Filamentous Type

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* (Cyanobacteria) (Figure 1.10), *Spirogyra* (Chlorophyta) (Figure 1.11), or *Ulothrix* (Chlorophyta) (Figure 1.12), have false branching as in *Tolypothrix* (Cyanobacteria) (Figure 1.13) or *Scytonema* (Cyanobacteria) (Figure 1.14), or true branching as in *Cladophora* (Chlorophyta) (Figure 1.15). Filaments of *Stigonema ocellatum* (Cyanobacteria)



FIGURE 1.8 Motile coenobium of Eudorina sp. Scale bar: 10 µm.



FIGURE 1.9 Nonmotile coenobium of Pediastrum simplex.





FIGURE 1.11 Simple filament of Spirogyra sp.

2

FIGURE 1.12 Simple filament of Ulothrix variabilis.



FIGURE 1.13 False branched filament of Tolypothrix byssoidea.



FIGURE 1.14 False branched filament of *Scytonema* sp. Scale bar: 50µm.



FIGURE 1.15 True branched filament of Cladophora glomerata.



FIGURE 1.16 Uniseriate filament of Stigonema ocellatum.

FIGURE 1.17 Pluriscraite filament of Stigonema mamillosum.



Siphonocladous Type

The algae with this cytomorphological design have multicellular thalli, with a basically uniseriate filamentous, branched, or unbranched organization, composed of multinucleate cells as a consequence of uncoupled cell division and mitosis. The synchronously dividing nuclei are organized in nonmotile, regularly spaced nucleocytoplasmic domains that are maintained by perinuclear microtubule arrays. Despite lacking clear physical borders, such as a plasma membrane, these cytoplasmic domains behave like independent structural entities or pseudocells. This morphotype is present in members of the class Ulvophyceae (Chlorophyta) such as *Cladophora* sp. and *Anadyomene* sp.

Siphonous Type

Siphonous algae consist of a single giant tubular cell containing thousands to millions of nuclei dividing by asynchronous mitosis, and hence they are unicellular, but multinucleate (or coenocytic). No cross-walls are present and the algae often take the form of branching tubes. The sparsely branched tube of *Vaucheria* (Ochrophyta) (Figure 1.18) is an example of coenocyte or apocyte, a single cell containing many nuclei. *Bryopsis* (Chlorophyta) and *Acetabularia* sp. (Chlorophyta) (Figures 1.1t and 1.19) are other quite diverse examples; the first is a fern-like, asymmetrically branched, marine alga composed of a single, tubular-shaped cell which contains multiple nuclei and chloroplasts in a thin cytoplasmic layer surrounding a large central vacuole. The second is an umbrella-shaped alga, with a rhizoid, a stalk, and a cap-like whorl, growing in clusters attached on rocks. The single-compartment architecture of siphonous algae would suggest that they are particularly vulnerable to injury; but even if damage does occur, a complex, multistep wound response is triggered and a wound can be plugged in seconds, regenerating the lost tissue. Many species can even use a small bit of excised tissue to regenerate the rest of the plant.

This ability offers these algae considerable competitive advantage over other marine organisms. In some settings where they have been accidentally introduced, notably the Mediterranean Sea, certain species of siphonous green algae (e.g., *Caulerpa racemosa*; Figure 1.20) have proved all successful, displacing native marine flora over large areas.



Parenchymatous and Pseudo-Parenchymatous Type

These algae are mostly macroscopic with tissue of undifferentiated cells and growth originating 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 present in *Ulva* (Chlorophyta) (Figure 1.1r), where the thallus is simply organized in a two-cell layered sheet and in many of the brown algae as *Laminaria* or *Fucus*. Pseudo-parenchymatous algae are made up of a loose or close aggregation of numerous, intertwined, branched filaments that collectively form the thallus, held together by mucilage, especially in red algae. Thallus construction is entirely based on a filamentous construction with little or no internal



cell differentiation. *Palmaria* (Rhodophyta) (Figure 1.21) is a brown alga with a complex pseudoparenchymatous structure.

Palmelloid Type

This type of thallus organization consists of nonmotile, quite independent cells embedded within a common mucilaginous matrix. The name comes from the similarity with the algae belonging to the genus Palmella (Chlorophyta) which form gelatinous colonies, with nonflagellate, spherical, or ellipsoid cells uniformly arranged at the peripheral matrix. The palmelloid type can be present as a temporary phase of the life cycle in some species and as permanent feature in others. Under unfavorable conditions, algae Chlamydomonas (Chlorophyta), such as Haematococcus (Chlorophyta), or Euglena (Euglenozoa) (Figure 1.22) lose their flagella, round off, and undergo successive divisions, while the cells secrete mucus. Once favorable conditions are restored, the mucilage dissolves and cells revert to the flagellate conditions.

