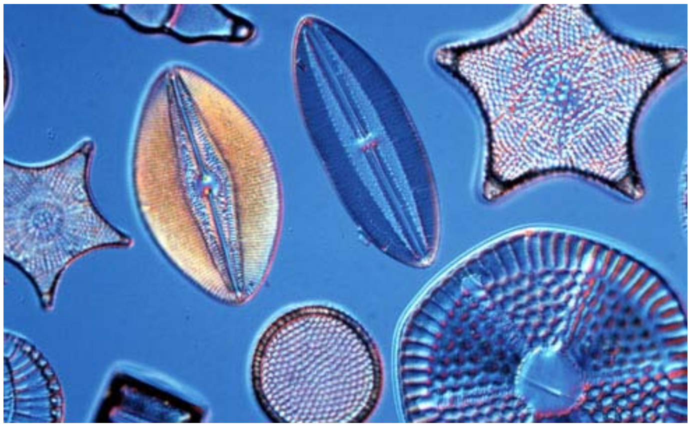
Chapter 21

The Protists



KEY CONCEPTS

1. The Linnaean kingdom Protista is not a monophyletic group but was created to contain all those eukaryotic organisms that were not plants, animals, or fungi. Modern evolutionary studies have discovered that these organisms represent the earliest diverging lineages of eukaryotes. We collectively call this artificial assemblage protists.

2. The protists are diverse. This chapter focuses on the photosynthetic protists, informally called algae. Although they are not closely related in their evolution, algae often have similar morphology, life cycle, and ecology. Collectively, they represent 20,000 to 30,000 species that are largely aquatic. They range from microscopic single cells to a visible tangle of filaments to large seaweeds, such as kelp, that are differentiated into stemlike and leaflike regions.

3. The protists consist of a number of well-supported lineages. The earliest lineage of protists to appear lacks mitochondria, and it includes a number of pathogens. Another early lineage includes the amoebas, slime molds, animals, and fungi. The remaining lineages all have at least some photosynthetic members.

4. The euglenoids typically are unicellular and can be photosynthetic. They may also have a unique organelle, called an eye-spot, that orients them to light. They have no known sexual reproduction and move by means of flagella or by a unique inching motion. They lack cell walls, but they have strips of proteins and microtubules under the cell membrane.

5. The alveolates all have small sacs beneath their cell membrane. They include a lineage of ciliated protists, such as *Paramecium*; a lineage of shelled protists, the foraminifera; a lineage of parasitic or pathogenic organisms called the apicomplexa; and an algal group called the dinoflagellates. Dinoflagellates have unusual chloroplasts that have multiple membranes around them. These may have resulted from the incorporation of another eukaryote that already had chloroplasts. The dinoflagellates cause red tides.

6. The heterokonts are single-celled or multicellular organisms with two unequally sized flagella. Many members tend to have brown or gold photosynthetic pigments. Heterokonts include the water molds, egg fungi, and several lineages of algae. Two major groups are the diatoms, typically single-celled algae with silica cell walls that create vast deposits over time, and brown algae, which comprise the kelps and rockweeds, among other seaweeds, and are important sources of commercial products.

7. A protist clade that this chapter refers to as the plants consists of red and green algae together with the land plants, which are derived within this clade. The red algae are seaweeds that are similar morphologically to the brown algae but smaller

in stature and possessing photosynthetic pigments that allow them to live at great depths. They are the sister group to the green plants.

8. Microscopic, floating forms of algae are ecologically important because they are at the base of aquatic food chains. Larger seaweeds and kelps are economically important because of cell wall materials such as agar, carrageenan, and alginates.

9. Algal life cycles include gametic, zygotic, and sporic types. In many cases, however, asexual reproduction (by cell division, fragmentation of filaments, or mitospores) is more common than sexual reproduction.

21.1 THE PROTISTS: THE FIRST EUKARYOTES

The kingdom Protista was created when biologists began to investigate the diversity of microscopic life. They realized that not all eukaryotic organisms could be easily categorized as plant, animal, or fungus. Protista became a catchall category for all eukaryotes that did not fit anywhere else. Modern biologists have realized from extensive evolutionary studies (initially based on morphology, cell structure, and biochemistry, but more recently on genetics) that these diverse organisms do not form a natural group as named. This is because the animal, plant, and fungus kingdoms are lineages derived from within the kingdom Protista (Fig. 21.1). A natural group must include an ancestor and all of its descendants.

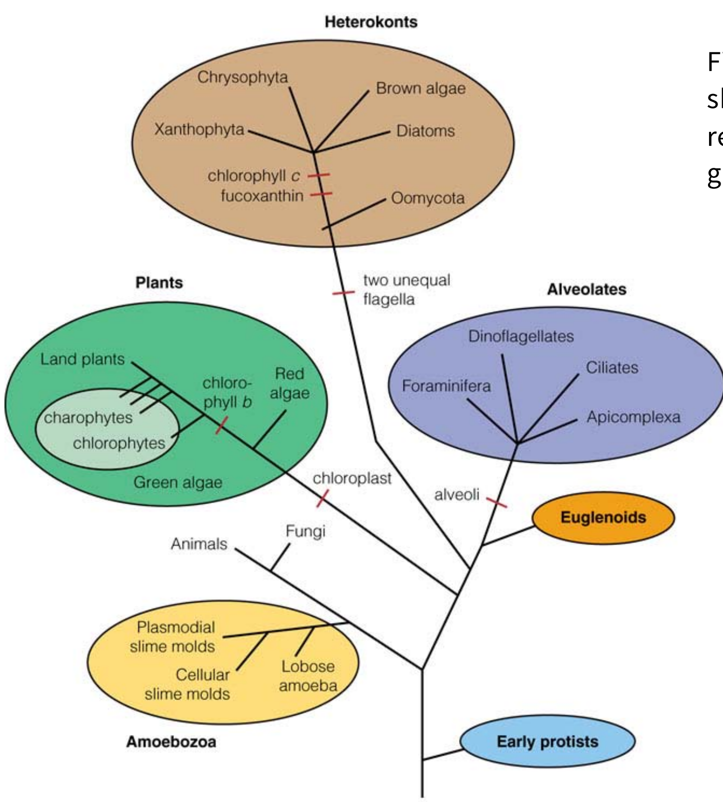


Figure 21.1. A cladogram showing phylogenetic relationships among some groups of protists.

As a result, biologists have largely abandoned the Protista, focusing instead on the various well-defined lineages that exist within it. Sometimes, however, it is useful to have a name for these organisms, even though they are not a clade. This chapter uses the common name **protist**. Protists are unicellular, colonial, or relative simple multicellular organisms that only rarely exhibit specialized cell types, or organs such as leaves or stems. Protist cells are eukaryotic with a double-membrane-enclosed nucleus, double-stranded DNA, and specialized organelles, such as chloroplasts and mitochondria, in the cytoplasm.

Some protists, such as *Paramecium* (Fig. 21.2a), swim actively with beating hairs called cilia and hunt for food in their environment. Other protists, such as various groups of amoebas, crawl along slowly and engulf whatever food they come across. Still other protists, such as the foraminiferans, are covered by a shell and often remain stationary. Some create sticky nets to trap their food, and others eat detritus. These diverse protists that have animal-like feeding strategies often are called *protozoa*.

Some protists are unlike any familiar organisms. Some euglenoids, for example, combine characteristics of animals and plants. Many euglenoids have chloroplasts and produce their own food, but they can also swim actively and consume food like an animal. Slime molds (Fig. 21.2b) can move through the forest like a small slug, and then produce sporangia like a fungus.

Many protists are photosynthetic. These all share the same photosynthetic pigment, chlorophyll *a*, located in the inner membranes of chloroplasts. However, the various lineages have different chloroplast structures, other forms of chlorophyll in addition to type *a*, and a wide variety of unique accessory photosynthetic pigments. Photosynthetic protists often are called algae, and their morphological and habitat diversity is great (Fig. 21.2c).

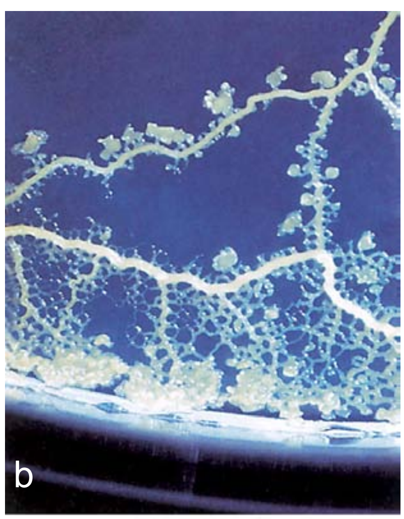
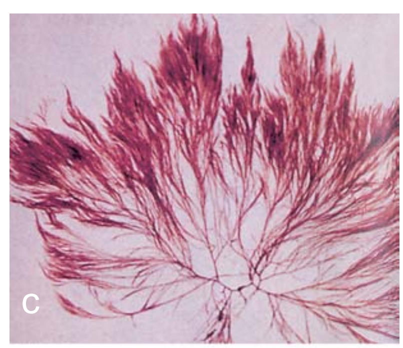


Figure 21.2. Diversity among protists. (a) *Paramecium*, a protozoan. (b) *Physarum*, a slime mold. (c) *Polysiphona*, a red alga.



Relationships among the Eukaryotes Are Incompletely Understood

Determining the relationships between the various eukaryotic groups--the protists, plants, animals, and fungi--has been a difficult problem. Some biologists have even predicted that the phylogeny will never be known. Part of the difficulty is that the splits between many of the lineages of eukaryotes are ancient. Another difficulty is that apparently there have been events in which organisms (or parts of organisms) that are not closely related have joined to form new organisms. In addition, not many characters are shared by all members of this group, and often the shared characters yield different results when analyzed cladistically. Recent (and ongoing) phylogenetic work using the genes coding for tubulin, actin, and a few other proteins has given biologists new hope for solving the problem. There are now well-supported phylogenies for the larger lineages of protists, and we are beginning to fill in the missing pieces at finer scales.

Fossils of multicellular coiled filaments of green algae date back to 2.1 billion years ago (Fig. 21.3). Biochemical markers that are distinctive to eukaryotes have been found in oil as old as 2.7 billion years. Undoubtedly, the eukaryotes are even older, but fossil evidence is lacking. The currently accepted scenario for the origin of eukaryotes relies on the endosymbiotic hypothesis (see Chapter 18 and the end note "IN DEPTH: The Mysterious Origin of Chloroplasts.")

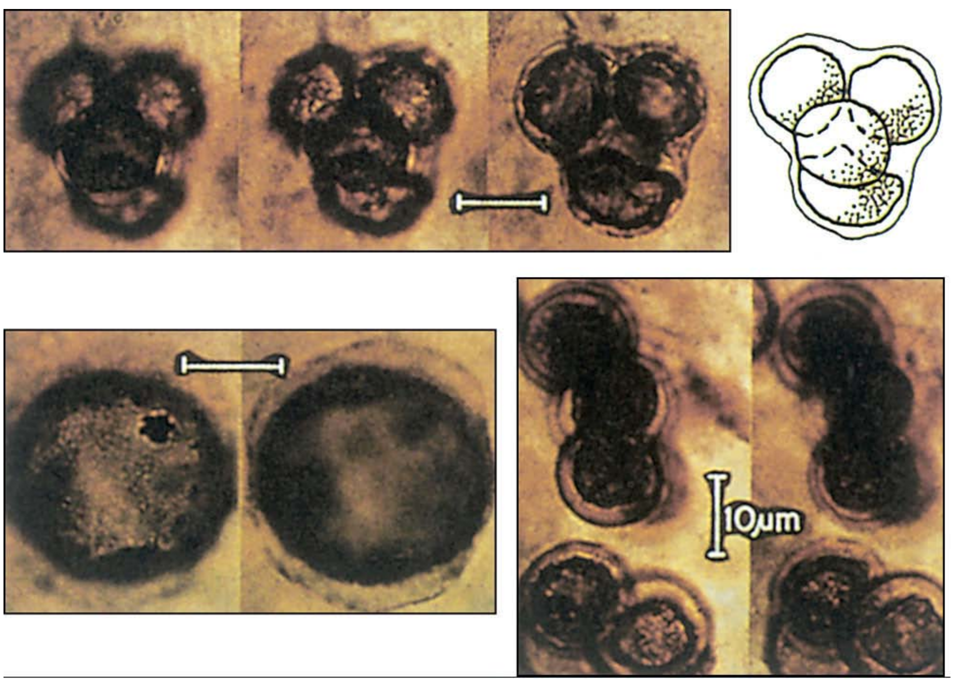


Figure 21.3. Microfossils of green algae in chert approximately 1 billion years old.

Since their ancient origin, eukaryotes have diversified into a series of lineages. At the base of the eukaryotic tree is a group of protists, some of which lack mitochondria and live as parasites on other organisms (nonmitochondrial protists in Fig. 21.1). The pathogen that causes giardia is in this group.

The rest of the eukaryotes are divided into two major clades. One clade includes the animals, fungi, slime molds, and a small group of amoeboid organisms. There are no photosynthetic members of this clade, and most are motile (the major exception being fungi). The other clade includes a variety of protist groups, many of which are photosynthetic. One of these lineages gave rise to the land plants. Both photosynthetic and nonphotosynthetic protists in this clade may swim about actively, hunting for food or moving toward bright light.

Photosynthetic Protists Are Commonly Called Algae

The photosynthetic protists in traditional taxonomy often were classified as about a dozen divisions representing 20,000 to 30,000 species. Although we now know these are not all closely related to each other, they are all still commonly called **algae** (singular, *alga*; Fig. 21.4). Algae have a great variety of life histories, body forms, and ecological roles.

