6- Algae

General Overview

**DEFINITION**
The term algae has no formal taxonomic standing. It is routinely used to indicate a polyphyletic (i.e., including organisms that do not share a common origin), noncohesive, and artificial assemblage of O₂-evolving, photosynthetic organisms. According to this definition, plants could be considered an algal division. Algae and plants produce the same storage compounds, use similar defense strategies against predators and parasites, and a strong morphological similarity exists between some algae and plants.

Then, how to distinguish algae from plants?
The answer is quite easy because the similarities between algae and plants are much fewer than their differences. Algae do not have roots, stems, leaves, no well-defined vascular tissues. Even though many seaweeds are plant-like in appearance and some of them show specialization and differentiation of their vegetative cells, they do not form embryos, their reproductive structures consist of cells that are potentially fertile and lack sterile cells covering or protecting them. Parenchymatous development is present only in some groups and have both monogenetic and digenetic life cycles. Moreover, algae occur in dissimilar forms such as microscopic single cell, macroscopic multicellular loose or filmy conglomerations, matted or branched colonies, or more complex leafy or blade forms, which contrast strongly with uniformity in vascular plants.
The profound diversity of size ranging from picoplankton only 0.2–2.0 µm in diameter to giant kelps with fronds up to 60 m in length, ecology and colonized habitats, cellular structure, levels of organization and morphology, pigments for photosynthesis, reserve and structural polysaccharides, and type of life history reflect the varied origins of this heterogeneous assemblage of organisms, including both prokaryote and eukaryote species. The term algae refers to both macroalgae and a highly diversified group of microorganisms known as microalgae. The number of algal species has been estimated to be one to ten million, and most of them are microalgae.

**CLASSIFICATION**
No easily definable classification system acceptable to all exists for algae because taxonomy is under constant and rapid revision at all levels following every day new genetic and ultrastructural evidence.
Prokaryotic members of this assemblage are grouped into two divisions: Cyanophyta and Prochlorophyta, whereas eukaryotic members are grouped into nine divisions: Glaucophyta, Rhodophyta, Heterokontophyta, Haptophyta, Cryptophyta, Dinophyta, Euglenophyta, Chlorarachniophyta, and Chlorophyta (Table 1.1).
OCCURRENCE AND DISTRIBUTION

Algae can be aquatic or subaerial, when they are exposed to the atmosphere rather than being submerged in water. Aquatic algae are found almost anywhere from freshwater spring to salt lakes, with tolerance for a broad range of pH, temperature, turbidity, and O₂ and CO₂ concentration. They can be **planktonic**, like most unicellular species, living suspended throughout the lighted regions of all water bodies including under ice in polar areas. They can be also **benthic**, attached to the bottom or living within sediments, limited to shallow areas because of the rapid attenuation of light with depth. Benthic algae can grow
attached on stones (epilithic), on mud or sand (epipelic), on other algae or plants (epiphytic), or on animals (epizoic). In the case of marine algae, various terms can be used to describe their growth habits, such as supralittoral, when they grow above the high-tide level, within the reach of waves and spray; intertidal, when they grow on shores exposed to tidal cycles; or sublittoral, when they grow in the benthic environment from the extreme low-water level to around 200 m deep, in the case of very clear water.

Oceans covering about 71% of earth’s surface contain more than 5000 species of planktonic microscopic algae, the phytoplankton, which forms the base of the marine food chain and produces roughly 50% of the oxygen we inhale. However, phytoplankton is not only a cause of life but also a cause of death sometimes. When the population becomes too large in response to pollution with nutrients such as nitrogen and phosphate, these blooms can reduce the water transparency, causing the death of other photosynthetic organisms. They are often responsible for massive fish and bird kills, producing poisons and toxins. The temperate pelagic marine environment is also the realm of giant algae, the kelp. These algae have thalli up to 60 m long, and the community can be so crowded that it forms a real submerged forest; they are not limited to temperate waters, as they also form luxuriant thickets beneath polar ice sheets and can survive at very low depth. The depth record for algae is held by dark purple red algae collected at a depth of 268 m, where the faint light is blue-green and its intensity is only 0.0005% of surface light. At this depth the red part of the sunlight spectrum is filtered out from the water and sufficient energy is not available for photosynthesis. These algae can survive in the dark blue sea as they possess accessory pigments that absorb light in spectral regions different from those of the green chlorophylls a and b and channel this absorbed light energy to chlorophyll a, which is the only molecule that converts sunlight energy into chemical energy. For this reason the green of their chlorophylls is masked and they look dark purple. In contrast, algae that live in high irradiance habitat typically have pigments that protect them against the photo-damages caused by singlet oxygen. It is the composition and amount of accessory and protective pigments that give algae their wide variety of colors and for several algal groups, their common names such as brown algae, red algae, and golden and green algae. Internal freshwater environment displays a wide diversity of microalgae forms, although not exhibiting the phenomenal size range of their marine relatives. Freshwater phytoplankton and the benthic algae form the base of the aquatic food chain.

A considerable number of subaerial algae have adapted to life on land. They can occur in surprising places such as tree trunks, animal fur, snow banks, hot springs, or even embedded within desert rocks. The activities of land algae are thought to convert rock into soil to minimize soil erosion and to increase water retention and nutrient availability for plants growing nearby.