In members of the genus *Tetraspora* (Chlorophyta), this organization is a permanent feature: colonies are vesicular and sac-like, containing many hundreds of cells at the periphery, with long pseudocilia extending beyond the mucilaginous matrix. The palmelloid organization is present also in the members of the Palmophyllales, an early-diverging chlorophytic lineage restricted to dimly lit habitats and deep water. These algae possess a unique type of multicellularity: they form well-defined macroscopic bodies composed of small spherical cells embedded in a firm gelatinous matrix.



FIGURE 1.22 Palmelloid phase of Euglena gracilis. Scale bar: 5µm.

NUTRITION

Following our definition of the term *algae*, most algal groups should be considered photoautotrophs, that is, depending entirely on their photosynthetic apparatus for their metabolic necessities, using sunlight as the source of energy, and CO2 as the carbon source to produce carbohydrates and adenosine triphosphate. 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 such as particulate prey (phagotrophy). There also exist some algae that cannot synthesize essential components such as the vitamins of the B12 complex, or fatty acids, 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. This ability is referred to as mixotrophy. The relative contribution of autotrophy and heterotrophy to growth within mixotrophic species varies along a gradient from algae whose dominant mode of nutrition is phototrophy, through those for which phototrophy or heterotrophy provide 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. Others 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 as well as 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 can be important for the acquisition of carbon when light is limiting and, conversely, autotrophy can maintain a cell during periods when particulate food is scarce.

On the basis of their nutritional strategies, we can classify algae into four groups:

- 1. *Obligate heterotrophic algae*: they are primarily heterotrophic, but are capable of sustaining themselves by phototropy when prey concentrations limit heterotrophic growth (e.g., *Gymnodium gracilentum*, Myzozoa);
- 2. *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*, Ochrophyta);
- 3. *Facultative mixotrophic algae*: they can grow equally well as photoautotrophs and as heterotrophs (e.g., *Fragilidium subglobosum*, Myzozoa);
- 4. *Obligate mixotrophic algae*: their primary mode of nutrition is phototrophy, but phagotrophy and/or osmotrophy provide substances essential for growth (in this group, we can include photoautoxotrophic algae) (e.g., *Euglena gracilis*, Euglenozoa).

REPRODUCTION

Methods of reproduction in algae may be vegetative by division of a single cell or fragmentation of a colony, asexual by production of motile spore, or sexual by union of gametes. Vegetative and asexual mode allows 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 for 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 parents. In unicellular algae, cell division may be longitudinal as in *Euglena* (Euglenozoa) (Figure 1.23) 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 has leveled off (see Figure 6.3). In multicellular algae or in algal colonies, this process eventually leads to growth of the individual.



FIGURE 1.23 Cell division in Euglena sp. Scale bar: 5 µm.



FIGURE 1.24 Zoospores of Tetraselmis sp. within the parental cell wall. Scale bar: 5 µm.

Zoospore, Aplanospore, and Autospore

Zoospores are flagellate motile spores that may be produced within a parental vegetative cell as in *Tetraselmis* (Chlorophyta) (Figure 1.24). 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 zoospospores. Examples of autospore-forming genera are *Nannochloropsis* (Ochrophyta) and *Chlorella* (Chlorophyta). Spores may be produced within and by 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; Figure 1.7) and *Pediastrum* (Chlorophyta; Figure 1.25). In *Volvox*, 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 cell forms flagella at their apical poles, and it is released by rupture of the parent sphere. In *Pediastrum*, 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

A more or less random process whereby noncoenobic 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 hypnospores, hypnozygotes, statospores, and akinetes.

Hypnospores and hypnozygotes, which have thickened walls, are produced ex novo by protoplasts which previously separated from the walls of the parental cells. Hypnospores are present in *Ulotrix* spp. (Chlorophyta) and *Chlorococcum* spp. (Chlorophyta), whereas hypnozygotes are



FIGURE 1.25 Nonmotile coenobium of Pediastrum sp. Scale bar: 100 µm.



