used in locomotion and feeding. The most familiar ciliates are freshwater forms such as *Paramecium*. Marine ciliates are usually found creeping over seaweeds and in bottom sediments. Some live on the gills of clams, in the intestines of sea urchins, on the skin of fish, and in other unusual places. Other ciliates live attached to surfaces, even forming branched colonies of tiny individuals. **Tintinnids** are common ciliates that build vase-like cases, or **loricas**, loosely fitting shells that drift in the water (Fig. 5.12). The cases may be transparent or made of bits of particles.



**FIGURE 5.12** *Tintinnopsis* is a marine tintinnid that forms a vase-like lorica made of sand grains. Specialized cilia on one end are used in feeding.

## FUNGI

**Fungi** (kingdom **Fungi**) are eukaryotic and mostly multicellular, although some, such as molds and yeasts, are unicellular. Many fungi appear superficially plant-like but are heterotrophs that lack chloroplasts and chlorophyll and cannot perform photosynthesis.

There are at least 500 known species of marine fungi. They are mostly microscopic. Many, like bacteria, are decomposers of dead organic matter. They are the most important decomposers of mangrove plants and thus contribute to the recycling of nutrients in mangrove forests (see “Mangroves,” p. 115). Some are parasites of seagrasses or borers in mollusc shells. Others are parasites that cause diseases of economically important seaweeds, sponges, shellfish, and fish. Some marine fungi are being investigated as a source of antibiotics for use in medicine. Still others live in close association with algae to form unique entities, the **lichens**. In lichens the long, filament-like growths of the fungi provide support, while the algae provide food manufactured by photosynthesis. Marine lichens can be found as thick, dark-brown or black patches in the wave-splashed zone of rocky shores, particularly on North Atlantic shores. By comparison with the multitude of lichen species on land, there are very few species of marine lichens.



# interactive exploration

Check out the Online Learning Center at [www.mhhe.com/marinebiology](http://www.mhhe.com/marinebiology) and click on the cover of *Marine Biology* for interactive versions of the following activities.

## Do-It-Yourself Summary

A fill-in-the-blank summary is available in the Online Learning Center, which allows you to review and check your understanding of this chapter's subject material.


## Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

## Critical Thinking

1. Scientists use the particular structure of nucleic acids and other chemical differences to separate the archaea from the bacteria. Can you think of other characteristics that could be used to separate not only these two kingdoms but also between them and members of the kingdom Protista?
2. An autotrophic protist, such as a diatom or a dinoflagellate, can evolve into a heterotrophic protist (and therefore a protozoan) simply by losing its chloroplasts. Under what conditions could such a situation take place?

## For Further Reading

Some of the recommended readings listed below may be available online. These are indicated by this symbol , and will contain live links when you visit this page in the Online Learning Center.

### General Interest

- Burkholder, J. M., 1999. The lurking perils of *Pfiesteria*. *Scientific American*, vol. 281, no. 2, August, pp. 42–49. The life cycle and other aspects of the biology of this potentially harmful parasite.
- Furlow, B., 2001. The freelance poisoner. *New Scientist*, vol. 169, no. 2274, 20 January, pp. 30–33. As in the case of the deadly toxins found in pufferfishes, similar toxic chemicals in other marine organisms may actually be produced by bacteria.
- Hoppert, M. and F. Mayer, 1999. Prokaryotes. *American Scientist*, vol. 87, no. 6, November–December, pp. 518–525. Prokaryotic cells show a complex organization, even when organelles are absent.

- Jarrell, K. F., D. P. Bayley, J. D. Correia and N. A. Thomas, 1999. Recent excitement about the Archaea. *BioScience*, vol. 49, no. 7, July, pp. 530–541. The archaea are useful tools in efforts to understand some of the basic characteristics of life.
- Knight, J., 1999. Blazing a trail. *New Scientist*, vol. 164, no. 2213, 20 November, pp. 28–32. Bioluminescent phytoplankton is used to study the swimming ability of dolphins.
- Leslie, M., 2001. Tales of the sea. *New Scientist*, vol. 169, no. 2275, 27 January, pp. 32–35. New techniques allow the sampling of previously unknown unicellular organisms in the ocean.
- Zimmer, C., 2000. Sea sickness. *Audubon*, vol. 102, no. 3, May–June, pp. 38–45. Bacteria, fungi, and other microorganisms cause serious diseases in marine life, from seagrasses and corals to cetaceans.

### In Depth

- Cahoon, L. B., 1999. The role of benthic microalgae in neritic ecosystems. *Oceanography and Marine Biology: An Annual Review*, vol. 37, pp. 47–86.
- Fleming, L. E., J. Easom, D. Baden, A. Rowan and B. Levin, 1999. Emerging harmful algal blooms and human health: *Pfiesteria* and related organisms. *Environmental Toxicologic Pathology*, vol. 27, pp. 573–581.
- Hyde, K. D., E. B. G. Jones, E. Leano, S. B. Pointing, A. D. Poonyth and L. L. Vrijmued, 1998. Role of fungi in marine ecosystems. *Biodiversity and Conservation*, vol. 7, pp. 1147–1161.
- McFall-Ngai, M. J., 1999. Consequences of evolving with bacterial symbionts: Insights from the squid-Vibrio associations. *Annual Review of Ecology and Systematics*, vol. 30, pp. 235–256.
- Rowan, R., 1998. Diversity and ecology of zooxanthellae on coral reefs. *Journal of Phycology*, vol. 34, pp. 407–417.

### See It in Motion

Video footage of the following animals and their behaviors can be found for this chapter on the Online Learning Center.

- Brown algae moving in surge (Honduras)

## ***Marine Biology on the Net***

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Photosynthetic marine organisms
- Diversity of algae
- Economic and ecological importance of algae
- Diversity of eubacteria
- Cyanobacteria

- *Pfiesteria*
- Diversity of archaea
- Marine protozoans and invertebrates
- Diversity of fungi
- Lichens

## ***Quiz Yourself***

Take the online quiz for this chapter to test your knowledge.