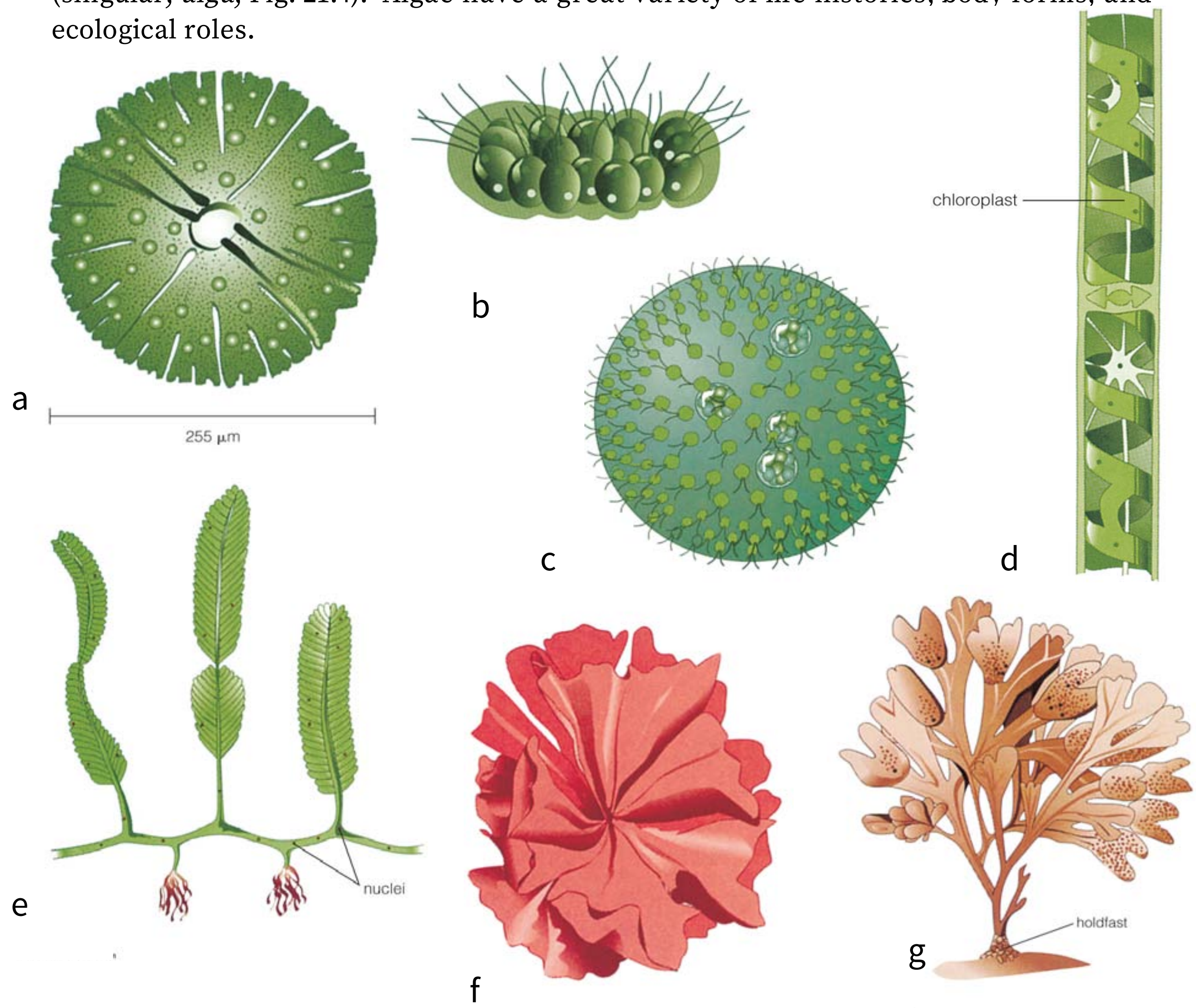


Figure 24.4. Algal diversity. (a) A unicellular *Micrasteria*. (b) A colonial *Gonium*. (c) A colonial *Volvox*. (d) Filaments of *Spirogyra*. (e) *Caulerpa* with differentiation into rootlike, stemlike, and leaflike regions. All of the foregoing are green algae. (f) *Porphyra* is a red alga. (g) *Fucus* is a brown alga.

The various groups of algae often are named for their distinctive colors (red, green, brown, golden, yellow-green), a result of the photosynthetic pigments they possess. Algae range in shape from unicellular to colonial (clusters of cells) to filamentous or sheetlike. A few are complex enough to exhibit marked differentiation into specialized tissues or even organs. Some species drift or swim in open water; others attach to the bottoms of streams or shallow seas, to surface soil particles, to tree trunks, to other algae, or to rocky cliffs battered by surf. Still others form symbiotic associations with fungi, higher plants, or animals. We commonly see algae growing on the sides of fish tanks, around leaking faucets, in garden pools, and as scum on the surface of ponds in summertime. Table 21.1 summarizes the habitats, morphology, pigments, and storage products of major algal groups.

Table 21.1 The Algae Organized by Evolutionary Groups and Traditional Taxonomic Names

Evolutionary Group	Taxonomic Name	No. Species	Key Characteristics
Euglenoids	Euglenophyta	500	Two equal, anterior flagella; no cell wall; chlorophylls *a* and *b;* unicellular; mainly in polluted freshwater
Alveolates			
Dinoflagellates	Pyrrophyta	1,000	Two unequal lateral flagella; no cell wall or wall of cellulose plates; chlorophylls *a* and *b;* unicellular; mainly in marine phytoplankton
Heterokonts			
Brown algae	Phaeophyta	1,500	Two unequal lateral flagella; cell wall of algin + cellulose; chlorophylls *a* and *c;* filamentous to complex large kelps; mainly in shallow, cool, marine water
Diatoms	Bacillariophyta	8,000	Usually no flagella; cell wall of silica + pectin; chlorophylls *a* and *c;* carbohydrates stored as oil; mainly unicellular and free-floating; prominent as freshwater or saltwater phytoplankton
Xanthophyta	Xanthophyta	400	Two flagella (various); cellulose cell wall; chlorophyll *a* (+ *c* in some), oil stored; mainly unicellular; mainly in freshwater
Chrysophyta	Chrysophyta	300	Two unequal anterior flagella; cellulose cell wall (+ silica in some); chlorophylls *a* and *c;* mainly unicellular and in freshwater
Plants			
Red algae	Rhodophyta	4,000	No flagella; cell wall cellulose + agar or carrageenan; chlorophylls *a* and *d*; phycobilin accessory pigments; mostly multicellular seaweeds in deep, warm, marine water
None	Green algae (Chlorophyta and Charophytes)	7,000	Two equal anterior flagella; cellulose cell wall; starch as a storage product; chlorophylls *a* and *b;* carotene accessory pigment; diverse morphology; mainly freshwater

Multicellular algae occur in wet habitats, where their simple bodies are supported by buoyancy in water. They have no water-conducting or stiffening cells strengthened by a secondary cell wall. Every cell in most algal bodies can carry on photosynthesis and obtain water and nutrients directly from its surroundings by diffusion. Such a simple body is called a **thallus**. Some unicellular algae occur in the most severe habitats on Earth: on snow with perpetually freezing temperatures; in hot springs with temperatures of 70ºC; in extremely saline bodies of water, such as the Great Salt Lake in Utah; beneath 274 m of seawater; even surviving--within 1 km of ground zero--a 20-kiloton atomic bomb explosion in Nevada. Many algal species have a semiterrestrial existence by going dormant between wet seasons. The following sections consider five major lineages of protists.

21.2 THE PROTISTS MOST CLOSELY RELATED TO ANIMALS AND FUNGI

The subclade of the eukaryote tree that includes animals and fungi also includes a clade of protists called the Amoebozoa (Fig. 21.1). This clade consists of amoebas and slime molds. These are a diverse group with a unique set of traits that seem to combine aspects of fungi and animals. These are two groups of slime molds: the Myxomycota, or plasmodial slime molds, with contain thousands of nuclei with no membranes separating them; and the Acrasiomycota, or cellular slime molds, which are smaller, have fewer nuclei, and do have membranes between the nuclei.

Slime molds resemble animals in that they lack cell walls, engulf food, and have motile cells at some phase of the life cycle. On the other hand, they resemble fungi and plants in that they form sporangia and nonmotile spores with cell walls.

21.3 ALVEOLATES

Modern molecular systematics has recognized several big groups that were not identified in earlier taxonomic schemes. In retrospect, there often were good nonmolecular indications that these clades existed. The **alveolates** are one example. Members of this group share a system of alveoli, or tiny membrane-enclosed sacs lying beneath the plasma membrane. These provide structural support and can give rise to distinctive coverings, such as the plates on the surface of dinoflagellates (Fig. 21.5).

The alveolate clade is composed of four ecologically and economically significant groups (Fig. 21.1). The **ciliates** include many of the actively swimming protists seen in freshwater bodies. Some, such as *Paramecium,* are commonly used in biology laboratories. These protists typically possess cilia and feed by engulfing their food in much the same manner as animals. For this reason, they often are called protozoa. The **foraminifera** are common and diverse protists with a hard shell. Their feeding strategies range from active predation to scavenging to creating sticky webs for trapping food. Their shells are common fossils and are important in dating geological strata and in oil exploration. The **apicomplexa** consist almost entirely of parasitic or pathogenic protists. This group includes *Plasmodium,* the organism that causes malaria, and *Toxoplasma*, the cause of toxoplasmosis. The apicomplexa recently have been found to contain vestigial plastids, and thus may be derived from a photosynthetic ancestor. The fourth group of alveolates is the photosynthetic dinoflagellates.

Dinoflagellates Cause Red Tides

The **dinoflagellates** are important members of the phytoplankton. Most species are unicellular, motile, and marine. Some species have plates on their exterior made of cellulose (Fig. 21.5), whereas other lack a cell wall entirely and are enclosed only by a thickened cell membrane. A few are colonial or filamentous. Usually, two flagella are present; both emerge from the same pore, but otherwise they are different. One is flat and ribbonlike and encircles the cell in a groove around the middle; it provides rotational movement. The second flagellum trails behind and provides forward movement.

Dinoflagellates contain chlorophylls *a* and *c* and a brown pigment called fucoxanthin, which gives the cells a green-brown or orange-brown color. They have unusual chloroplasts that are surrounded by three or four membranes and may contain a remnant nucleus--evidence that the dinoflagellates likely acquired their chloroplasts by engulfing other eukaryotic algae.

Some forms produce a bioluminescence and contribute to the glow of water when it is disturbed at night by surf or in the wake of a ship. At certain times of year

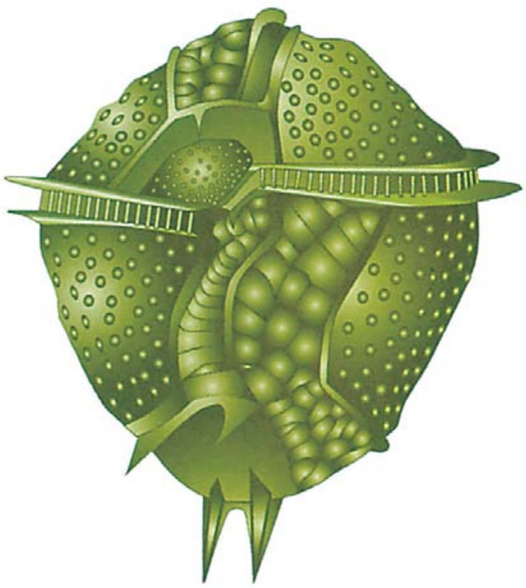


Figure 21.5. The dinoflagellate *Ceratocorys aultii*. Flagella, which ordinarily lie within the grooves or trail behind, are not shown.

and along some coasts, the density of dinoflagellates in the phytoplankton multiplies, turning the water a reddish color. This effect is known as a *red tide* (see "PLANTS, PEOPLE, AND THE ENVIRONMENT: Algal Blooms" at the end of the chapter.) Some dinoflagellates release toxins into the water, which can kill fish, marine mammals, and even humans if they are consumed in great enough quantities.

21.4 EUGLENOIDS

When a stagnant swimming pool or pond turns into a pea-green soup, the most likely cause is a bloom of **euglenoids**. These organisms have puzzled biologists because they combine characteristics of different lineages, and their relationship to other eukaryotes has been uncertain until the recent use of molecular characteristics.

Euglenoids are typically single-celled organisms (one small genus is colonial) that live primarily in freshwater, but they also can be found in salt or brackish water, and even in soil (Fig. 21.6). A few are parasitic. Euglenoids lack a cell wall, but they have flexible strips of proteins and microtubules under their cell membrane. They have two flagella, although in many forms only one emerges from the cell. They also can move by a unique inching motion.

About one third of the 1,000 species of euglenoids have chloroplasts. These contain chlorophylls *a* and *b* and carotenoids, like green plants. Most likely, they obtained this set of pigments through secondary endosymbiosis with a green alga. Three membranes surround euglenoid chloroplasts, supporting the secondary endosymbiosis hypothesis. Many euglenoids also contain a unique red or orange light-sensitive organelle called an **eyespot** that enables the organism to orient itself toward the light. The pigment in the eyespot (astaxanthin) is a carotenoid that has strong antioxidant properties. It is extracted and sold as a health supplement.

Figure 21.6. Two *Euglena* cells with chloroplasts and red eyespots.

The remaining two-thirds of euglenoids must find food in their environment. They ingest their food though a pocket-like cavity at one end of the cell.

Euglenoids have never been observed to reproduce sexually. How so many species formed among these asexual organisms remains a mystery, but it may be that euglenoids had some form a genetic recombination in the past. Euglenoids are important in the food chains of freshwater ecosystems, and they can be useful ecological indicators of water rich in organic matter.