FIGURE 1.26 Dinoflagellate hypnozygote. Scale bar: 10 µm.

present in *Spyrogyra* spp. (Chlorophyta) and Dinophyceae (Myzozoa) (Figure 1.26). Hypnospores 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 dinoflagellate cysts have a similar function.

Statospores are endogenous cysts formed within the vegetative cell by member 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 a nucleus, chloroplasts and abundant reserve material lie within the cyst. After a period of dormancy, the cyst germinates and liberates its content in the form of one to several flagellated cells.

Akinetes is 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 1.27 shows the akinetes of *Anabaena cylindrica* (Cyanophyta). They are extremely resistant to drying and freezing, as well as function as a long-term anaerobic



FIGURE 1.27 Akinetes (arrows) of Anabaena sp. Scale bar: 10 µm.

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.

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 which 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: anysogamy, where both gametes are motile, but one is small (sperm) and one is large (egg); oogamy, when only one gamete is motile (sperm), which fuses with one nonmotile and very large (egg).

Algae exhibit three different life cycles with variation inside the different groups. The main difference is the point where meiosis occurs and the type of cells it produces, and whether or not there is more than one free-living stage present 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 1.28) exhibits this type of life cycle.

Diplontic or Gametic Life Cycle

This cycle has a single predominant vegetative diploid phase, and the meiosis gives rise to haploid gametes. Diatoms (Figure 1.29) and *Fucus* (Ochrophyta) (Figure 1.30) have a diplontic cycle.

Diplohaplontic or Sporic Life Cycles

These cycles present an alternation of generation between two different phases consisting of a haploid gametophyte and a diploid sporophyte. The gametophyte produces gametes by mitosis, and 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 1.31) or heteromorphic, with predominance of the sporophyte as in *Laminaria* (Ochrophyta) (Figure 1.32), or with predominance of the gametophyte as in *Porphyra* (Rhodophyta) (Figure 1.33).



FIGURE 1.28 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.



FIGURE 1.29 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. RI: meiosis.



FIGURE 1.30 Life cycle of *Fucus* sp.: 1, sporophyte; 2, anteridium; 2', oogonium; 3, sperm; 3', egg; 4, zygote; 5, young sporophyte. R!: meiosis.

SUMMARIES OF THE 11 ALGAL PHYLA

Historically, the major groups of algae were classified on the basis of pigmentation, chemical nature of photosynthetic storage product, photosynthetic membrane (thylakoids) organization and other features of the chloroplasts, chemistry and structure of the cell wall, number, arrangement, and ultrastructure of flagella (if any), occurrence of any other special features, and sexual cycles. Recently revised classifications incorporate advances resulting from the widespread use of phylogenomic-scale phylogenetic analyses and massively increased taxon sampling in rRNA phylogenies. All these studies tend to assess the internal genetic coherence of the major phyla such as Cyanobacteria, Glaucophyta, Rhodophyta, Chlorophyta, Charophyta, Haptophyta, Cryptophyta, Ochrophyta, Cercozoa, Myzozoa, and Euglenozoa, confirming that these divisions are nonartificial. Table 1.4 attempts to summarize the main characteristics of the different algal groups.

Cyanobacteria

All blue-green algae (Figures 1.1a and 1.34) and prochlorophytes (Figure 1.35) are nonmotile Gram-negative eubacteria. In structural diversity, blue-green algae range from unicells to 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 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



FIGURE 1.31 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.

There are approximately 10^{24} 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 both chlorophyll *a*, blue and red phycobilins (phycoerythrin, phycocyanin, allophycocyanin), 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 aspartic acid. 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 1.36). 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 freeliving components of pelagic nanoplankton 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 chlorophyll a and b, as euglenoids and land plants, but lack phycobilins, and this is the most significant difference between them and cyanobacteria, which extends the light-harvesting capacity of these algae into the blue and orange/red regions of the visible light spectrum. Other pigments are β -carotene and several xantophylls (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 from 25% to 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-1,5bisphosphate carboxylase/oxygenase, the enzyme that converts inorganic carbon into reduced organic carbon in all oxygen-evolving photosynthetic organisms) and have similar cell walls characterized by a peptidoglycan layer. Blue-green algae and prochlorophytes can be classified as obligate photoautotrophic organisms. Reproduction in both divisions is strictly asexual, by simple cell division, fragmentation of the colony, or filaments.



FIGURE 1.32 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. RI: meiosis.

