Chapter 1

DEFINITION

The term *algae* has no formal taxonomic standing; however, it is routinely used to indicate a polyphyletic (i.e., including organisms that do not share a common origin, but follow multiple and independent evolutionary lines), non-cohesive, and artificial assemblage of O2-evolving, photosynthetic organisms (with several exceptions of colorless members undoubtedly related to pigmented forms). According to this definition, plants could be considered an algal division. Algae and plants produce the same storage compounds as well as use similar defense strategies against predators and parasites. A strong morphological similarity exists between some algae and plants; however, distinguishing algae from plants is quite easy since the similarities we have listed between algae and plants are much fewer than their differences. Plants show a very high degree of differentiation, with roots, leaves, stems, and xylem/phloem vascular network, their reproductive organs are surrounded by a jacket of sterile cells, they have a multicellular diploid embryo stage that remains developmentally and nutritionally dependent on the parental gametophyte for a significant period (and this feature is the source of the name embryophytes given to plants), and tissue-generating parenchymatous meristems at the shoot and root apices producing tissues that differentiate in a wide variety of shapes. Moreover, all plants have a digenetic life cycle, with an alternation between a haploid gametophyte and a diploid sporophyte. Algae do not have any of these features, they do not have roots, stems, leaves, nor 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 all 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 cells, 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. Evolution may have worked in two ways: one for shaping similarities and one for shaping differences. The same environmental pressure led to the parallel, independent evolution of similar traits in both plants and algae, while the transition from relatively stable aquatic environment to a gaseous medium exposed plants to new physical conditions that resulted in key physiological and structural changes necessary to be able to invade upland habitats and fully exploit them. The bottom line is that plants are a separate group with no overlapping with the algal assemblage.

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, type of life history reflect the varied evolutionary origins of this heterogeneous assemblage of organisms, including both prokaryote and eukaryote species. The term *algae* refers to macroalgae and a highly diversified group of microorganisms known as microalgae. Estimates of the number of living algae varies from 30,000 to more than 1 million species, but most of the reliable estimates refer to the numbers given in AlgaeBase, which currently documents 32,260 species of organisms generally regarded as algae of an estimated 43,918 described species of algae, corresponding to about 73%. According to the AlgaeBase estimate of 28,500 species waiting for description, the total number of algal species is likely to be about 72,500, of which more than 20,000 will be diatomic.

CLASSIFICATION

Over the past 30 years, molecular phylogenetic studies have led to extensive modification of traditional classification schemes for algae; nowadays no easily definable classification system acceptable to all exists for this group of organisms, since taxonomy is under constant and rapid revision at all levels following everyday new genetic and ultrastructural evidence. Keeping in mind that the polyphyletic nature of the algal group is somewhat inconsistent with traditional taxonomic groupings, though they are still useful to define the general characteristics and levels of organizations, and aware of the fact that taxonomic opinion may change as information accumulates, we will adopt a tentative scheme of classification mainly based on the most recently published classifications. In particular, we will integrate the most recent publications on revised classifications of eukaryotes and specific groups to obtain a classification scheme highlighting the presence of algae in the four kingdoms of Bacteria, Plantae, Chromista, and Protozoa. The main purpose of the classification here reported is to categorize the diversity of the algae in a very practical manner, providing names useful for teaching students and searching the literature. Prokaryotic members of this assemblage are grouped into the kingdom Bacteria, phylum Cyanobacteria, with the single class of Cyanophyceae. Members of the proposed division Prochlorophyta, considered artificial, are currently included in this class.

Eukaryotic members are grouped into the three kingdoms of Plantae, with four phyla, Chromista, with four phyla, and Protozoa, with two phyla. Table 1.1 shows the different classes comprised in the 11 phyla. Figure 1.1 shows examples of representatives of each class.

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 everywhere from freshwater spring to salt lakes, with tolerance for a broad range of pH, temperature, turbidity, O2, and CO2 concentration. They can be planktonic, as most unicellular species do, living suspended throughout the lighted regions of all water bodies including under ice in polar areas. They can also be benthonic, 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, other terms can also 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 the 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 sometimes a cause of death. 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 (more than 200 m), where the faint light is bluish-green and its intensity is only 0.0005% that of surface light. At these depths, the red part of the sunlight spectrum is filtered out from the water and not enough energy is available for photosynthesis. These algae can survive in the dark blue sea since 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 into chlorophyll *a*, which is the only molecule able to convert 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 habitats typically have pigments that protect them against the photo-damages caused by the presence of 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, golden, and green algae. Internal freshwater environment displays a wide diversity of form of microalgae, although not exhibiting the phenomenal size range of their marine relatives. Freshwater phytoplankton and the benthonic 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 as well as 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.