21.5 HETEROKONTS

Another large clade recently identified in molecular studies is the **Heterokonta** (also sometimes called Stramenopiles or Chromista). The heterokonts include the **Oomycota** (the water molds and downy mildews), and several algal groups, all of which share a variant of chlorophyll called chlorophyll *c* and a brown accessory pigment called fucoxanthin. Recall that the dinoflagellates also have fucoxanthin and chlorophyll *c*. The heterokonts all have two unequally sized flagella. The heterokonts and alveolates share a common ancestor (Fig. 21.1). In addition to the Oomycota, heterokonts include two lines of golden algae, **Xanthophyta** and **Chrysophyta**; the diatoms,; and the brown algae.

Oomycota Have a Great Impact on Humans

Oomycota include egg fungi, downy mildews, and water molds. In the past, they often have been classified as fungi, which they resemble in having hyphae, producing spores, and lacking chlorophyll. However, they share cellulose cell walls, swimming spores, certain cellular details, and unique metabolic pathways with some algal groups.

Most Oomycota are benign decomposers that live in soil or freshwater habitats, but a few are pathogens of important crops. Downy mildews, for example, infect beans, grasses, and melons, among other plants. They are easily identified by the dense web of sporangia-bearing hyphae (sporangiophores) that make the infected leaf appear to be covered with soft down (Fig. 21.7).

Downy mildew of grape, *Plasmopora viticola*, nearly destroyed French vineyards in the nineteenth century. Before this time, the disease had been restricted to North America, where it infected wild grapes. These wild species were seen to be valuable rootstocks for European grapes, so they were imported to France. Some carried spores of downy mildew, which spread to European plants and caused disease symptoms that were first noticed in 1878. The disease then spread rapidly. Investors began planting vineyards in countries outside France, believing the French wine industry was doomed. But the mycologist Alexis Millardet discovered that a mix of lime and copper sulfate, applied as a dust on leaves and stems, killed downy mildew. The French wine industry recovered, and opportunistic owners who had overplanted vineyards in other countries, such as Italy, went bankrupt. Millardet called his mixture Bordeaux mix, and it is still used.

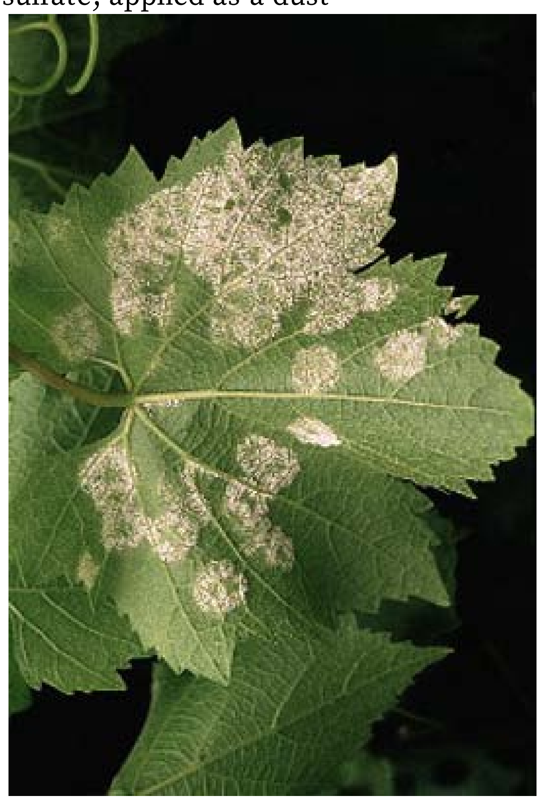


Figure 21.7. Grape leaves infected with downy mildew, *Plasmopora viticola.*

Another Oomycota changed the history of Ireland. The potato blight of the 1840s was caused by *Phytophthora infestans* (the genus name literally means "plant destroyer"). The potato is a New World plant, originally restricted to the cold, rocky soils of farms in the Andes. Its value as a food crop on marginal farmland elsewhere was obvious, and it soon became the main crop in Ireland. One farm family could subsist on an acre of potatoes and a cow. An unusual series of warm, humid summers allowed the downy mildew to become epidemic, rotting the potatoes and killing the plants. A quarter of a million people died of starvation, and a million more immigrated to the United States, adding an important new ethnic component to U.S. culture. Decades later, mycologists learned that potato blight could be controlled by spraying infected fields with poisons that kill the blight and by carefully disposing of infected potato tubers.

Diatoms Are Encased in Glass

Diatoms are important members of the **phytoplankton**, which are floating, photosynthetic, microscopic algae. Diatoms are unique in that they produce cell walls out of silica, the main component of glass. Viewed from above, their silica walls are exquisitely ornamented with perforations (Fig. 21.8). The silica is embedded in a pectin matrix. The shape of the cell can be circular, triangular, oval, diamond shaped, or even more elaborate (Fig. 21.14). In cross section, the cell wall has two parts (valves) that fit over each other like the halves of a Petri dish. Like other heterokonts, diatoms contain chlorophylls *a* and *c* and the accessory pigment fucoxanthin. Fucoxanthin gives these cells their characteristic color, ranging from olive brown to golden brown. Diatoms store food reserves as oils. Some diatoms move along surfaces, even out of water, with a unique gliding motion, though cilia and flagella are absent.

Diatoms also exist as attached, stalked single cells or as filaments. Many stalked diatoms grow as **epiphytes** ("on other plants") on seaweeds and kelps. They do not parasitize the host plant but use it as a base to gain access to light near the water's surface.

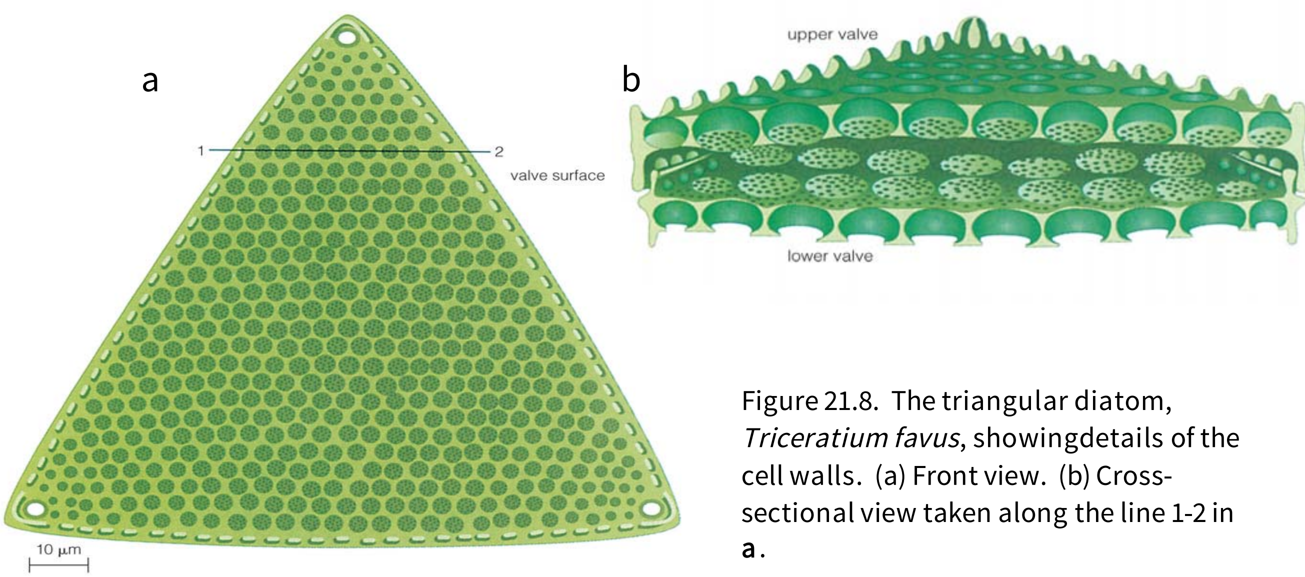


Figure 21.8. The triangular diatom, *Triceratium favus*, showingdetails of the cell walls. (a) Front view. (b) Cross-sectional view taken along the line 1-2 in **a**.

It is estimated that the productivity of the extra layer of epiphytes can be as great as that of their larger hosts. Thus, epiphytes add greatly to the first tier of the food chain (the transfer of energy in an ecosystem) in shallow water.

Diatoms may also become attached to nonliving surfaces. For example, the undersurface of icebergs is coated with diatoms, particularly ones in the genera *Navicula, Nitzschia*, and *Podosira*. Diatoms are abundant enough to stain ice a yellow-brown color, and the base of the arctic food chain is enriched because of them. Diatoms also create *algal turfs*, which coat shallow rocks in quiet freshwater or marine habitats. These turfs have as high a daily productivity per square meter of surface as a tropical rain forest; therefore, they play an important role in the food chain of these habitats. The surfaces of salt marsh mudflats also are dominated by diatoms, which are grazed on by insects.

Diatoms have an extensive fossil record and are important indicator fossils for paleontologists and petroleum exploration geologists. Their accumulated silica shells have created distinctive deposits.

The Brown Algae Include the Kelps

The **brown algae** are almost exclusively marine; but in contrast to red algae, they are most diverse and abundant in cool, shallow waters. The simplest brown algae are filamentous and sheetlike; the most complex are kelps (Fig 21.9). **Kelps** are large seaweeds with well-differentiated regions that resemble stems and leaves and with internally distinctive tissues and regions (see "PLANTS, PEOPLE, AND THE ENVIRONMENT: *The Kelp Forest Ecosystem*" at the end of the chapter). Some brown algae such as *Fucus* (rockweed) are the most common seaweeds on rocky shores. Brown algae provide important food supplements, medicines, and industrial chemicals.

Like the other heterokonts, kelps have chlorophylls *a* and *c* and the pigmentfucoxanthin. Carbohydrates, stored as mannitol or laminaran, accumulate as granules in the cytoplasm. Chloroplasts do not contain grana. Cell walls are made from cellulose and tough flexible polymers called alginates. Motile cells have two unequal flagella attached along the side of the cell.

Macrocystis is the largest kelp known, and it has one of the fastest growth rates of any multicellular alga. In the course of a single growing season, it grows from a single-celled zygote into a mature, giant, 60-meter-long kelp, attached to a rocky bottom with much of the upper part floating on the surface. A mature *Macrocystis* (Fig. 21.9) consists of an anchoring **holdfast**, stemlike **stipes**, and numerous leaflike **blades** that arise all along the stipes. The base of each blade is inflated into a gas-filled bladder, which increases buoyancy.

Kelps are complex anatomically and morphologically. If the stipe is sectioned and examined under the microscope, several regions are apparent (Fig. 21.10). Cells in the outermost layer are protective; they also are meristematic and contain chloroplasts. To distinguish this unique tissue from the much simpler epidermis of

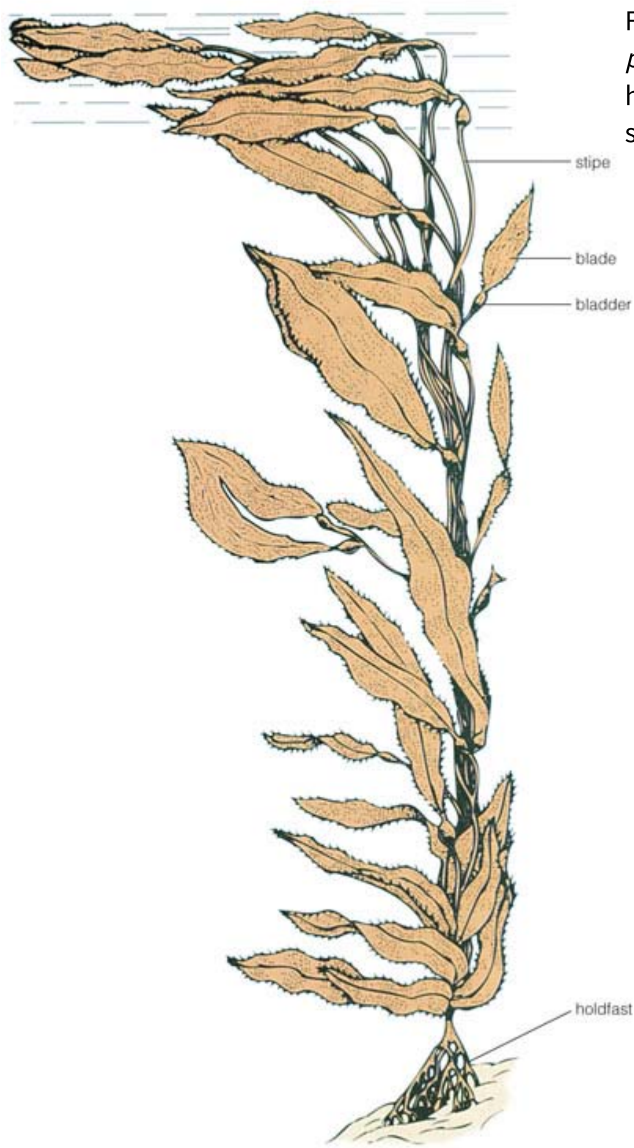


Figure 21.9. The giant kelp *Macrocystis pyrifera* growing in water 4 m deep. The holdfast, stipes, blades, and bladders are shown.

land plants, it is called **meristoderm**. A broad region of cortex beneath the meristoderm is composed of parenchyma-like cells. Mucilage-secreting cells line canals through the cortex. Loosely packed filaments of cells fill the innermost part of the stipe, a region called the **medulla**. Some cells in the transition zone between cortex and medulla function as sieve elements. They have sieve plates, form callose, and adjoin to one another to form continuous tubes, and mannitol moves through them at a rate resembling sugar movement in vascular land plants. The value of a photosynthate-conducting system in these large plants is easy to understand: the mass of floating fronds on the surface shades the lower part of the stipes and the holdfast so much that the shaded parts cannot produce enough carbohydrate to maintain themselves and must have additional amounts translocated to them. Because they live immersed in water, kelps contain no tissue that resembles xylem.