Glaucophyta

Glaucophyceae (Figures 1.1b and 1.37) are basically unicellular flagellates with a dorsiventral construction; they bear two unequal flagella, which are inserted into a shallow depression just below the apex of the cell. Glaucophyceae are rare freshwater inhabitants, sometimes collected from soil samples also. They possess only chlorophyll *a*; accessory pigments such as phycoerythrocyanin, phycocyanin, and allophycocyanin are organized in phycobilisomes. Carotenoids such as β -carotenes and xantophyll zeaxanthins are also present in their chloroplast. This unusual chloroplast lies in a special vacuole and presents a thin peptidoglycan wall located between the two plastid outer membranes. Thylakoids are not stacked. The chloroplast DNA is concentrated at the center of the chloroplast, where typical 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. Glaucophyceae live photoautotrophically with the aid of blue-green plastids often referred to as cyanelles. Cyanelles are presumed to be phylogenetically derived from endosymbiotic cyanobacterium. Sexual reproduction is unknown in this division.



FIGURE 1.33 Life cycle of *Porphyra* sp.: 1, male gametophyte; 1', female gametophyte; 2, sperm; 2', egg; 3, fertilization and zygote; 4, spores; 5, sporophyte; 6, male spore; 6', female spores; 7, young male gametophyte; young female gametophyte. R!: meiosis.

Rhodophyta

This phylum is currently divided into two subphyla, Cyanidiophytina, with the single class of Cyanidiophyceae, and Rhodophytina with the remaining six classes. Red algae consist mostly of seaweed, but including genera of free-living unicellular microalgae. They inhabit prevalently marine ecosystems, but are also present in freshwater and terrestrial environment. The lack of any flagellate stages, the lack of centrioles, and the presence of accessory phycobiliproteins (allophycocyanin, phycocyanin, and phycoerythrin) organized in phycobilisomes (shared with Cyanobacteria, Cryptophyta, and Glaucophyta) are unique features of these algae; 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's internal membrane. The chloroplastic DNA is organized in blebs scattered throughout the whole chloroplast. The most important storage product is the floridean starch, an α -1,4-glucan polysaccharide, which is deposited in the cytoplasm. 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. In the great majority of red algae, cytokinesis is incomplete. Daughter cells are separated by the pit connection, a proteinaceous plug that fills the junction between cells; this connection successively becomes a plug. Species in which sexual reproduction is known generally have an isomorphic or heteromorphic diplohaplontic life cycle; haplontic life cycle is considered an exception.

The class Bangiophyceae includes all multicellular genera, in which the gametophyte has chloroplasts lacking a peripheral encircling thylakoid, and the Golgi is associated with both endoplasmic reticulum (ER) and mitochondrion. Many economically important genera found in intertidal and subtidal habitats, such as *Porphyra purpurea* and *P. umbilicalis*, belong to this class; they are harvested for human food across the North Atlantic and are under development as aquaculture crops for human and animal foods. *Porphyra* species (Figures 1.1c and 1.33) are important reference red algae because of their multicellularity, high stress tolerance (e.g., to heat, freezing, high light, osmotic stress, and desiccation), ancient fossil record of the Bangiales, and capacity to synthesize an array of storage carbohydrates and light-protection compounds. The life history of Bangiales such as *Porphyra* spp. involves an alternation between the economically important foliose blade (haploid gametophyte) and the microscopic, filamentous, diploid conchocelis phase.

The class Compsopogonophyceae includes microscopic filamentous algae (e.g., *Erythrocladia*; Figure 1.1d) to macroscopic multicellular species (e.g., *Compsopogon*). They live in coastal seawater or freshwater. They possess two distinctive ultrastructural characters in combination: the association of Golgi bodies with ER instead of mitochondria, typical of almost all red algae, and the presence of a peripheral encircling thylakoid in the chloroplast. The color of chloroplasts is variable from greenish blue to red. Asexual reproduction occurs by monospores generated by the oblique division of vegetative cells. Sexual reproduction and alternation of generations are reported in the Erythropeltidales.

The Cyanidiophyceae are all unicellular, spherical, or elliptical in shape, growing in volcanic and thermal areas under extremely low pH (0.05–5) and relatively high temperature (35–56°C). Unlike most eukaryotes, they are also capable of tolerating a large array of toxic chemical compounds such as sulfuric acid, arsenic, and other heavy metals. They reproduce by binary fission (*Cyanidioschyzon*; Figure 1.1e) or by formation of endospores (*Cyanidium*, *Galdieria*); they can be facultative heterotrophs or obligate photoautotrophs.