Algae also form mutually beneficial partnership with other organisms. They live with fungi to form lichens or inside the cells of reef-building corals, in both cases providing oxygen and complex nutrients to their partner and in return receiving protection and simple nutrients. This arrangement enables both partners to survive in conditions that they could not endure alone. Table 1.2 summarizes the different types of habitat colonized by the algal divisions.
STRUCTURE OF THALLUS
Examples of the distinctive morphological characteristics within different divisions are summarized in Table 1.3.

| TABLE 1.2 |
| Distribution of Algal Divisions |
| Division | Common Name | Marine | Freshwater | Terrestrial | Symbiotic |
| Cyanophyta | Blue-green algae | Yes | Yes | Yes | Yes |
| Prochlorophyta | n.a. | Yes | n.d. | n.d. | Yes |
| Glaucochlora | n.a. | n.d. | Yes | Yes | Yes |
| Rhodophyta | Red algae | Yes | Yes | Yes | Yes |
| Heterokontophyta | Golden algae | Yes | Yes | Yes | Yes |
| | Yellow-green algae | | | | |
| | Diatoms | | | | |
| | Brown algae | | | | |
| Haptophyta | Coccolithophorids | Yes | Yes | Yes | Yes |
| Cryptophyta | Cryptomonads | Yes | Yes | n.d. | Yes |
| Chlorarachniophyta | n.a. | Yes | n.d. | n.d. | Yes |
| Dinophyta | Dinoflagellates | Yes | Yes | n.d. | Yes |
| Euglenophyta | Euglenoids | Yes | Yes | Yes | Yes |
| Chlorophyta | Green algae | Yes | Yes | Yes | Yes |

Note: n.a., not available; n.d., not detected.

| TABLE 1.3 |
| Thallus Morphology in the Different Algal Divisions |
| Division | Unicellular and non-motile | Unicellular and motile | Colonial and non-motile | Colonial and motile | Filamentous | Siphonous | Parenche-matous |
| Heterokontophyta | Nannochloris | Ochromonas | Chlororhabdos | Symura | Corynebella | n.d. | Fucus |
| Haptophyta | n.d. | Chrysochro- malina | | | | | |
| Chlorophyta | Dinoflagellate | Pseudosphaerocystis | | | | | |

Note: n.d., not detected.

UNICELLS AND UNICELL COLONIAL ALGAE
Many algae are solitary cells, unicells with or without flagella, hence motile or non-motile. Nannochloropsis (Heterokontophyta) (Figure 1) is an example of a non-motile unicell, while Ochromonas (Heterokontophyta) (Figure 2) is an example of motile unicell. Other algae exist as aggregates of several single cells held together loosely or in a highly organized fashion, the colony. In these types of aggregates, the cell number is indefinite, growth occurs by cell division of its components, there is no division of labor, and each cell can survive on its own.
Hydrurus (Heterokontophyta) (Figure 3) forms long and bushy non-motile colonies with cells evenly distributed throughout a gelatinous matrix, while Synura (Heterokontophyta) (Figure 4) forms freeswimming colonies composed of cells held together by their elongated posterior ends. When the number and arrangement of cells are determined at the time of origin and remain constant during the life span of the individual colony, colony is termed coenobium.

Volvox (Chlorophyta) (Figure 5) with its spherical colonies composed of up to 50,000 cells is an example of motile coenobium, and Pediastrum (Chlorophyta) (Figure 6) with its flat colonies of cells characterized by spiny protuberances is an example of non-motile coenobium.
FILAMENTOUS ALGAE
Filaments result from cell division in the plane perpendicular to the axis of the filament and have cell chains consisting of daughter cells connected to each other by their end wall. Filaments can be simple as in *Oscillatoria* (Cyanophyta) (Figure 7), *Spirogyra* (Chlorophyta) (Figure 8), or *Ulothrix* (Chlorophyta) (Figure 9), have false branching as in *Tolypothrix* (Cyanophyta) (Figure 10) or true branching as in *Cladophora* (Chlorophyta) (Figure 11). Filaments of *Stigonema ocellatum* (Cyanophyta) (Figure 12) consists of a single layer of cells and are called uniseriate, and those of *Stigonema mamillosum* (Cyanophyta) (Figure 13) made up of multiple layers are called multiseriate.

![FIGURE 7 Simple filament of *Oscillatoria* sp.](image1)

![FIGURE 8 Simple filament of *Spirogyra* sp.](image2)

![FIGURE 9 Simple filament of *Ulothrix variabilis*.](image3)
SIPHONOUS ALGAE

These algae are characterized by a siphonous or coenocytic construction, consisting of tubular filaments lacking transverse cell walls. These algae undergo repeated nuclear division without forming cell walls; hence they are unicellular, but multinucleate (or coenocytic). The sparsely branched tube of *Vaucheria* (Heterokontophyta) (Figure 14) is an example of coenocyte or apocyte, a single cell containing many nuclei.
PARENCHYMATOUS AND PSEUDOPARENCHYMATOUS ALGAE
These algae are mostly macroscopic with undifferentiated cells and originate from a meristem with cell division in three dimensions. In the case of parenchymatous algae, cells of the primary filament divide in all directions and any essential filamentous structure is lost. This tissue organization is found in Ulva (Chlorophyta) (see life cycle in Figure 22) and many of the brown algae. Pseudoparenchymatous algae are made up of a loose or close aggregation of numerous, intertwined, branched filaments that collectively form the thallus, held together by mucilages, especially in red algae. Thallus construction is entirely based on a filamentous construction with little or no internal cell differentiation. Palmaria (Rhodophyta) (Figure 15) is a red alga with a complex pseudoparenchymatous structure.