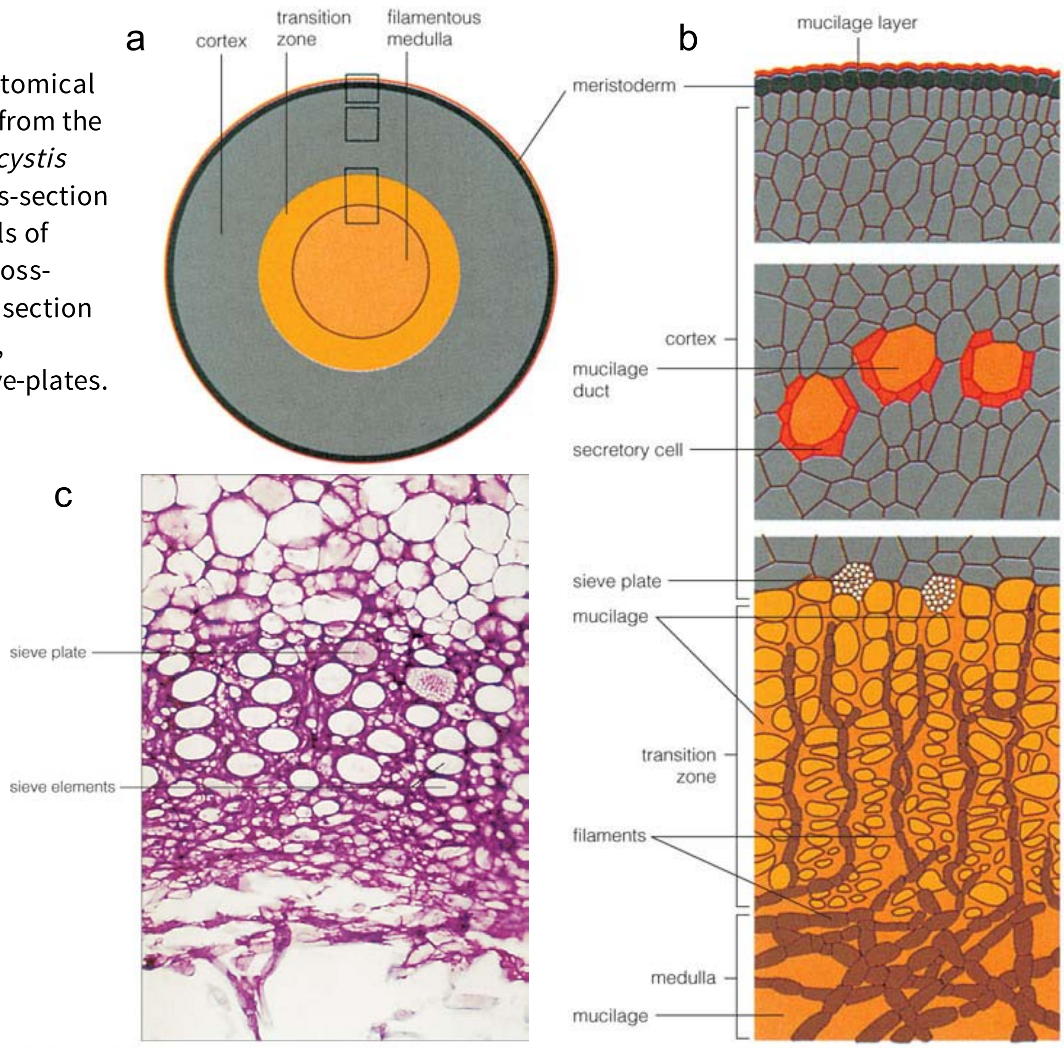


Figure 21.10. Anatomical details of a stipe from the giant kelp *Macrocystis pyrifera*. (a) Cross-section of stipe. (b) Details of portions of the cross-section. (c) Cross section of sieve elements, showing two sieve-plates.

21.6 THE PLANTS

A great wealth of molecular data supports the idea that red algae, green algae, and land plants belong in the same clade. Biologists have long suspected--on the basis of cellular details, biochemistry, life cycles, and morphology--that green algae gave rise to land plants. Analyses of proteins and nucleic acids have provided overwhelming support for this suspicion and also showed that red algae belong in this clade. Now that we know these organisms form a clade, it seems likely that their common ancestor was the group originally associated with a photosynthetic prokaryote to form the chloroplast. This original endosymbiosis was passed on to all the descendants.

Green algae are not a natural (monophyletic) group because they gave rise to land plants. To solve this problem, phylogenetic taxonomists simply include at least some green algae in the plant kingdom. Now that we know red algae are sister to this clade and share many characteristics with it, particularly chloroplasts derived from a primary endosymbiotic event, it makes sense to call them plants as well. In this system, the clade that includes plants and green algae can be called simply **green plants** (Fig. 21.1).

Red Algae Are Adapted to Live at Great Depths

Red algae are almost exclusively marine and are most abundant in warm water. They can grow to considerable depth. Most are multicellular and large enough to be called **seaweeds**. The simplest red algae are small, branched, delicate filaments (Figs. 21.2c and 21.4f). More complex forms have a parenchyma-like tissue, forming a body with a holdfast that anchors the plant to a substrate, a stemlike stipe, and a leaflike blade. Unlike the brown algae, the stipes of red algae are never very long and the blades never have gas bladders. Some forms are encrusted with lime (calcium carbonate) and become parts of tropical reefs. Cell walls contain cellulose, sometimes augmented with agar or carrageenan.

The chloroplasts of red algae retain some characteristics of the prokaryotic cyanobacteria from which they were probably derived. Both typically contain only chlorophyll *a* and have similar accessory pigments called phycobilins. The red algae have a unique food storage molecule called floridean starch.

The accessory pigments of red algae (and cyanobacteria) allow them to grow at greater depths than other photosynthetic organisms. Both the quality and the quantity of light change with passage though water. Red light is completely absorbed in the upper layers leaving a blue-green twilight to prevail farther down. Experiments have revealed that aquatic algae have adjusted their metabolism to the light at different depths. The action spectrum of photosynthesis for the green alga *Ulva taeniata*, which grows at shallow depths along rocky coasts, and the red alga *Myriogramme spectabilis*, which grows permanently submerged in deeper water, are different (Fig. 21.11). You can see that the most important wavelength of light for photosynthesis shifts with depth to center around the blue-green region, 440 to 580 nm. The phycobilins in red algae are able to trap light in this region of the spectrum, transferring the energy to chlorophyll.

Eventually, at about 170 m in water of average clarity, the amount of light becomes so depleted that no alga--regardless of pigments--can scavenge enough light to support growth. The record depth for a red alga is 268 m in an unusually clear part of the Caribbean Sea. Algae in such low light grow slowly and are probably hundreds of years old.

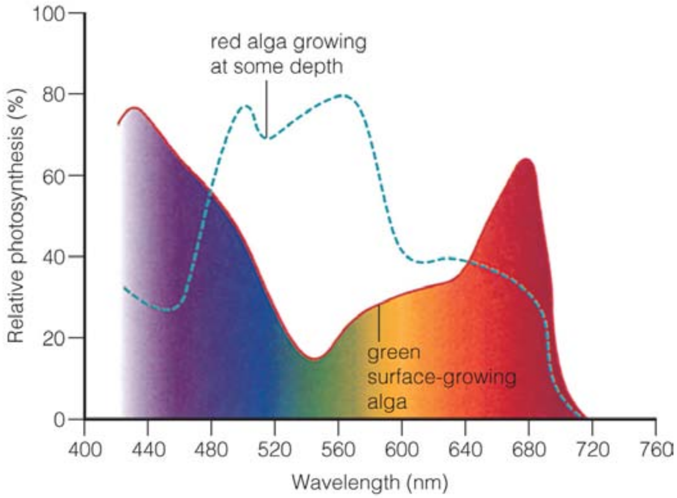


Figure 21.11. Action spectrum of photosynthesis for a green, surface growing alga and a red alga growing at depth. The red alga can use blue-green light (wavelengths 440-550 nm) that pass through the upper layers of water.

Green Algae Gave Rise to the Land Plants

Green algae occur predominantly in freshwater habitats. They also exist in saltwater, on snow in hot springs, on soil, and on the leaves and branches of terrestrial plants. All green plants (green algae and land plants) share a great number of characteristics that distinguish them as a clade. They have chlorophylls *a* and *b*, similar carotenoid accessory pigments, starch as a food storage molecule, and cell walls made primarily of cellulose. They also have a unique type of cell division during mitosis (the formation of a phragmoplast) and asymmetrically attached flagella, among other traits.

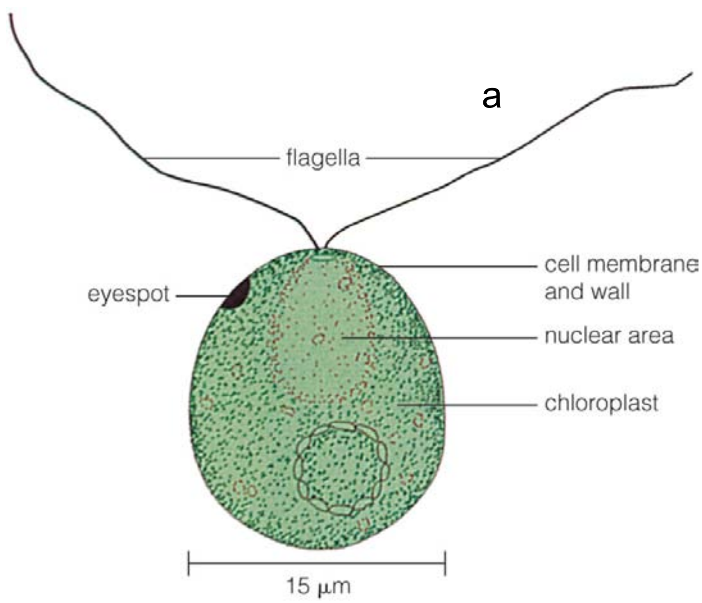
Before the appearance of land plants, ancient green algae apparently split into two lineages. One lineage, the **chlorophytes**, persists as a clade that is sister to the land plants in addition to the rest of the green algae. The chlorophytes include several monophyletic groups, including the Chlorophyceae and the Ulvophyceae. The other lineage, the **charophytes**, is the group from which land plants are derived.

CHOROPHYCEAE The Chlorophyceae are distinguished by few morphological characters but many different molecules. This group includes *Chlamydomonas* (Fig. 21.12). Each cell has two flagella at the anterior end and a single, large, cup-shaped chloroplast. Most species have a red-colored carotene eyespot, which is capable of sensing light. The two flagella enter the cell at an angle, and they end in basal bodies, which are connected by a bridge of many microtubules. Forward movement results from flagellar motion resembling a swimmer's breaststroke--the flagella extend straight ahead, sweep backward without bending, and then fold and come back to the forward position.

Chlamydomonas-like cells may link together into permanent multicellular colonies; *Gonium* and *Volvox* are examples (Fig. 21.4b,c). *Volvox* is a hollow sphere of cells connected to each other by plasmodesmatal strands of cytoplasm. One colony may contain as many as 20,000 cells. It is clear that the cells of a colony are coordinated, because their flagella are synchronized and able to move the colony in a given direction.

ULVOPHYCEAE The Ulvophyceae typically are small, green seaweeds composed of thalli growing attached to a substrate in shallow water. Species in the genus *Ulva*, called sea lettuces, consist of an irregularly shaped, bright green, ruffled sheet or thallus two cell layers in thickness attached to a rocky substrate by a rudimentary holdfast. The holdfast often is persistent, whereas the thallus is lost and regrown on an annual basis. Sea lettuces are consumed as a food in many places.

Some filamentous forms of Ulvophyceae have complex morphologies that resemble land plants. *Caulerpa*, for example, forms extensive mats on the bottom of shallow bays beneath the Mediterranean Sea (Fig. 21.4e). Each individual consists of a horizontal, creeping portion, which sends branching filaments down into the substrate,



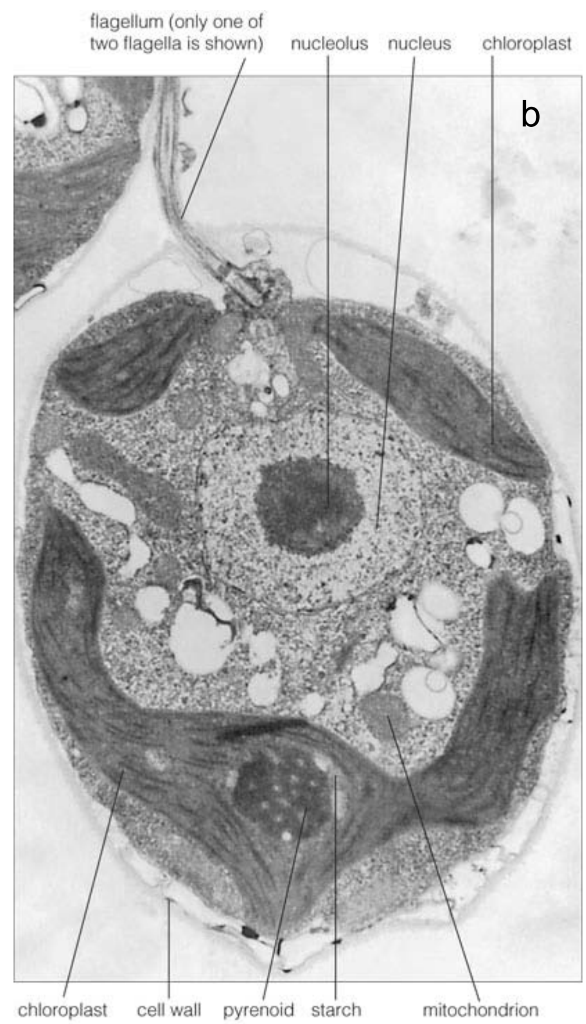


Figure 21.12. The unicellular green alga *Chlamydomonas*. (a) Diagram. (b) Transmission electron micrograph. X 19,000

and feather-like or sheet-like blades that reach upward into the water. Thus, there are rootlike, stemlike, and leaflike regions. This plant was accidentally imported to the Mediterranean Sea from tropical oceans where it grew singly or in small colonies. Apparently, in its new environment, it is free from natural limits to growth, and therefore it has multiplied explosively, pushing out native algae. Even worse, *Caulerpa* produces toxins that are lethal to urchins and some fish, which are important elements of ecosystem food chains. In summary, *Caulerpa* has wreaked ecological havoc in the Mediterranean region. In 2000, *Caulerpa* was discovered off the coast of California.