The Florideophyceae (Figures 1.1f and 1.38) includes all multicellular genera, both marine and freshwater, in which the gametophytes have chloroplasts with a peripheral encircling thylakoid, and the Golgi is associated with both ER and mitochondrion. The class contains species as seemingly different as the coralline algae, characterized for the presence of calcite and *Botryocladia*, known as sea-grapes, and parasitic taxa. These algae show a triphasic reproduction cycle: an isomorphic gametophyte and sporophyte generations are separated by the carposporophyte, a very different sporophyte is a set of small filaments that terminate in diploid spores, carpospores. These disperse and germinate to form the sporophyte. This is generally pseudoparenchymatous and identical to the gametophyte.

The three classes of Porphyridiophyceae (Figure 1.1g), Rhodellophyceae (Figure 1.1h), and Stylonematophyceae (Figure 1.1i) include the 10 recognized genera of unicellular red algae of the subphylum Rhodophytina. In the Porphyridiophyceae, the Golgi bodies are invariably associated with ER and a mitochondrion, while in the Rhodellophyceae the Golgi association can be either with ER or the functionally equivalent outer membrane of the nuclear envelope. The class Stylonematophyceae also includes pseudofilamentous or filamentous red algae. In the first two classes,

E1.4					
Pigments, Storage Produ	ucts, and	Cell Coverings of th	e Algal Divisions		
		Pigment	s (See Figures 3.5-3.9)		
с г	lorophylls	Phycobilins	Main Carotenoids	Main Xantophylls	Storage Products
bacteria a	<i>a</i> , <i>b</i>	C-phycoerythrin	β-carotene	Myxoxanthin	Cyanophycin (arginine and aspartic acid)
		C-phycocyanin		Zeaxanthin	Cyan ophyce an starch (α-1,4 glucan)
		Allophycocyanin			
a alydy	2	Phycoerythrocyanin	β-carotene	Zeaxanthin	Starch (cc-1,4-glucan)
		C-phycocyanin			
		Allophyc oc yanin			
phyta a		B-phycoerythrin	or- and B-carotone	Lutein	Floridean starch (0-1,4-glucan)
		R-phycoerythrin			
		R-phycocyanin			
		Allophycocyanin			
phyta	<i>t</i> , <i>b</i>	Absent	a., b., and y-carotene	Lutein	Starch (cc-1,4-glucan)
				Prasinoxanthin	
ahyta a	<i>d</i> ,1	Absent	or., B., and y-carotene	Lutein	Starch (cc-1,4-glucan)
				Prasinoxanthin	
abyta	1, c1, c2	Absent	or and B-carotone	Fue exanthin	Chryso kmiraran (3-1, 3-glucan)
phyta a	1, C2	B-phycoerytrin (545)	or-, β-, and ε-carotene	Alloxanthin	Starch (cc-1,4-glucan)
		R-phycocyanin			
		Allophyc oc yanin			
phyta	i, c ₁ , c ₂ , c ₃	Absent	or, B-, and e-carotene	Fucceanthin, violaxanthin	Chrysolamiraran (β-1,3-glucan)
toa (Chlorarachniophyceae) a	<i>a</i> , <i>b</i>	Absent	Absent	Lutein, neoxanthin, violaxanthin	Paramylon (§-1,3-glucan)
oa (Dynophyceae) a	1, c ₁ , c ₂	Absent	β-carotene	Peridinin	Starch (0-1,4-gluc an)
				Fucceanthin	
				Diadinoxanthin	
				Dinoxanthin	
				Gyroxanthin	
iozoa (Eugenophycene) 6	2, 0	Absent	5- and Y-carotene	Diadinoxanthin	Paramylon (p-1,3-glucan)
iozoa (redzienobulyceac) e	<i>a</i> * <i>a</i>	TIDEOU	p- and 7-carotene		

reproduction occurs by cell division, while in the Stylonematophyceae reproduction occurs by both cell division and monospores.



FIGURE 1.34 Cells of Cyanothece sp. Scale bar: 10 µm.



FIGURE 1.35 Cells of Prochloron sp. Scale bar: 10 µm.



FIGURE 1.36 Heterocyst (arrow) of Anabaena azollae. Scale bar: 10 µm.



FIGURE 1.37 A group of eight autospores of *Glaucocystis nostochinearum* still retained within the parent cell wall. Scale bar: 10 µm.



FIGURE 1.38 Frond of Rhodophyllis acanthocarpa. Scale bar: 5 cm.