FIGURE 14 Siphonous thallus of Vaucheria sessilis.

FIGURE 15 Pseudoparenchymatous thallus of Palmaria palmata.

NUTRITION
Following our definition of the term algae, most algal groups are considered photoautotrophs, that is, depending entirely upon their photosynthetic apparatus for their metabolic necessities, using sunlight as the source of energy, and CO₂ as the carbon source to produce carbohydrates and ATP. Most algal divisions contain colorless heterotrophic species that can obtain organic carbon from the external environment either by taking up dissolved substances (osmotrophy) or by engulfing bacteria and other cells as particulate prey (phagotrophy). Algae that cannot
synthesize essential components such as the vitamins of the B12 complex or fatty acids also exist, and have to import them; these algae are defined auxotrophic. However, it is widely accepted that algae use a complex spectrum of nutritional strategies, combining photoautotrophy and heterotrophy, which is referred to as mixotrophy. The relative contribution of autotrophy and heterotrophy to growth within a mixotrophic species varies along a gradient from algae whose dominant mode of nutrition is phototrophy, through those for which phototrophy or heterotrophy provides essential nutritional supplements, to those for which heterotrophy is the dominant strategy. Some mixotrophs are mainly photosynthetic and only occasionally use an organic energy source. Other mixotrophs meet most of their nutritional demand by phagotrophy, but may use some of the products of photosynthesis from sequestered prey chloroplasts. Photosynthetic fixation of carbon and use of particulate food as a source of major nutrients (nitrogen, phosphorus, and iron) and growth factors (e.g., vitamins, essential amino acids, and essential fatty acids) can enhance growth, especially in extreme environments where resources are limited. Heterotrophy is important for the acquisition of carbon when light is limiting and, conversely, autotrophy maintains a cell during periods when particulate food is scarce.

On the basis of their nutritional strategies, algae are into classified four groups:

- **Obligate heterotrophic algae.** They are primarily heterotrophic, but are capable of sustaining themselves by phototrophy when prey concentrations limit heterotrophic growth (e.g., *Gymnodium gracilentum*, Dinophyta).
- **Obligate phototrophic algae.** Their primary mode of nutrition is phototrophy, but they can supplement growth by phagotrophy and/or osmotrophy when light is limiting (e.g., *Dinobryon divergens*, Heterokontophyta).
- **Facultative mixotrophic algae.** They can grow equally well as phototrophs and as heterotrophs (e.g., *Fragilidium subglobosum*, Dinophyta).
- **Obligate mixotrophic algae.** Their primary mode of nutrition is phototrophy, but phagotrophy and/or osmotrophy provides substances essential for growth (photoauxotrophic algae can be included in this group) (e.g., *Euglena gracilis*, Euglenophyta).

**REPRODUCTION**

Methods of reproduction in algae may be vegetative by the division of a single cell or fragmentation of a colony, asexual by the production of motile spore, or sexual by the union of gametes.

Vegetative and asexual modes allow stability of an adapted genotype within a species from a generation to the next. Both modes provide a fast and economical means of increasing the number of individuals while restricting genetic variability. Sexual mode involves plasmogamy (union of cells), karyogamy (union of nuclei), chromosome/gene association, and meiosis, resulting in genetic recombination. Sexual reproduction allows variation but is more costly because of the waste of gametes that fail to mate.

**VEGETATIVE AND ASEXUAL REPRODUCTION**

**Binary Fission or Cellular Bisection**

It is the simplest form of reproduction; the parent organism divides into two equal parts, each having the same hereditary information as the parent. In unicellular algae, cell division may be longitudinal as in *Euglena* (Euglenophyta) (Figure 16) or
transverse. The growth of the population follows a typical curve consisting of a lag phase, an exponential or log phase, and a stationary or plateau phase, where increase in density is leveled off. In multicellular algae or in algal colonies this process eventually leads to the growth of the individual.

**Zoospore, Aplanospore, and Autospore**

Zoospores are flagellate motile spores that may be produced within a parental vegetative cell as in *Chlamydomonas* (Chlorophyta) (Figure 17). Aplanospores are aflagellate spores that begin their development within the parent cell wall before being released; these cells can develop into zoospores. Autospores are aflagellate daughter cells that will be released from the ruptured wall of the original parent cell. They are almost perfect replicas of the vegetative cells that produce them and lack the capacity to develop in zoospores. Examples of autospore forming genera are *Nannochloropsis* (Heterokontophyta) and *Chlorella* (Chlorophyta). Spores may be produced within ordinary vegetative cells or within specialized cells or structures called sporangia.

**Autocolony Formation**

In this reproductive mode, when the coenobium/colony enters the reproductive phase, each cell within the colony can produce a new colony similar to the one to which it belongs. Cell division no longer produces unicellular individuals but multicellular groups, a sort of embryonic colony that differs from the parent in cell size but not in cell number. This mode characterizes green algae such as *Volvox* (Chlorophyta) and *Pediastrum* (Chlorophyta). In *Volvox* (Figure 5) division is restricted to a series of cells which produce a hollow sphere within the parent colony, and with each mitosis each cell becomes smaller. The new colony everts, its cells form flagella at their apical poles, which is released by the rupture of the parent sphere. In *Pediastrum* (Figure 6) the protoplast of some cells of the colony undergoes divisions to form biflagellate zoospores. These are not liberated but aggregate to form a new colony within the parent cell wall.
**Fragmentation**
This is a more or less random process whereby non-coenobic colonies or filaments break into two to several fragments having the capacity of developing into new individuals.