CHAROPHYTES Charophytes are a group of ancient green algae composed of a series of lineages that in Linnaean taxonomy were in the Charophyta. However, the full clade consists of a grade of many other lineages, one of which gave rise to land plants. Among living charophytes, *Coleochaete* has long been cited as the closest living relative of the land plants. It shares many characters with land plants. For example, like land plants, *Coleochaete* retains its egg and zygote on the parent plant, although there is no multicellular diploid phase. A recent study, however, based on molecular characters, showed that another alga, *Chara*, is actually more closely related to land plants than *Coleochaete*. *Chara*, or stonewort, is a complex filamentous charophyte with an anchoring region and a stemlike region differentiated into nodes and internodes (Fig. 21.13). *Chara* also possesses multicellular gametangia structures, in which the gametes are protected by a shell of sterile cells.

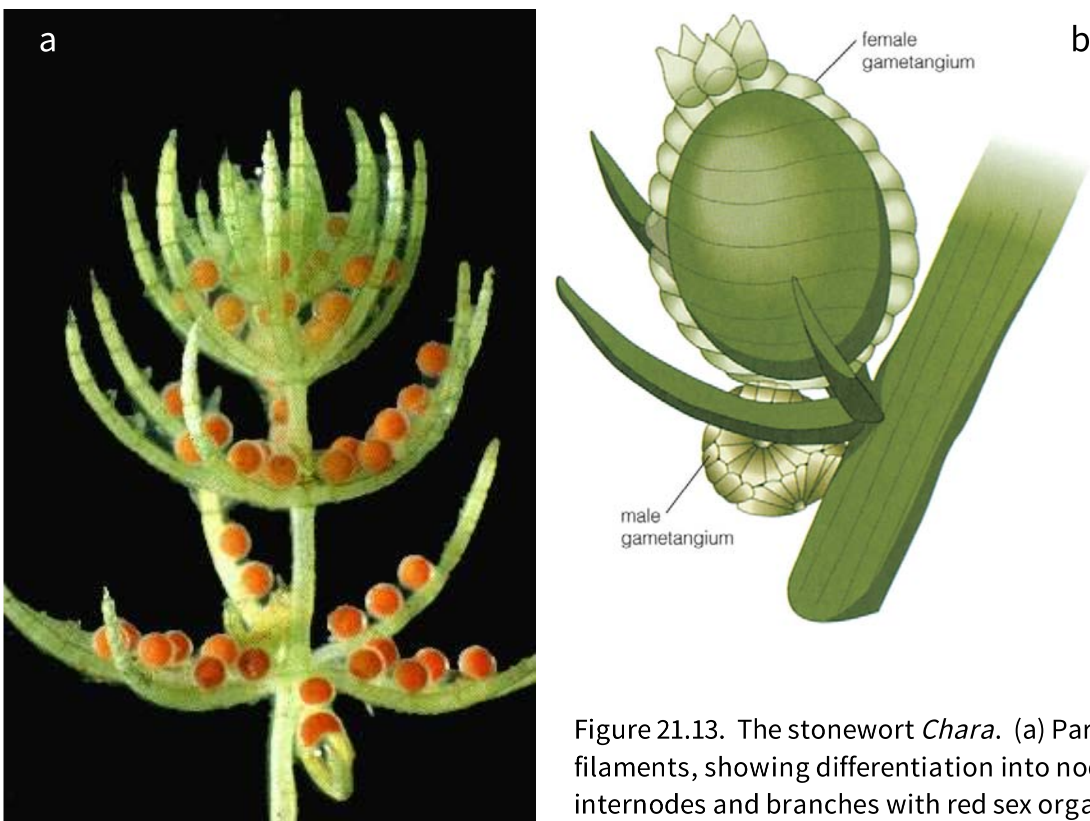


Figure 21.13. The stonewort *Chara*. (a) Part of a cluster of filaments, showing differentiation into nodes and internodes and branches with red sex organs. (b) The female gametangium. Note the shell of sterile cells surrounding and protecting the gametangium.

21.7 THE ECOLOGICAL AND ECONOMIC IMPORTANCE OF ALGAE

Algae are important in two basic but quite different ways. They are important to the entire biosphere because they are photosynthetic--that is, they create carbohydrates and release oxygen, and in so doing form the base of aquatic food chains and build tropical reefs. They also are economically important to humans because they serve as food, fodder, and fertilizer and have many industrial and pharmaceutical uses.

Planktonic Algae Are at the Base of Aquatic Food Chains

Microscopic floating algae called phytoplankton (Fig. 21.14) occur in such great numbers over such a large surface of water that they are said to be "the grasses of the sea"; that is, they produce the vegetation that feeds grazing animals, which in turn feed predators and, ultimately, humans. Phytoplankton are at the base of aquatic, and especially oceanic, food chains. Phytoplankton are unicellular. They must stay close to the surface and avoid sinking below the photosynthetic zone by swimming, storing buoyant oil droplets, altering their ionic balance, and developing fine projections that extend out from the cell wall. The average life span of a given cell is probably measured in hours or days; death is cause by the organism eventually sinking below the photosynthetic zone and ultimately coming to lie on the ocean bottom.

The density of phytoplankton is normally low in the open ocean, perhaps a few thousand cells per liter, but the oceanic expanse is enormous. As a result, on a global scale, phytoplankton produce 3.26 quintillion kcal (3.26×10^{18}) photosynthate each year, which is four times that produced by the earth's croplands. This production of food energy would be even greater if such limiting factors as temperature and mineral nutrients were ameliorated. Deep oceans and freshwater lakes tend to be cool and low in nutrients. Continental edges and shallow lakes are warmer, have more mixing of water through all depths, and have more nutrients; there, productivity by plankton is greater. If nitrogen- or phosphorus-rich wastewater is added to such areas--or if water temperature increases for some natural reason--a tremendous increase in the density of phytoplankton called a bloom occurs (see "PLANTS, PEOPLE, AND THE ENVIRONMENT: Algal Blooms" end note.)

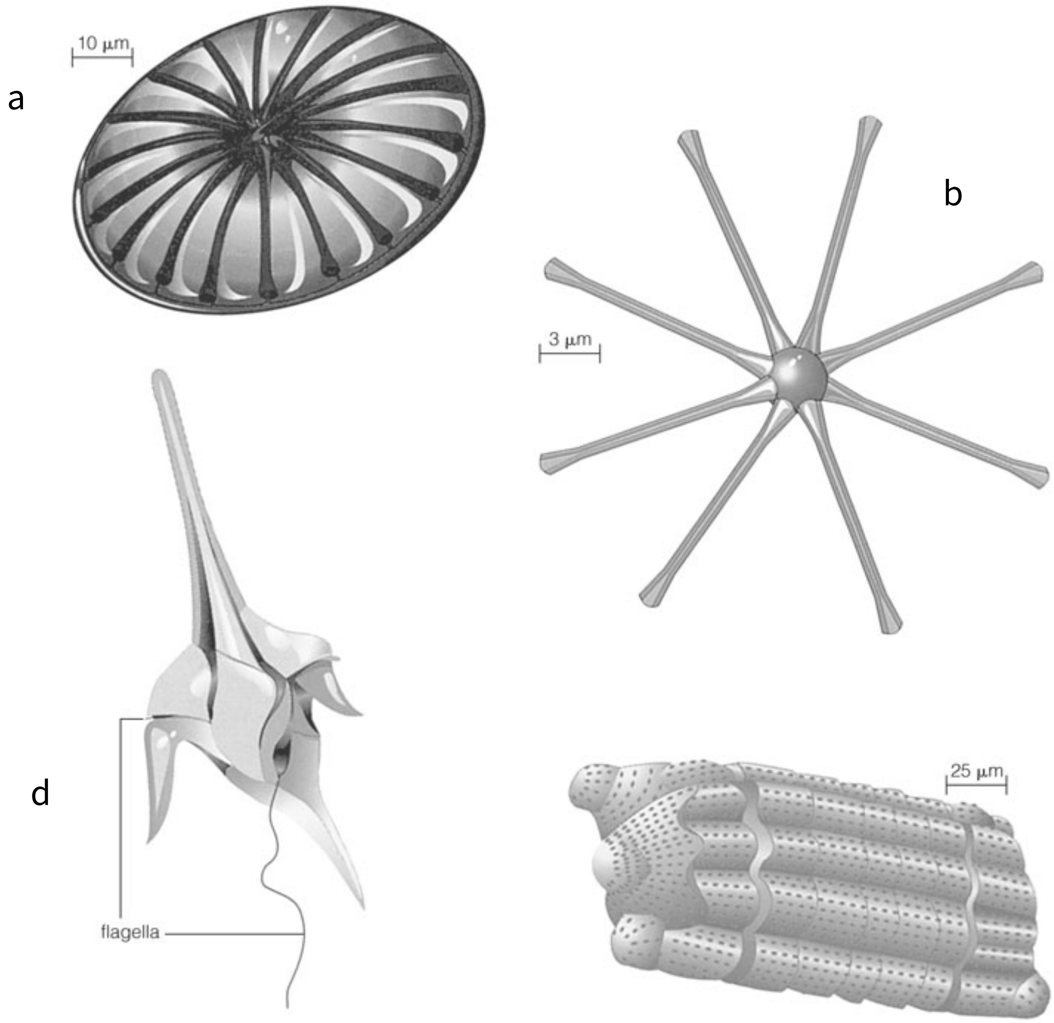


Figure 21.14. Examples of phytoplankton. Diatoms include (a) *Asteromphalos elegans*, (b) *Asterionella formosa*, and (c) *Biddulphia biddulphia*. (d) The dinoflagellate *Ceratium*.

Algae Help Build Tropical Reefs

Reefs, which form in shallow tropical seas, most often near islands or on continental shelves, provide an important habitat for an incredible variety of marine life. Partly composed of the stony remains of coralline animals, reefs also are constructed by algae. Certain red and green **coralline algae** create a carbonate exoskeleton resembling coral around their filaments. This exoskeleton becomes a physical part of the reef after the algae die. Coralline algae also help build the reef by connecting the corals' exoskeletons. More than half of the bulk of many reefs is from algae.

In addition, a few species of algae grow symbiotically within the tissues of coralline animals. The tissue of these invertebrate reef-forming animals is photosynthetic because it contains these symbiotic algal cells. The alga, usually the dinoflagellate *Symbiodinium microadriaticum,* has a photosynthetic rate 10 times greater than phytoplankton, probably because it is protected and nourished by the animal cytoplasm around it. The relationship between corals and algae is mutualistic--that is, both organisms benefit. The alga produces sugar and oxygen for the animal, exporting more than 90% of the sugar into the animal's tissue and retaining only a small balance for its own growth and maintenance. In exchange, the cells of the coral contribute carbon dioxide, nitrogen, and mineral nutrients to the alga. Together, both prosper.

Algae Serve as Medicine, Food, and Fertilizer

Seaweeds are marine forms of red, brown, and green algae of moderate size. They usually grow in the rocky intertidal zone, alternately exposed by low tides and covered by high tides. Seaweeds are an important part of the human diet and medicine chest in several parts of the world. In East Asia, seaweed harvesting has been known for 5,000 years. Shen Nong, the legendary Chinese "father of medicine" prescribed seaweed for a variety of ailments in texts dating back to 3,600 years ago. Much later, Confucius also praised their curative value. A million metric tons a year of the brown seaweed *Laminaria* is harvested off the China coast as a source of iodine, which is added in trace amounts to the diet for the prevention of goiter (an enlargement of the thyroid gland).

For centuries, the Japanese have used algae as a testy supplement to their rice diet. The demand for nori, the red alga *Porphyra*, has grown to such an extent that it is cultivated (Fig. 21.15). The Polynesians in Hawaii used and named at least 75 species of *limu* (seaweed) as food sources. Some rare species were cultivated only in marine fishponds belonging to nobility. Dulce, the red seaweed *Palmaria palmate*, has been used as a food for 1,200 years in the British Isles. The Irish discovered that when boiled with milk, small quantities of Irish moss--another red alga, *Chondrus crispus*--would produce a jelly dessert that the French later called *blancmange*.

Nevertheless, with some exceptions, algae do not have much nutritive value; in fact, their major constituents are largely indigestible. Today, algae are used more as condiments, garnishes, or desserts than as staples--much as we use watercress, celery, or herbs.

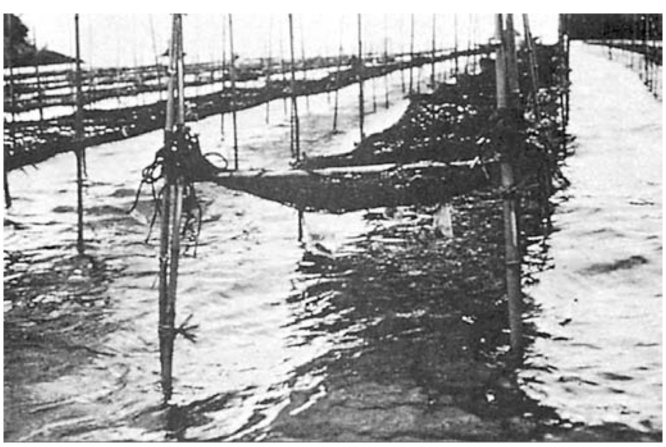


Figure 21.15. Harvesting nori, red alga *Porphyra tenera*, in Sendai Prefecture, Honshu Island, Japan. Hibi nets sit about 30 cm above mean low tide in September, at the beginning of the growing season for nori. Harvest time is in January.

Seaweeds do contain large amounts of potassium, nitrogen, phosphorus, and other minerals characteristic of good fertilizer or cattle feed supplements. In historic times, Native Americans and the Scotch-Irish used Irish moss as a fertilizer to build up poor soils for such crops as corn and potatoes. As a fertilizer, seaweed compares favorably with barnyard manure: it enhances germination, increases the uptake of nutrients in plants, and seems to import a degree of resistance to frost, pathogens, and insects.

Algal Cell Walls Have Industrial Uses

Physical and chemical characteristics of the cell walls of some algae lead to products with many industrial, pharmaceutical, and dietary applications. It is through these cell wall components--primarily diatomite, agar, carrageenan, and algin--that algae have their greatest direct economic value.

Diatomite (or diatomaceous earth) is a sedimentary rock composed of fossilized diatom cell walls. Recall that diatoms are important members of the phytoplankton. As they flourish and die, their empty walls sink and accumulate as bottom sediments. One of the richest deposits of diatomite is a 300-m-think layer near Lompoc, California. It formed this way about 15 million years ago beneath a warm, shallow sea. In more recent geologic time, the Lompoc area was uplifted above sea level, and the diatomite deposit was revealed by erosion. Several companies mine the diatomite for industrial and pharmaceutical use. Diatomite makes a superior filter or clarifying material, both because the microscopic wall pores create a large surface area (230 g contain the area of a football field) and because the rigid walls are incompressible. It is used in laboratory and swimming pool filters. Diatomite is inert, and it can be added to many materials to provide bulk, improve flow, and increase stability: diatomite is used in cement, stucco, plaster, grouting, dental impressions, paper, asphalt, paint, and pesticides. Diatomite also is used as an abrasive.

Agar (or agar-agar) is a polysaccharide analogous to starch or cellulose but chemically different. With cellulose, it is a component of the walls of certain red algae, mainly *Gelidium* and *Gracilaria*. Currently, agar is a common medium on which bacteria are grown. This use was discovered a century ago by a physician's wife, Frau Hesse, who used agar to thicken her jam. The noted microbiologist Robert Koch presented Hesse's idea to the world in his scientific writings during the late nineteenth century. Agarose, purified from agar, is used for gel electrophoresis, a valuable technique of modern molecular biology.

Seaweeds containing agar are commercially harvested by divers who descend 3 to 12 m into warm nearshore waters off Australia, California, China, Japan, Mexico, South America, and the southeastern United States. Some red algae are cultivated for agar production using rocks dropped into shallow bays or ropes suspended from floats. Weeds are removed, and at times solid fertilizer is added to the water to increase production. Agar-producing algae have been cultivated for more than 300 years in Japan.

In addition to its bacteriological use, agar is important in the bakery trade. When added to icing, it retards drying in open air or melting in cellophane packages.

Agar is made into a gelatin for consumption in parts of Asia. Because agar is virtually indigestible, it also is used as a bulk laxative.

Carrageenan is another polysaccharide that accompanies cellulose in the walls of red algae, mainly Irish moss. The substance takes its name from the town of Carragheen, County Cork, along the south shore of Ireland, where its properties were first documented. Carrageenan reacts with the proteins in milk to make a stable, creamy, think solution or gel. Consequently, it is used commercially in ice cream, whipped cream, fruit syrups, chocolate milk, custard, evaporated milk, bread, and even macaroni. It is added to dietetic, low-calorie foods to provide the appropriate "mouth feel." Carrageenan also is used in toothpaste, pharmaceutical jellies, and lotions of many sorts. Irish moss is commercially harvested in the United States off the shore of Maine.

Brown algae have a commercially valuable compound called **algin**, a long-chain polymer made up of repeating organic acid units that is their principal cell wall component. Algin constitutes up to 40% of the cell wall by weight. Water is strongly adsorbed by algin, creating a think solution. When added to 1 L of water, one tablespoon of powdered algin increases the viscosity to that of honey. In nature, algin may be valuable to intertidal algae during low tide because of its ability to retain water. Commercially, it is used as an additive to beer, water-based paints, textile sizing, ceramic glaze, syrup, toothpaste, and hand lotion. Hundreds of algal species contain algin, but only a few are commercially harvested: *Macrocystis pyrifera* along the California coast; species of *Ascophyllum, Fucus,* and *Laminaria* off Maritime Canada, the northeastern United States, England, and the China coast; and *Durvillea* in Australian waters.

21.8 ALGAL REPRODUCTION

The life cycles of many algae are still unknown, but the three basic life cycles, zygotic, gametic, and sporic, have all been documented to exist among algal species. Each life cycle has sexual and asexual portions. Asexual reproduction occurs more often than sexual reproduction; therefore, it is more commonly seen by researchers. Typical methods of asexual reproduction are cell division (for single-celled algae) and fragmentation (the splitting apart of a filament). Asexual reproduction also can be achieved by the formation, liberation, and germination of motile or non-motile spores produced in sporangia. In many algae, sporangia show little, if any, difference in appearance from ordinary vegetative cells, except that they may be larger. The parent nucleus divides by mitosis several times, and each resulting nucleus accumulates cytoplasm about itself and secretes a surrounding wall, forming a spore.

Ulothrix Typifies the Zygotic Life Cycle in Algae

The filamentous green alga *Ulothrix* has a **zygotic life cycle**, meaning that the only diploid phase of the life cycle is the single-celled zygote (Fig. 21.16).

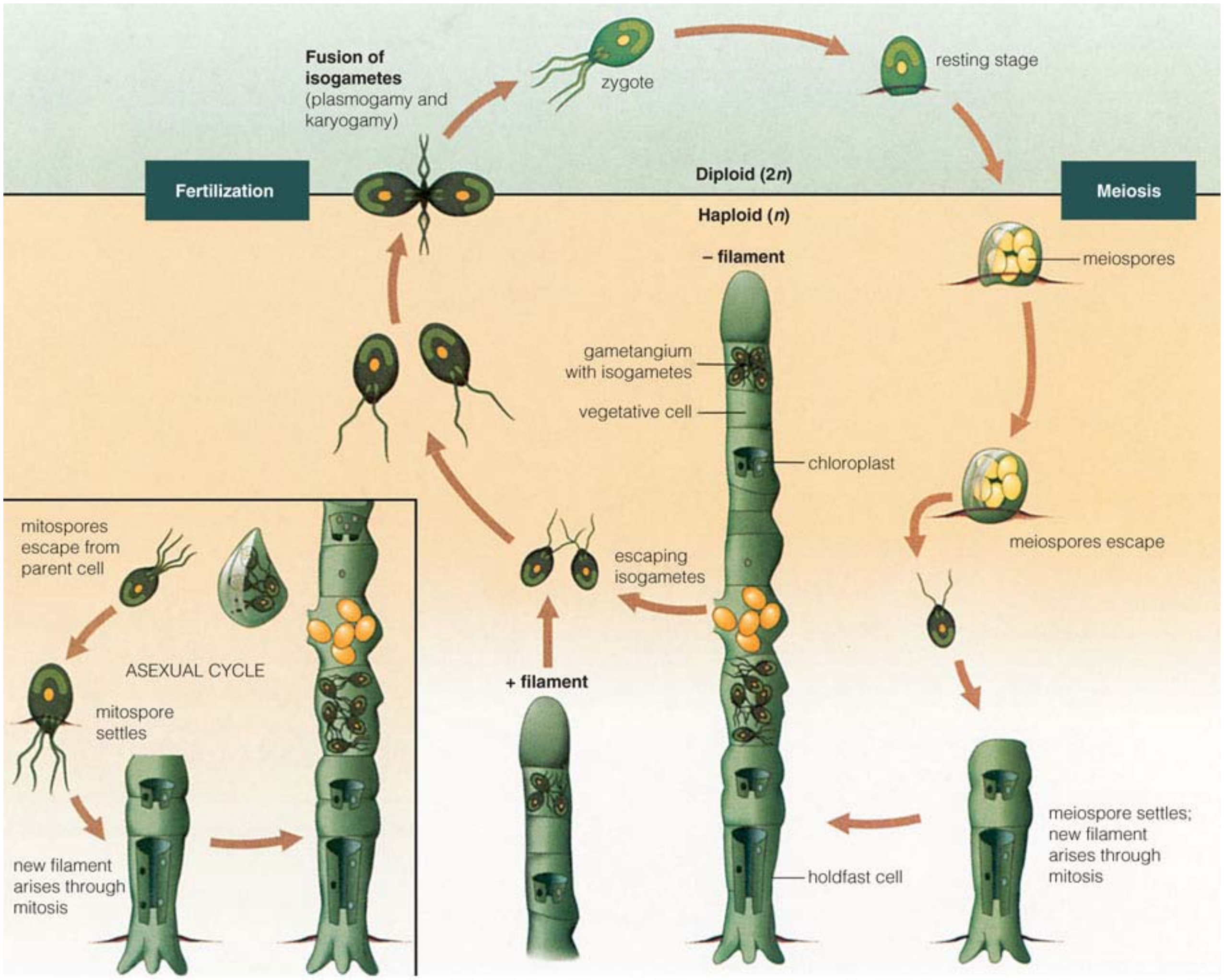


Figure 21.16. The zygotic life cycle of the filamentous green alga Ulotrix. Algal filaments are haploid. The nucleus of some cells can divide to produce mitospores (inset). Other cells produce + or - gametes, which fuse to form a resting zygote. The zygote eventually undergoes meiosis, producing meiospores, which germinate to form new algal filaments.

The nucleus of each *Ulothrix* cell is haploid. When sexual reproduction begins, some of the nuclei will divide by repeated mitotic divisions, producing many motile gametes inside the wall of the parent cell. In this case, the parent cell is a *gametangium*. The gametes of *Ulothrix* look very much like individual *Chlamydomonas* cells: they have two anterior flagella, and they swim about in water. If a *Ulothrix* gamete approaches another suitable gamete, the two will pair and fuse, producing a diploid zygote cell with four flagella. Although all *Ulothrix* gametes are isogametes, meaning they look alike under the microscope, there must be genetic differences recognizable by *Ulothrix* that make fusion possible among some, but not all, gametes--that is, there appear to be two mating types of gametes, known as plus (+) and minus (-). Because a given *Ulothrix* individual produces only plus or minus gametes, gametes form the same individual will not fuse, whereas gametes from different individuals may be able to fuse.

The zygote resulting from gametic fusion becomes spherical, loses its flagella, and enters a resting stage during which it is resistant to such environmental extremes as exposure to dry air. Once growing conditions return, the zygote becomes metabolically active and divides by meiosis to produce plus and minus meiospores, each of which is capable of producing a new individual by itself. The meiospores are dispersed, and each can germinate, divide by mitosis, and produce a plus or minus haploid plant.

When *Ulothrix* begins to reproduce asexually, a vegetative cell becomes a sporangium. Eventually 16 to 64 pear-shaped mitospores are produced by mitosis and released: each has 4 flagella. After a period of activity, these motile mitospores settle to the bottom of a pond, lose their flagella, and begin to produce a new plant by mitosis. Some mitospores may enter a dormant phase and become resistance to environmental stress during that time.

Diatoms have a Gametic Life Cycle

Diatom cells are diploid. Diatoms reproduce asexually by cell division. Recall that each cell has two wall segments that fit together like the top and bottom of a Petri dish. After division, a new wall forms within the old one (Fig. 21.17a). This means that the progeny cell that inherits the smaller wall segment will make a new wall that is smaller yet. As this pattern continues from generation to generation, one line of cells become ever smaller. Eventually, a critically small size is reached and division stops.

The cell must then reproduce sexually. The nucleus undergoes meiosis, producing four haploid nuclei (Fig. 21.17b). Only one or two of the nuclei may survive and become gametes. The parental cell has served as a gametangium. If two diatom gametangia are near each other, they open, and the two gametes emerge and fuse, forming a diploid zygote. The zygote increases greatly in size and may rest for a short time. It then secretes a normal, two-part silicate wall around itself and becomes a vegetative diploid diatom. This life cycle, in which the only haploid phase is represented by the single-celled gametes, is a **gametic life cycle**.

The common intertidal rockweed *Fucus* and many other brown algae also have a gametic life cycle.