**Resting Stages**
Under unfavorable conditions, particularly of desiccation, many algal groups produce thick-walled resting cells, such as hypnosores, hypnozygotes, statospores, and akinetes. Hypnosores and hypnozygotes, which have thickened walls, are produced ex novo by protoplasts that previously separated from the walls of the parental cells. Hypnosores are present in *Ulotrix* spp. (Chlorophyceae) and *Chlorococcum* spp. (Chlorophyceae), whereas hypnozygotes are present in *Spyrogyra* spp. (Chlorophyceae) and Dinophyta. Hypnosores and hypnozygotes enable these green algae to survive temporary drying out of small water bodies and also allow aerial transport from one water body to another for instance via birds. It is likely that dinophyceae cysts have a similar function.

Statospores are endogenous cysts formed within the vegetative cell by members of Chrysophyceae such as *Ochromonas* spp. The cyst walls consist predominantly of silica and so are often preserved as fossils. These statospores are spherical or ellipsoidal, often ornamented with spines or other projections. The wall is pierced by a pore, sealed by an unsilicified bung, and within the cyst lie a nucleus, chloroplasts, and abundant reserve material. After a period of dormancy the cyst germinates and liberates its contents in the form of one to several flagellated cells.

Akinetes are of widespread occurrence in the blue-green and green algae. They are essentially enlarged vegetative cells that develop a thickened wall in response to limiting environmental nutrients or limiting light. Figure 1.18 shows the akinetes of *Anabaena cylindrica* (Cyanophyta). They are extremely resistant to drying and freezing and function as a long-term anaerobic storage of the genetic material of the species. Akinetes can remain in sediments for many years, enduring very harsh conditions, and remain viable to assure the continuance of the species. When suitable conditions for vegetative growth are restored, the akinete germinates into new vegetative cells.

![Akinetes (arrows) of Anabaena cylindrica. (Bar: 10 mm.)](image)
SEXUAL REPRODUCTION
Gametes may be morphologically identical with vegetative cells or markedly differ from them, depending on the algal group. The main difference is obviously the DNA content that is haploid instead of diploid. Different combinations of gamete types are possible. In the case of isogamy, gametes are both motile and indistinguishable. When the two gametes differ in size, we have heterogamy.
This combination occurs in two types: anisogamy, where both gametes are motile, but one is small (sperm) and the other is large (egg); oogamy, where only one gamete is motile (sperm) and fuses with the other that is non-motile and very large (egg).
Algae exhibit three different life cycles with variation within different groups. The main difference is the point where meiosis occurs and the type of cells it produces, and whether there is more than one free-living stage in the life cycle.

Haplontic or Zygotic Life Cycle
This cycle is characterized by a single predominant haploid vegetative phase, with the meiosis taking place upon germination of the zygote. Chlamydomonas (Chlorophyta) (Figure 19) exhibits this type of life cycle.

FIGURE 19 Life cycle of Chlamydomonas sp.: 1, mature cell; 2, cell producing zoospores; 2', cell producing gametes (strain + and strain -); 3, zoospores; 3', gametes; 4, fertilization; 5, zygote; 6, release of daughter cells. R!, meiosis; a.r., asexual reproduction; s.r., sexual reproduction.
Diplontic or Gametic Life Cycle
This cycle has a single predominant vegetative diploid phase, and the meiosis gives rise to haploid gametes. Diatoms (Figure 20) and Fucus (Heterokontophyta) (Figure 21) have a diplontic cycle.

FIGURE 20 Life cycle of a diatom: 1, vegetative cell; 2, 3, vegetative cell division; 4, minimum cell size; 5, gametogenesis; 6, 7, fertilization; 8, auxospores; 9, initial cells. R!, meiosis.

FIGURE 21 Life cycle of Fucus sp.: 1, sporophyte; 2, anteridium; 2', oogonium; 3, sperm; 3', egg; 4, zygote; 5, young sporophyte. R!, meiosis.
**Diplohaplontic or Sporic Life Cycles**

These cycles present an alternation of generation between two different phases consisting in a haploid gametophyte and a diploid sporophyte. The gametophyte produces gametes by mitosis; the sporophyte produces spores through meiosis. Alternation of generation in the algae can be isomorphic, in which the two phases are morphologically identical as in *Ulva* (Chlorophyta) (Figure 22) or heteromorphic, with the predominance of the sporophyte as in *Laminaria* (Heterokontophyta) (Figure 23) or with the predominance of the gametophyte as in *Porphyra* (Rhodophyta) (Figure 24).

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**FIGURE 22 Life cycle of *Ulva* sp.:** 1, sporophyte; 2, male zoospore; 2', female zoospore; 3, young male gametophyte; 3', young female gametophyte; 4, male gametophyte; 4', female gametophyte; 5, male gamete; 5', female gamete; 6–8, syngamy; 9, young sporophyte. R!, meiosis.

**FIGURE 23 Life cycle of *Laminaria* sp.:** 1, sporophyte; 2, male zoospore; 2', female zoospore; 3, male gametophyte; 3', female gametophyte; 4, sperm; 4', egg and fertilization; 5, zygote; 6, young sporophyte. R!, meiosis.
SUMMARIES OF THE TEN ALGAL DIVISIONS

Historically, the major groups of algae are classified into Divisions (the equivalent taxon in the zoological code was the Phylum) on the basis of pigmentation, chemical nature of photosynthetic storage product, photosynthetic membranes’ (thylakoids) organization and other features of the chloroplasts, chemistry and structure of cell wall, number, arrangement, and ultrastructure of flagella (if any), occurrence of any other special features, and sexual cycles. Recently, all the studies that compare the sequence of macromolecules genes and the 5S, 18S, and 28S ribosomal RNA sequences tend to assess the internal genetic coherence of the major divisions such as Cyanophyta and Prochlophyta and Glaucophyta, Rhodophyta, Heterokontophyta, Haptophyta, Cryptophyta, Dinophyta, Euglenophyta, Chlorarachniophyta, and Chlorophyta. This confirms that these divisions are non-artificial, even though they were originally defined on the basis of morphology alone. Table 1.4 attempts to summarize the main characteristics of the different algal divisions.
CYANOPHYTA AND PROCHLOROPHYTA

All blue-green algae (Figure 25) and prochlorophytes (Figure 26) are non-motile Gramnegative eubacteria. In structural diversity, blue-green algae range from unicells through branched and unbranched filaments to unspecialized colonial aggregations and are possibly the most widely distributed of any group of algae. They are planktonic, occasionally forming blooms in eutrophic lakes, and are an important component of the picoplankton in both marine and freshwater systems; benthic, as dense mats on soil or in mud flats and hot springs, as the “black zone” high on the seashore, and as relatively inconspicuous components in most soils; and symbiotic in diatoms, ferns, lichens, cycads, sponges, and other systems. Numerically these organisms dominate the ocean ecosystems.

There are approximately 1024 cyanobacterial cells in the oceans. To put that in perspective, the number of cyanobacterial cells in the oceans is two orders of magnitude more than all the stars in the sky. Pigmentation of cyanobacteria includes chlorophyll a, blue and red phycobilins (phycoerythrin, phycoecyanin,
allophycocyanin, and phycoerythrocyanin), and carotenoids. These accessory pigments lie in the phycobilisomes, located in rows on the outer surface of the thylakoids. Their thylakoids, which lie free in the cytoplasm, are not arranged in stacks, but singled and equidistant, in contrast to prochlorophytes and most other algae, but similar to Rhodopyta and Glaucophyta.

The reserve polysaccharide is cyanophycean starch, stored in tiny granules lying between the thylakoids. In addition, these cells often contain cyanophycin granules, that is, polymer of arginine and asparagine. Some marine species also contain gas vesicles used for buoyancy regulation. In some filamentous cyanobacteria, heterocysts and akinetes are formed. Heterocysts are vegetative cells that have been drastically altered (loss of photosystem II, development of a thick, glycolipid cell wall) to provide the necessary anoxygenic environment for the process of nitrogen fixation (Figure 27). Some cyanobacteria produce potent hepato- and neurotoxins.
Prochlorophytes can be unicellular or filamentous, and depending on the filamentous species, they can be either branched or unbranched. They exist as free-living components of pelagic nanoplancton and obligate symbionts within marine didemnid ascidians and holothurians, and are mainly limited to living in tropical and subtropical marine environments, with optimal growth temperature at about 24°C. Prochlorophytes possess chlorophylls a and b similar to euglenoids and land plants, but lack phycobilins, and this is the most significance difference between these and cyanobacteria; other pigments are β-carotene and several xanthophylls (zeaxanthin is the principal one). Their thylakoids, which lie free in the cytoplasm, are arranged in stacks. Prochlorophytes have a starch-like reserve polysaccharide. These prokaryotes contribute a large percentage of the total organic carbon in the global tropical oceans, making up to 25–60% of the total chlorophyll a biomass in the tropical and subtropical oceans. They are also able to fix nitrogen, though not in heterocysts. Both blue-green algae and prochlorophytes contain polyhedral bodies (carboxysomes) containing RuBisCo (ribulose bisphosphate carboxylase/oxygenase, the enzyme that converts inorganic carbon to reduced organic carbon in all oxygen evolving photosynthetic organisms), and have similar cell walls characterized by a peptoglycan layer. Blue-green algae and Prochlorophytes can be classified as obligate photoautotrophic organisms. Reproduction in both divisions is strictly asexual, by simple cell division of fragmentation of the colony or filaments.

Glaucophyta

Glaucophytes (Figure 28) are basically unicellular flagellates with a dorsiventral construction; they bear two unequal flagella, which are inserted in a shallow depression just below the apex of the cell. Glaucophytes are rare freshwater inhabitants, sometimes collected also from soil samples. They posses only chlorophyll a and accessory pigments such as phycerothrinocyanin, phycocyanin, and allophycocyanin are organized in phycobilisomes. Carotenoids such as β-carotene and xanthophylls such as zeaxanthin are also present in their chloroplast. This unusual chloroplast lies in a special vacuole and presents a thin peptoglycan wall located between the two plastid outer membranes. Thylakoids are not stacked. The chloroplast DNA is concentrated in the center of the chloroplast, where typically carboxysomes are present, which contain the RuBisCo enzyme. Starch is the reserve polysaccharide, which is accumulated in granular form inside the cytoplasm, but outside the chloroplast. Glaucophytes live photoautotrophically with the aid of blue-green plastids often referred to as cyanelles. Sexual reproduction is unknown in this division.