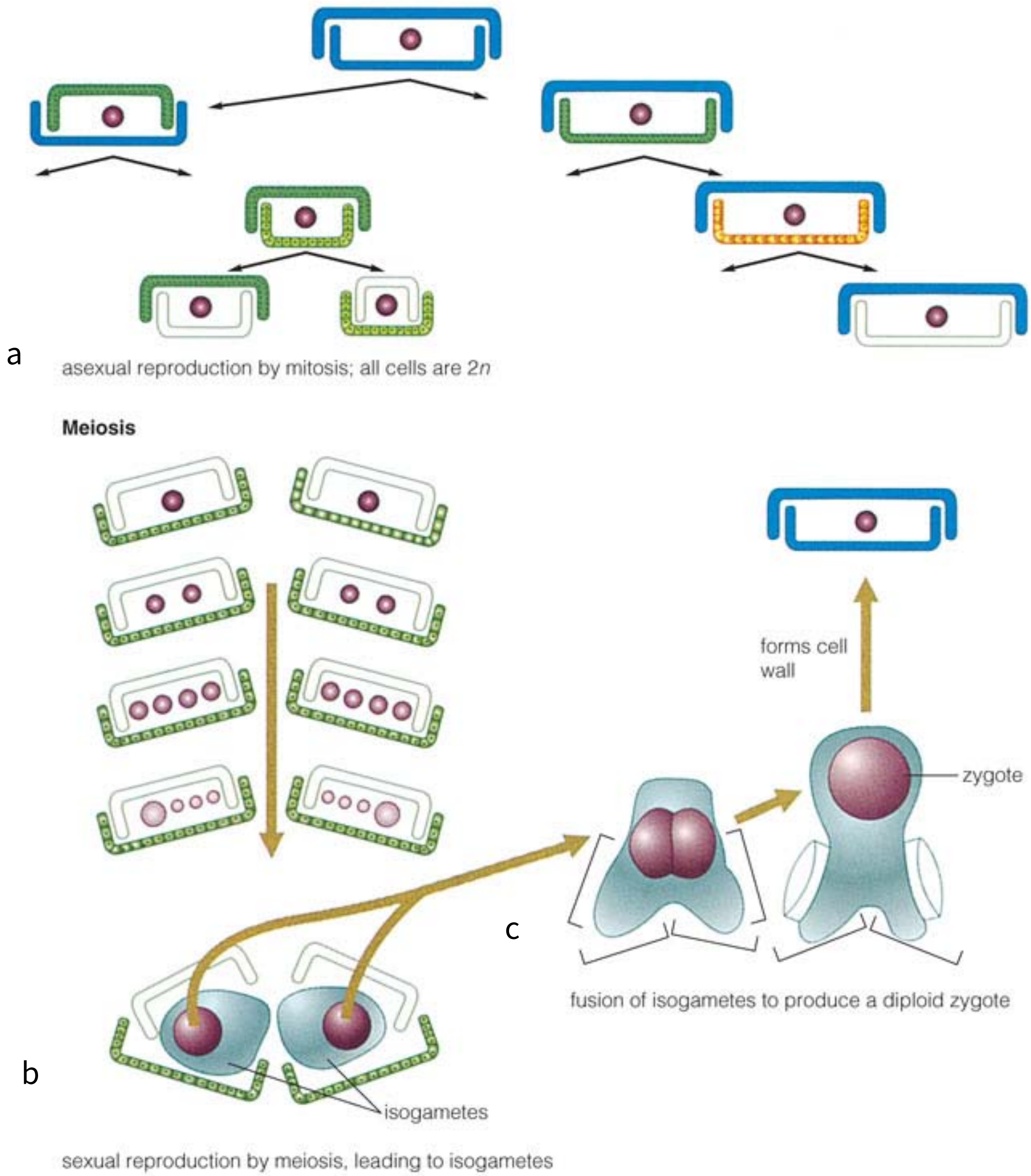


Figure 21.17. The gametic life cycle of a diatom. (a) Repeated asexual cell division results in smaller diploid cells because one of the progeny cells is formed within the wall of the smaller half of the parent cell wall. (b) When cells become critically small, meiosis occurs. The products of meiosis are four haploid nuclei within the old cell's membrane and wall. Three of the haploid nuclei degenerate and the single remaining one becomes the nucleus of a gamete. (c) The fusion of two gametes forms a diploid zygote.

Ectocarpus Has a Sporic Life Cycle with Isomorphic Generations

Ectocarpus is a filamentous brown alga commonly found in cool coastal saltwater. This alga has a **sporic life cycle**, meaning that there are multicellular gametophytes and sporophytes. The life cycle begins with the haploid phase (Fig. 21.18a), which has curved clusters of gametangia on side branches. Mitosis within each gametangium produces many gametes, which swim when released using two unequal flagella that arise from the middle of the cells. The gametes all look alike, even though they represent plus and minus mating types (they are isogametes). Fusion of a plus isogamete and minus isogamete in open water yields a diploid zygote.

The zygote settles to the bottom, germinates, and divides by mitosis to produce a diploid organism (Fig. 21b,c). The diploid sporophyte looks identical to the haploid gametophyte. The only difference is the chromosome number within every nucleus. Seaweeds such as *Ectocarpus* that have identical-looking gametophytes and sporophytes are said to have **isomorphic generations**. The sporophyte produces two kinds of reproductive cells.

In one reproductive process, clusters of cells on side branches liberate motile cells. These side branches look identical to the gametangia on gametophytes but are called asexual sporangia because of their function. Although the cells they shed look like gametes, they do not pair and produce zygotes. Instead, each is capable of producing a new individual by itself--that is, each is a diploid mitospore. The individual that each mitospore produces is another sporophyte, identical to the parent sporophyte. A second reproductive process produces a kind of sporangium that is spherical. Meiosis occurs

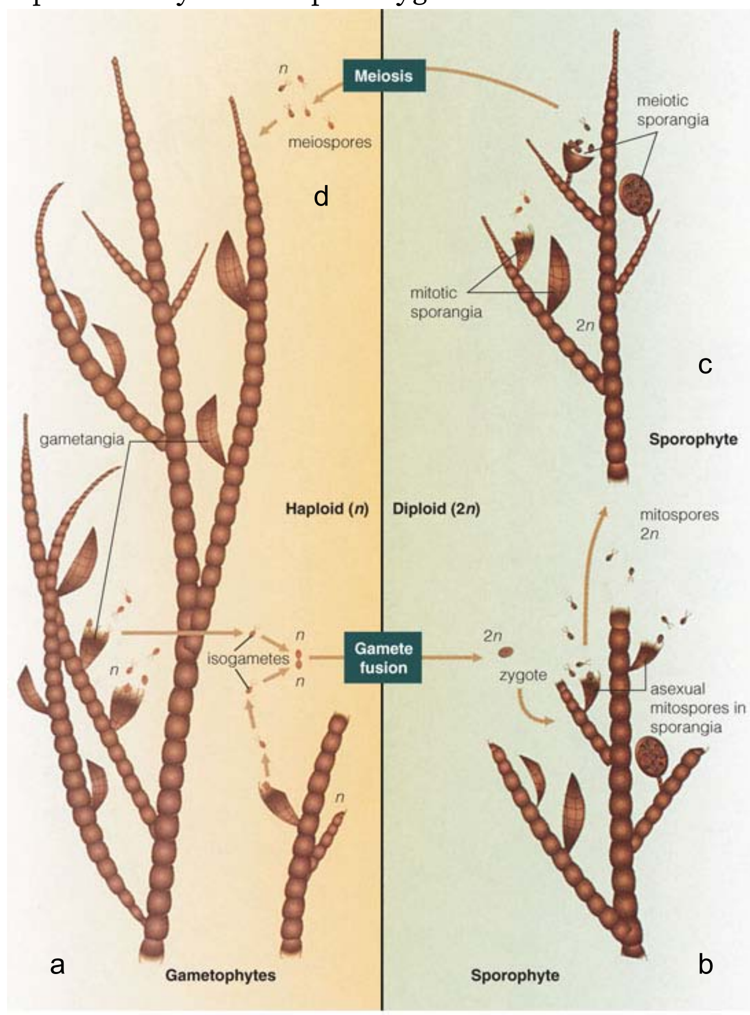


Figure 21.18. The sporic life cycle of the brown alga *Ectocarpus*, which has isomerous generations. (a) The gametophyte generation releases + and - gametes. These fuse in pairs to form diploid zygotes. Each zygote produces a sporophyte (b), which can generate asexual mitospores or (c,d) meiospores that will germinate to form a gametophyte.

within this sporangium, producing many meiospores (Fig. 21.18d). The meiospores, when released, look just like gametes and mitospores. Each one can settle down to the bottom, germinate, and produce a gametophyte, completing the life cycle.

Laminaria Has a Sporic Life Cycle with Heteromorphic Generations

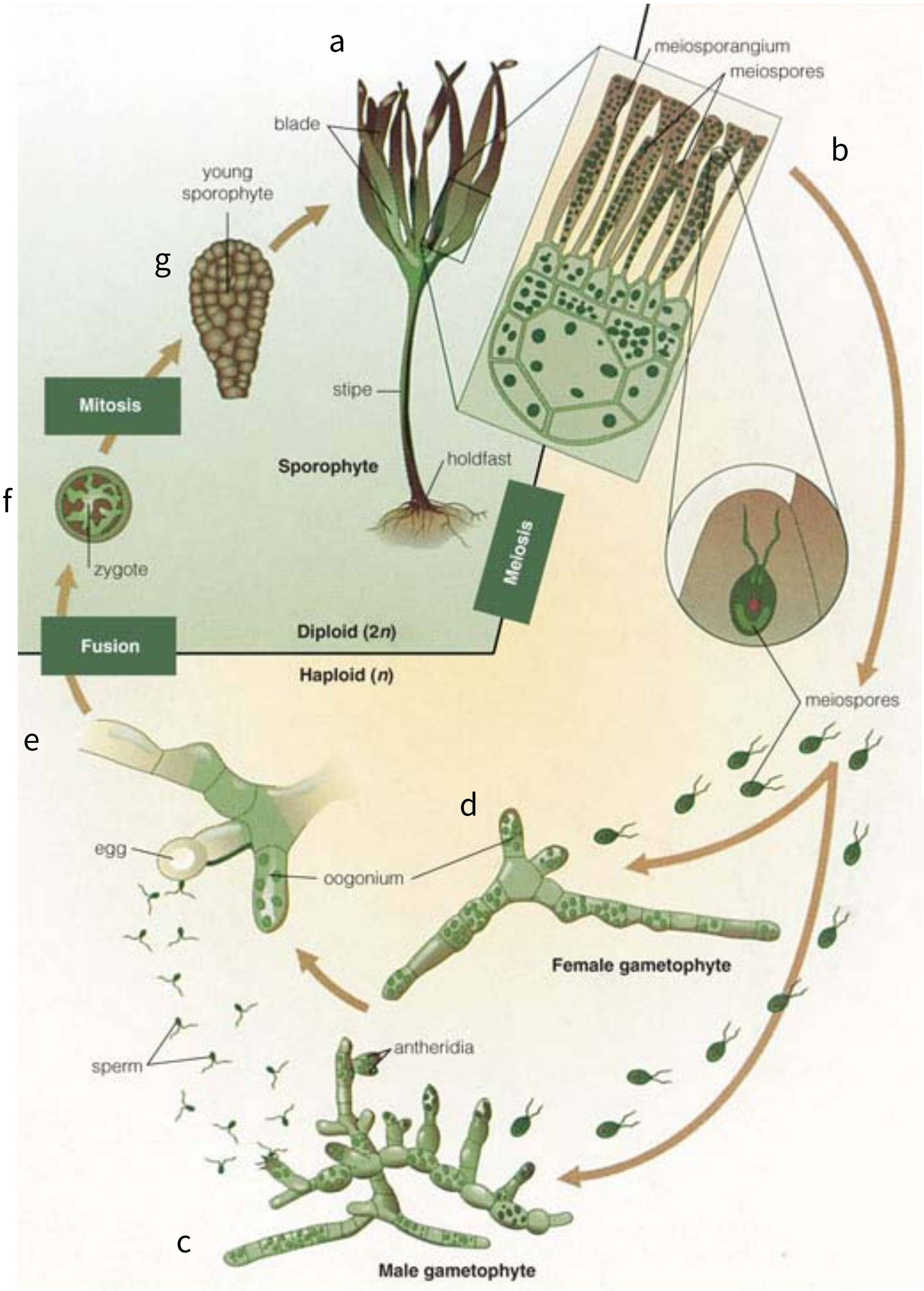


Figure 21.19. The sporic life cycle of the kelp *Laminaria*, which has heteromorphic generations. (a) The sporophyte plant. (b) Meiosis occurs in sporangia in the blade, producing male and female meiospores. Each meiospore will produce either (c) a male or (d) a female gametophyte individual. The male gametophytes produce antheridia and sperm. The females produce oogonia and eggs. (e) The fusion of gametes creates (f) a diploid zygote that then forms (g) a young sporophyte.

Plants in which the gametophyte and sporophyte are not identical have **heteromorphic generations**. Many groups of algae exhibit this kind of life cycle, but it is most highly developed in the brown algae, particular in the kelps. The kelp *Laminaria* has a sporophyte generation with a well-developed holdfast and a long unbranched stipe with a cluster of narrow blades extending from the end (Fig. 21.19a). Sporangia usually occur in groups just below the meristoderm on a blade (Fig. 21.19b). Each sporangium is a single cell within which meiosis occurs, followed by one to several rounds of mitosis, producing 8 to 64 meiospores. The meiospores are released, swim about, settle to the bottom, and produce gametophytes.

The gametophytes are small, branched filaments, quite unlike the sporophytes. Some of the gametophytes will produce male gametes (Fig. 21.19c); others will produce female gametes (Fig. 21.19d). The cells at the tips of some filaments on male gametophytes enlarge and function as **antheridia** (male gametangia). Their nuclei undergo mitosis, producing many motile sperm. Other cells of filaments of female gametophytes enlarge and function as **oogonia** (female gametangia); their nuclei undergo mitosis, producing one to several large **eggs**. The eggs are extruded nearly out of the oogonium, but they remain attached. A **sperm cell** will fuse with an egg cell, producing a zygote, which develops into a sporophyte (Fig. 21e-g). At this stage, the sporophyte separates from the gametophyte, is carried passively by currents to the bottom, and begins to develop into a mature *Laminaria* sporophyte. The life cycle is completed.