FIGURE 28 A group of eight autospore of *Glaucocystis nostochinearum* still retained within parent cell wall. (Bar: 10 mm.)
RHODOPHYTA
The red algae mostly consist of seaweeds but also include the genera of free-living unicellular microalgae. The morphological characters of the class Bangiophyceae (Figure 24) range from unicells to multicellular filaments or sheet-like thalli. The Floridophyceae (Figure 29) includes morphologically complex red algae. Rhodophyta inhabit prevalently marine ecosystems but they are also present in freshwater and terrestrial environment. The lack of any flagellate stages and the presence of accessory phycobiliproteins organized in phycobilisomes (shared with Cyanobacteria, Cryptophyta, and Glaucophyta) are unique features of this division; chlorophyll a is the only chlorophyll. Chloroplasts are enclosed by a double unit membrane; thylakoids do not stack at all, but lie equidistant and singly within the chloroplast. One thylakoid is present around the periphery of the chloroplast, running parallel to the chloroplast internal membrane.
The chloroplastic DNA is organized in blebs scattered throughout the whole chloroplast. The most important storage product is floridean starch, an $\alpha$-1,4-glucan polysaccharide. Grains of this starch are located only in the cytoplasm, unlike the starch grains produced in the Chlorophyta, which lie inside the chloroplasts. Most rhodophytes live photoautotrophically. Species in which sexual reproduction is known generally have an isomorphic or heteromorphic diplohaplontic life cycle; haplontic life cycle is considered an exception.

HETEROKONTOPHYTA
One of the defining features of the members of this division is that when two flagella are present, they are different. Flagellate cells are termed heterokont, that is, they possess a long mastigonemate flagellum, which is directed forward during swimming, and a short smooth one that points backwards along the cell. Chrysophyceae contain single-celled individuals (Figure 2) as well as quite colonial forms. Xanthophyceae can be unicellular (coccoids or not) filamentous, but the most distinctive species are siphonous (Figure 14). All known species of Eustigmatophyceae are green coccoid unicells either single (Figure 1), in pairs or in colonies. Bacillariophyceae are a group of unicellular brown pigmented cells that are encased by a unique type of silica wall, composed of two overlapping frustules that fit together like a box and lid (Figure 30 and Figure 31). Raphidophyceae are unicellular wall-less heterokonts (Figure 32). Dictyochophyceae, known as silicoflagellates, are unicells that bear a single flagellum with mastigonemes (Figure 33).
Phaeophyceae are multicellular, from branched filaments to massive and complex kelp (Figure 34). Other groups of algae have been described as belonging to this division, such as Pelagophyceans and Sarcinochrysidaeans sensu and Parmales sensu. Heterokontophyta are mostly marine; but they can be found also in freshwater and terrestrial habitats. They show a preponderance of carotenoids over chlorophylls that result in all groups having golden rather than grass green hue typical of other major algal divisions. The members of this division possess chlorophylls a, c₁, c₂, and c₃ with the exception of the Eustigmatophyceae that have only chlorophyll a. The principal accessory pigments are β-carotene, fucoxanthin, and vaucheriaxanthin. The thylakoids are grouped into stacks of three, called lamellae. One lamella usually runs along the whole periphery of the chloroplast, which is termed girdle lamella, absent only in the Eustigmatophyceae. The chloroplasts are enclosed in their own double membrane and also by a fold of the endoplasmic reticulum. The chloroplastic DNA is usually arranged in a ring-shaped nucleoid. Dictyochophyceae species possess several
nucleoids scattered inside the chloroplast. The main reserve polysaccharide is chrysolaminarin, a β-1,3-glucan, located inside the cytoplasm in special vacuoles. The eyespot consists of a layer of globules, enclosed within the chloroplast, and together with the photoreceptor, located in the smooth flagellum, forms the photoreceptive apparatus. The members of this division can grow photoautotrophically but can also combine different nutritional strategies such as heterotrophy. The Heterokontophyta species that reproduce sexually have a haplontic (Chrysophyceae), diplontic (Bacillariophyceae) or diplohaplontic (Phaeophyceae) life cycle.

HAPTOPHYTA
The great majority of Haptophyta are unicellular, motile, palmelloid, or coccoid (Figure 35), but a few form colonies or short filaments.