KEY TERMS

agar
algae
algin
alveolates
antheridia
apicomplexa
blades
brown algae
carrageenan
charophytes
chlorophytes
chrysophyta
ciliates
coralline algae
diatomite
diatoms
dinoflagellates
eggs
epiphyte
euglenoids
eyespot
foraminifera
gametic life cycle
green algae
green plants
Heterokonta
heteromorphic generations
holdfast
isomorphic generations
kelp
medulla
meristoderm
oogonia
Oomycota
phytoplankton
protist
red algae
seaweeds
sperm cell
sporic life cycle
stipes
thallus
Xanthophyta
zygotic life cycle

SUMMARY

1. The traditional (Linnaean) kingdom Protista includes nonphotosynthetic organisms and photosynthetic organisms. All organisms are eukaryotic, most are microscopic, and most have simple bodies. Ancestors of the animal, fungi, and land plants are all protists; consequently, the group is not monophyletic.

2. Molecular studies have shown the relationships among the various protist groups and the animals, fungi, and land plants. The photosynthetic protists are the most important for understanding land plant evolution. These are commonly called algae.

3. "Algae" is a common name for a diverse group of about 20,000 to 30,000 species of photosynthetic organisms. Algae can be generally characterized as follows: their gametangia are single cells, lacking any protective layer of sterile cells around the gametes; they lack an embryo stage; they do not have an epidermis with cuticle and stomata; they are more often aquatic than terrestrial; and their bodies usually are simple and relatively undifferentiated. Body shapes include single-celled forms, colonies, filaments, sheets, and three dimensional packages of cells. The various groups of algae differ in cell wall construction, number and placement of flagella, types of chlorophylls and pigments, morphology, and habitat ranges.

4. The protists contain a number of well-defined lineages. One clade includes the slime molds, amoebas, animals, and fungi. The four other major clades all include at least some photosynthetic members.

5. Euglenoids are a common algal group that also includes many non-photosynthetic species. Even the photosynthetic euglenoids can engulf food in the manner of an animal. They are motile (by flagella), may have a unique organ called an eyespot that orients them toward light, and have never been observed to reproduce sexually.

6. Alveolates are a large clade characterized by minute sacs beneath their cell membranes. There are four major subclades: ciliates; foraminifera; apicomplexa; and an algal group, the dinoflagellates. Dinoflagellates have chloroplasts surrounded by multiple membranes that may have been derived from multiple endosymbiotic events. Dinoflagellates cause red tides.

7. Heterokonts are a large protist clade with many photosynthetic members, some of which are multicellular. All heterokonts are characterized by two unequally sized flagella. On important nonphotosynthetic group of heterokonts is the Oomycota, the water molds, which have had a great impact on people as plant pathogens. Diatoms are single-celled, have the brown photosynthetic pigment fucoxanthin in addition to chlorophyll, and have silica cell walls. The brown algae are a group of marine seaweeds that also contain fucoxanthin. Their cell walls are impregnated with algin, an elastic polymer.

8. Red and green algae comprise a group of algal protists that are particularly important because they gave rise to land plants. Red algae are seaweeds that are capable of living at great depths in the ocean because of their red phycobilin photosynthetic pigments. Green algae primarily occupy freshwater. They comprise two groups: the diverse chlorophytes and the charophytes, which are most closely related to land plants. All green algae contain chlorophylls *a* and *b*, carotenoids, starch as a storage product, and cellulose cell walls. The fossil record of green algae extends back to nearly 1 billion years.

9. Algae are ecologically important in aquatic ecosystems by being at the base of the food chain. Most of their productivity comes from phytoplankton. In polluted or warm, shallow water, phytoplankton can become dense enough to color the water, poison vertebrates, and create noxious odors. Algae also are important as reef builders, both as coralline green and red algae and as symbionts with coral animals.

10. Seaweeds have some economic importance to humans as medicine, food, and fertilizer. However, their major value comes in the physical and chemical properties of the cell walls of diatoms (diatomite), red algae (agar, carrageenan), and brown algae (algin).

11. Algae can reproduce sexually by zygotic, gametic, and sporic life cycles. *Ulothrix* is a example of an alga with a zygotic life cycle. Diatoms have a gametic life cycle. *Ectocarpus* and *Laminaria* have sporic life cycles.

Questions

1. Why is the traditional kingdom Protista no longer considered a valid evolutionary group?

2. Characterize the group of organisms defined as protists in this chapter.

3. What evidence do biologists have to support their hypothesis that land plants evolved from green algae?

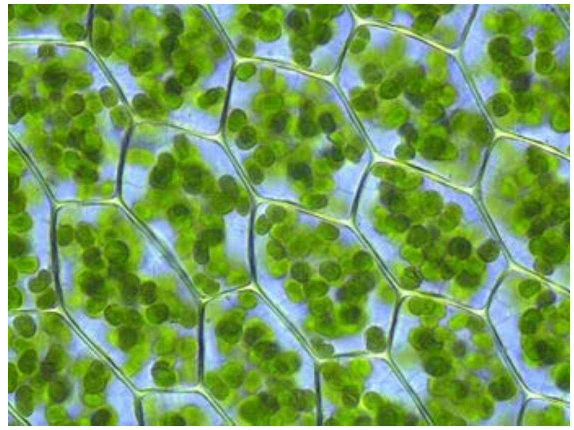
4. Make up your own short dichotomous key that separates members of the following algal groups: euglenoids, dinoflagellates, brown algae, red algae, and green algae.

5. How is it possible for microscopic algae to be important enough to fuel oceanic food chains, which culminate in large carnivorous fish and aquatic mammals such as whales? Why is it possible to say that reefs are built by algae as much as they are built by coral animals?

6. Some brown algae are complex marine organisms called kelps. Describe their specialized body regions, their unusual anatomy, and their sporic life cycle.

7. What impact have Oomycota had on humans?

IN DEPTH: ***The Mysterious Origin of Chloroplasts***



Chloroplasts are so fundamental to plants and the various algal groups that the question of their origin has been the subject of intense research and debate. The subclade that includes the land plants also includes two major algal groups: green and red algae. Biologists agree that the land plants derived their chloroplasts directly from a green alga; however, the question of whether green and red algae both derived their chloroplasts from a single common ancestor is still debated.

Cladistic analysis based on several genes, including those coding for proteins involved in photosynthesis, suggests that chloroplasts appeared only once and were then passed down to the other plant groups. However, evidence from recent analyses of chloroplast genomes also is consistent with chloroplasts evolving multiple times. One complicating factor is that lateral gene transfer (movement of genes among distantly related groups) is known to have occurred and may confound efforts to reveal the evolutionary history of chloroplasts.

Another related question concerns how many times secondary endosymbiotic events occurred to produce the great diversity of algal groups present today. Solid evidence from comparisons of DNA indicate that all the "non-plant" algae, such as the brown algae, dinoflagellates, euglenoids, and diatoms, acquired their chloroplasts from plants, either green or red algae. Extra sets of membranes surrounding the chloroplasts of the non-plant algae, and in some cases vestigial nuclei, support the idea that secondary endosymbioses have occurred.

Some researchers argue that secondary endosymbioses are rare, and that a mere two events (one involving a green alga and one involving a red alga) are enough to explain the appearance of chloroplasts in all non-plant algal groups. Other researchers maintain that secondary endosymbioses are more common and have occurred as many as seven times.

In some cases, all involving dinoflagellates, there is good evidence for tertiary endosymbiotic events--an organism with a secondarily acquired chloroplast comes to live inside a different organism and functions as a chloroplast. These events are revealed by extra sets of membranes surrounding the chloroplasts.

How many secondary endosymbiotic events occurred to create the great diversity of photosynthetic protists and whether a single primary endosymbiotic event can ultimately account for all chloroplasts remain open questions and the subjects of active research.

PLANTS, PEOPLE, AND THE ENVIRONMENT: *The Kelp Forest Ecosystem*

The California coast is one of the richest areas in the world for kelp. There, giant kelp ("sequoia of the sea," *Macrocystis pyrifera*) dominates nearshore waters on the continental shelf. This is the largest kelp species in the world, and it forms stands so magnificent in size and so dense that they have been called kelp forests or kelp beds (Figure).

Figure. A kelp forest off the California coast, viewed from underwater.

The range of this species in the northern hemisphere extends from near San Francisco south to the midpoint of the Baja California peninsula. In the southern hemisphere, it is found along the Chilean coast, off scattered islands in the South Atlantic and Indian Oceans, and into the western Pacific all the way to Tasmania and New Zealand.

The species is well known because of its economic importance as a source of algin. Kelp boats cruise offshore, harvesting the blades and stipes that float on, or just below, the surface. The material is then processed onshore to extract and purify the alginates. Giant kelp grows so rapidly that the same bed may be reharvested every 6 weeks. Kelco Company, the largest California-based firm to harvest giant kelp commercially, has monitored kelp bed acreage for many decades, and the data show dynamic fluctuations over time. What has caused these changes, and why haven't kelp beds been stable? The answer seems to be that the environment has not been stable: there have been fluctuations in temperature, turbidity, sewage, sea urchins, and sea otters.

Giant kelp grows in water between 5 and 20 m deep; only the uppermost blades lie partly exposed to air when they float on the surface. The water in which giant kelp grows is relatively cold because local upwelling currents bring deep, cold water to the surface. This deep water also is rich in nutrients. Water temperatures off the California coast normally change little from month to month or year to year, staying in the range of 12 to 20°C. Experiments show that young kelp grow poorly when the water temperature is greater than 20°C and when dissolved nitrate becomes low.

Giant kelp's sensitivity to high temperatures and low nutrient levels means that it experiences declines during El Nino events. Every 3 to 8 years, changes in the pattern of wind and water circulation in the Pacific Ocean cause surface water temperatures to increase several degrees, which produces phytoplankton blooms that use up nitrate in the water. Phytoplankton blooms also reduce the amount of solar radiation that penetrates into water. Mature kelp requires light intensity of about half that of full sun to achieve light saturation and maximum growth rate. Normally, a depth of 20 m in clear water has light at this level, but even moderate turbidity in the water from phytoplankton or sewage means that optimal light penetrates to only 10 m.

Another factor that affects the vigor of kelp beds is sewage pollution. Sewage creates turbidity and muddy ooze on the nearshore ocean bottom. Young *Macrocystis* must attach to exposed rock. Ooze prevents the organisms from anchoring themselves and may also cover young kelps and kill them. Sewage also increases sea urchin populations; these bottom-dwelling invertebrates then graze more intensively on kelp. Their grazing may sever the upper body of the kelp from the holdfast, setting it free to be washed up as beach drift. Sea urchin populations used to be controlled by a natural predator, the sea otter. By the early twentieth century, this animal had been hunted nearly to extinction for its fur. There are now laws that protect sea otters, and their population numbers are increasing. Where sea otter populations are greatest, kelp forests are most vigorous; where sea otter populations are smallest, kelp forests have declined. The resurgence of sea otters, therefore, pleases kelp harvesters. At the same time, shellfish harvesters are displeased because another favorite prey item of sea otters is abalone, a commercially valuable marine animal highly desired as seafood.

PLANTS, PEOPLE, AND THE ENVIRONMENT: ***Algal Blooms***

Phytoplankton can reproduce extremely quickly, and sometimes their cells become so dense they color the water. Which alga is causing one these algal blooms often can indicate which environmental factor is responsible. Freshwater often turns a bright green when euglenoids bloom. The Red Sea was name for the frequent recurrence of dinoflagellate blooms. On U.S. coasts, marine dinoflagellate populations periodically bloom, causing red tides.

Algal blooms typically are beneficial because they increase the food supply at the base of the food chain. However, some blooms can adversely affect aquatic life. Sometimes algal blooms can deplete oxygen from the water, causing noxious odors and death of some aquatic life. Certain algae possess sharp spines that lodge in the gills of fish, causing death or disease. Other algae, such as some of the red tide dinoflagellates (*Gymnodinium, Dinophysis, Pseudonitzchia*, and *Alexandrium*), can produce potent, water-soluble toxins that affect vertebrate nervous systems. The toxins are similar to curare poison and are 10 times more toxic than cyanide. Massive fish kills can result from these red tides. Invertebrates such as shellfish can accumulate the toxin without being affected, but humans or other vertebrates that eat tainted shellfish are poisoned.

An illness in humans called *ciguatera poisoning* comes from eating poisoned fish, and *paralytic shellfish poisoning* comes from eating shellfish. The effect of the toxin can be acute, causing respiratory failure and cardiac arrest with 12 hours of consumption. Typically, however, the symptoms are less severe and include nausea, diarrhea, itching, headache, muscle pain, and unusual sensory phenomena such as numbness and the reversal of the sensations of hot and cold. These sensory phenomena can continue for many months after the poisoning.

Red tides often are reported along the warm coastal waters of southwest India, southern China, southwest Africa, the eastern United States, the Gulf of Mexico, southern California, Peru, and Japan.

Dinoflagellates are not the only phytoplankton to produce dangerous blooms. Blooms caused by the golden alga *Prymnesium parvum* can cause massive fish kills in fresh and brackish water, negatively affecting salmon and trout fisheries. Cyanobacteria, such as *Anabaena, Gloeotrichia*, and *Nostoc*, may also undergo blooms in freshwater. Some of these have poisoned large numbers of wild mammals and birds, as well as domestic animals that drink the contaminated water.

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