These algae are generally found in marine habitats, although there are a number of records from freshwater and terrestrial environments. Flagellate cells bear two naked flagella, inserted either laterally or apically, which may have different length. A structure apparently found only in algae of this division is the haptonema, typically a long thin organelle - between the two flagella- reminiscent of a flagellum but with a different ultrastructure. The chloroplast contains only chlorophylls a, c1, and c2. The golden yellow brown appearance of the chloroplast is due to accessory pigments such as fucoxanthin, β-carotene, and other xanthins. Each chloroplast is enclosed within a fold of endoplasmic reticulum, which is continuous with the nuclear envelope. Thylakoids are stacked in threes, and there are no girdle lamellae. The nucleic DNA is scattered throughout the chloroplast as numerous nucleoids. When present as in Pavlova, the eyespot consists in a row of spherical globules inside the chloroplast; no associated flagellar swelling is present. The most important storage product is the polysaccharide chrysolaminarine. The cell surface is typically covered with tiny cellulosic scales or calcified scales bearing spoke-like fibrils radially arranged. Most haptophytes are photosynthetic, but heterotrophic nutrition is also possible. Phagotropy is present in the forms that lack a cell covering. A heteromorphic diplohaplontic life cycle has been reported, in which a diploid planktonic flagellate stage alternates with a haploid benthic filamentous stage.
CRYPTOPHYTA
The unicellular flagellates belonging to the division Cryptophyta are asymmetric cells dorsiventrally constructed (Figure 36). They bear two unequal, hairy flagella, subapically inserted, emerging from above a deep gullet located on the ventral side of the cell. The wall of this gullet is lined by numerous ejectosomes similar to trichocysts. Cryptophytes are typically free-swimming in freshwater and marine habitats; palmelloid phases can also be formed, and some members are known to be zooxanthellae in host invertebrates or within certain marine ciliates. Cryptophyta possess only chlorophylls a and c2. Phycobilins are present in the thylakoid lumen rather than in phycobilisomes. The chloroplasts, one or two per cell, are surrounded by a fold of the endoplasmic reticulum. In the space between these membranes a peculiar organelle, the nucleomorph, is located. This organelle can be interpreted as the vestigial nucleus of the red algal endosymbiont that gave rise to the chloroplasts of the Cryptophyta. Thylakoids are arranged in pairs, with no girdle lamellae. The pyrenoid projects out from the inner side of the chloroplast. The chloroplast DNA is condensed in small nucleoids scattered inside the chloroplast. The reserve polysaccharide accumulates in the periplastidal space as starch granules. Sometimes an eyespot formed by spherical globules is present inside the plastid, but it is not associated with the flagella. The cell is enclosed in a stiff, proteinaceous periplast, made of polygonal plates. Most forms are photosynthetic, but heterotrophic nutrition also occurs. The primary method of reproduction is simply by longitudinal cell division, but sexual reproduction has recently been documented.

DINOPHYTA
The members of this division are typical unicellular flagellates (Figure 37) but can be also nonflagellate, ameboid, coccoid, palmelloid, or filamentous. Dinoflagellates have two flagella with independent beating pattern, one training and the other girdling that confers characteristic rotatory swimming whirling motion. Flagella are apically inserted (desmokont type) or emerge from a region close to the midpoint of the ventral side of the cell (dinokont type). Most dinoflagellates are characterized by cell-covering components that lie beneath the cell membrane. Around the cell there is a superficial layer of flat, polygonal vesicles, which can be empty or filled with
cellulose plates. In dinokont type dinoflagellates, these thecal plates generally form a bi-partite armor, consisting of an upper, anterior half and a lower, posterior half, separated by a groove known as cingulum where the transversal flagellum is located (Figure 38). A smaller groove, the sceleus, extends posteriorly from the cingulum, and hosts the longitudinal flagellum. The two flagella emerge from a pore located at the intersection of the two grooves. Very often they are important components of the microplankton of freshwater and marine habitats. Though most are too large (2–2000 µm) to be consumed by filter feeders, they are readily eaten by larger protozoa, rotifer, and planktivorous fishes. Some Dinoflagellates are invertebrate parasites, others are endosymbionts (zooxanthellae) of tropical corals. Dinoflagellates possess chlorophylls a, b, c₁, and c₂, fucoxanthin, other carotenoids, and xanthophylls such as peridinin, gyrooxanthin diester, dinoxanthin, diadinoxantin, and fucoxanthin. The chloroplasts, if present, are surrounded by three membranes. Within the chloroplasts the thylakoids are for the most part united in a stack of three. The chloroplast DNA is localized in small nodules scattered in the whole chloroplast, with typical pyrenoids. A really complex photoreceptive system is present in the dinophytes such as Warnowia polyphemus, Warnowia pulchra, or Erythropsidinium agile consisting of a “compound eye” composed of a lens and a retinoid. Most dinoflagellates are distinguished by a dinokaryon, a special eukaryotic nucleus involving fibrillar chromosomes that remain condensed during the mitotic cycles. The principal reserve polysaccharide is starch, located as grains in the cytoplasm, but oil droplets are present in some genera. At the surface of the cell there are trichocysts which discharge explosively when stimulated. Besides photoautotrophy, dinoflagellates exhibit an amazing diversity of nutritional types because about half of the known species lack plastids and are therefore obligate heterotrophic. Some are notorious for nuisance blooms and toxin production, and many exhibit bioluminescence. Dinophyceae have generally a haplontic life history.

FIGURE 38 Dorsal view of Gonyaulax sp., a brackish water dinoflagellate.
EUGLENOPHYTA

Euglenophyta include mostly unicellular flagellates (Figure 39) although colonial species are common. They are widely distributed, occurring in freshwater, brackish and marine waters, most soils, and mud. They are especially abundant in highly heterotrophic environments. The flagella arise from the bottom of a cavity called reservoir, located in the anterior end of the cell. Cells can also ooze their way through mud or sand by a process known as metaboly, a series of flowing movements made possible by the presence of the pellicle, a proteinaceous wall which lies inside the cytoplasm. The pellicle can have a spiral construction and can be ornamented.

The members of this division share their pigmentation with prochlorophytes, green algae, and land plants, because they have chlorophylls a and b, β- and γ-carotenes, and xanthins. However, plastids could be colorless or absent in some species. As in the Dinophyta the chloroplast envelope consists of three membranes. Within the chloroplasts, the thylakoids are usually in groups of three, without a girdle lamella and pyrenoids may be present. The chloroplast DNA occurs as a fine skein of tiny granules. The photoreceptive system consisting of an orange eyespot located free in the cytoplasm and the true photoreceptor located at the base of the flagellum can be considered unique among unicellular algae. The reserve polysaccharide is paramylon, β-1,3-glucan, stored in the granules scattered inside the cytoplasm and not in the chloroplasts like the starch of the Chlorophyta. Though these possess algae chlorophylls, they are not photoautotrophic but rather obligate mixotrophic, because they require one or more vitamins of the B group. Some colorless genera are phagotrophic, with specialized cellular organelle for capture and ingestion of prey; some others are osmotrophic. Some of the pigmented genera are facultatively heterotrophic. Only asexual reproduction is known in this division. Euglenophyta posses unique cellular and biochemical features that place these microorganisms closer to trypanosomes than to any other algal group.

FIGURE 39 Unicell of *Euglena mutabilis*. (Bar: 10 mm.)
CHLORARACHNIOPHYTA
They are naked, uninucleate cells that form a net-like plasmodium via filopodia (Figure 40). The basic life cycle of these algae comprises ameboid, coccoid, and flagellate cell stages. The ovoid zoospores bear a single flagellum that during swimming wraps around the cell. Chlorarachniophytes are marine. They possess chlorophylls a and b. Each chloroplast has a prominent projecting pyrenoid and is surrounded by four-membrane envelope. Thylakoids are grouped in stacks of one to three. A nucleomorph is present between the second and third membranes of the chloroplast envelope.

The origin of this organelle is different from the origin of the cryptophytes nucleomorph, because the chlorarachniophytes originated from a green algal endosymbiont. Paramylon (β-1,3-glucan) is the storage carbohydrate. They are phototrophic and phagotrophic engulfing bacteria, flagellates, and eukaryotic algae. Asexual reproduction is carried out by either normal mitotic cell division or zoospore formation. Sexual reproduction characterized by heterogamy has been reported for only two species.

CHLOROPHYTA
A great range of somatic differentiation occurs within the Chlorophyta, ranging from flagellates to complex multicellular thalli differentiated into macroscopic organs. The different level of thallus organization (unicellular, colonial, filamentous, siphonous, and parenchimatous) have traditionally served as the basis of classification of this division. Prasinophyceae are unicellular motile algae covered on their cell body and flagella by non-mineralized organic scales (Figure 41). The class Chlorophyceae comprises flagellated cells even naked or covered by a cell wall termed theca (Figure 42). All Ulvophyceae known to date are sessile organisms having walled vegetative cells. Except for a small group of species, the thalli are usually multicellular or coenocytic during at least some part of the life history. Many species have microscopic, filamentous thalli, but most are macroscopic seaweeds, capable of
considerable morphological differentiation (Figure 22). Cladophorophyceae take the form of branched or unbranched filaments of multinucleate cells with periodic cross walls (Figure 11). The organization of the thallus in the class of Briopsidophyceae is always syphonous; syphonous thalli can combine to form fairly complex tissues (Figure 43).

The Zygnematophyceae species are either coccoids or filamentous (Figure 8). In all the Trentepohliophyceae the thalli consist of branched or unbranched filaments with uninucleate cells (Figure 44). Klebsormidiophyceae have coccoid and branched or unbranched filamentous forms (Figure 45). Charophyceae have macroscopic thalli, which exhibit the characteristic of both the filamentous and syphonous levels of organization (Figure 46).

Dasycladophyceae have syphonous thalli in many species encrusted with calcium carbonate (Figure 47). Chlorophytes show a wide diversity in the number and arrangements of flagella associated with individual cells (one or up to eight in the apical or subapical region). Flagellated cells are isokont, which means the flagella are similar in structure, but could differ in length. These algae are ubiquitous in freshwater, marine, and terrestrial habitats. Chlorophyta possess chlorophylls a and b, β- and γ-carotene, and several xanthophylls as accessory pigments. Chloroplasts are surrounded by a two-membrane envelope without any endoplasmic reticulum membrane. Within the chloroplasts, thylakoids are stacked to form grana. Pyrenoids, if present, are embedded within the chloroplast and often penetrated by thylakoids. The circular molecules of chloroplast DNA are concentrated in numerous small blobs (1–2 μm in diameter).
The most important reserve polysaccharide is starch, which occurs as a grain inside the chloroplasts; glucan is present in the cell wall of Cladophorophyceae and Bryopsidophyceae and β-1,4 mannan in Dasycladophyceae. Eyespot, if present, is located inside the chloroplast, and consists of a layer of carotenoid-containing lipid droplets between the chloroplast envelope and the outermost thylakoids. Chlorophyta are photoautotrophic but can be also heterotrophic. No sexuality is known in Prasinophyceae but the genus Nephroselmis has a haplontic life cycle. In Chlorophyceae, reproduction is usually brought about through the formation of flagellate reproductive cells. The life cycle is haplontic. In Ulvophyceae the life cycle is haplontic, isomorphic, and diplohaplontic. In Cladophorophyceae and Trentepohliophyceae, the life cycle of reproductive species are diplohaplontic and isomorphic. In Bryopsidophyceae, Klebsormidiophyceae, Charophyceae, Zygnematophyceae, and Dasycladophyceae life cycle is haplontic. As the advanced land plants and the “modest” Trentepohliophyceae class possess the same mechanism of cell division, that is, using the phragmoplast disc where the cells will divide, plant evolution researchers believe that the land plants derived directly from this freshwater algae class.