Chapter 8 will describe in detail some of the many and unusual interaction algae establish with different and distant environmental settings and other organisms, to highlight the extreme physiological variability and plasticity of this heterogeneous assemblage.

Table 1.2 summarizes the different types of habitat colonized by the algae of the divisions.

TABLE 1.1
Classification Scheme of the Different Algal Groups

	Kingdom	Subkingdom	Infrakingdom	Phylum	Class	Representative	Image
Prokaryota	Bacteria	Negibacteria		Cyanobacteria	Cyanophyceae	*Arthrospira*	1.1a
Eukaryota	Plantae	Biliphyta		Glaucophyta	Glaucophyceae	*Cyanophora*	1.1b
				Rhodophyta	Bangiophyceae	*Porphyra*	1.1c
					Compsopogonophyceae	*Erythrocladia*	1.1d
					Cyanidiophyceae	*Cyanidioschyzon*	1.1e
					Florideophyceae	*Phyllophora*	1.1f
					Porphyridiophyceae	*Porphyridium*	1.1g
					Rhodellophyceae	*Glaucosphaera*	1.1h
					Stylonematophyceae	*Stylonema*	1.1i
		Viridiplantae	Chlorophyta	Chlorophyta	Prasinophytes	*Pyramimonas*	1.1l
					Mamiellophyceae	*Crustomastix*	1.1m
					Nephroselmidophyceae	*Nephroselmis*	1.1n
					Pedinophyceae	*Pedinomonas*	1.1o
					Chlorodendrophyceae	*Tetraselmis*	1.1p
					Chlorophyceae	*Scenedesmus*	1.1q
					Ulvophyceae	*Ulva*	1.1r
					Trebouxiophyceae	*Chlorella*	1.1s
					Dasycladophyceae	*Acetabularia*	1.1t
					Palmophyllales	*Palmophyllum*	1.1u
			Streptophyta	Charophyta	Mesostigmatophyceae	*Mesostigma*	1.1v
					Chlorokybophyceae	*Chlorokybus*	1.1z
					Klebsormidiophyceae	*Klebsormidium*	1.1aa
					Charophyceae	*Nitella*	1.1ab
					Coleochaetophyceae	*Coleochaete*	1.1ac
					Zygnematophyceae	*Cosmarium*	1.1ad
	Chromista	Hacrobia		Haptophyta	Coccolithophyceae (Prymnesiophyceae)	*Umbellosphaera*	1.1ae
					Haptophyta incertae sedis	*Coronocyclus*	1.1af
					Pavlovophyceae	*Pavlova*	1.1ag

continued

TABLE 1.1 (continued)
Classification Scheme of the Different Algal Groups

Kingdom	Subkingdom	Infrakingdom	Phylum	Class	Representative	Image
			Cryptophyta	Cryptophyceae	*Rhodomonas*	1.1ah
	Harosa	Heterokonta	Ochrophyta	Chrysophyceae	*Ochromonas*	1.1ai
				Xanthophyceae	*Vaucheria*	1.1al
				Eustigmatophyceae	*Nannochloropsis*	1.1am
				Bacillariophyceae	*Cylindrotheca*	1.1an
				Raphidophyceae	*Heterosigma*	1.1ao
				Dictyochophyceae	*Distephanus*	1.1ap
				Phaeophyceae	*Ascophyllum*	1.1aq
				Pelagophyceae	*Chrysophaeum*	1.1ar
				Bolidophyceae	*Tetraparma*	1.1as
				Schizocladiophyceae	*Schizocladia*	1.1at
				Chrysomerophyceae	*Gyraudiopsis*	1.1au
				Picophagophyceae	*Picophagus*	1.1av
				Pinguiophyceae	*Pinguiococcus*	1.1az
				Placidiophyceae	*Placidia*	1.1ba
				Phaeothamniophyceae	*Phaeothamnion*	1.1bb
				Synchromophyceae	*Synchroma*	1.1bc
				Synurophyceae	*Synura*	1.1bd
				Aurearenophyceae	*Aurearena*	1.1be
			Cercozoa	Chlorarachniophyceae	*Gymnochlora*	1.1bf
Protozoa	Biciliata	Alveolata	Myzozoa	Dinophyceae	*Prorocentrum*	1.1bg
					Lepidodinium	1.1bh
	Eozoa	Euglenozoa	Euglenozoa	Euglenophyceae	*Euglena*	1.1bi
					Phacus	1.1bl
					Trachelomonas	1.1bm
					Peranema	1.1bn

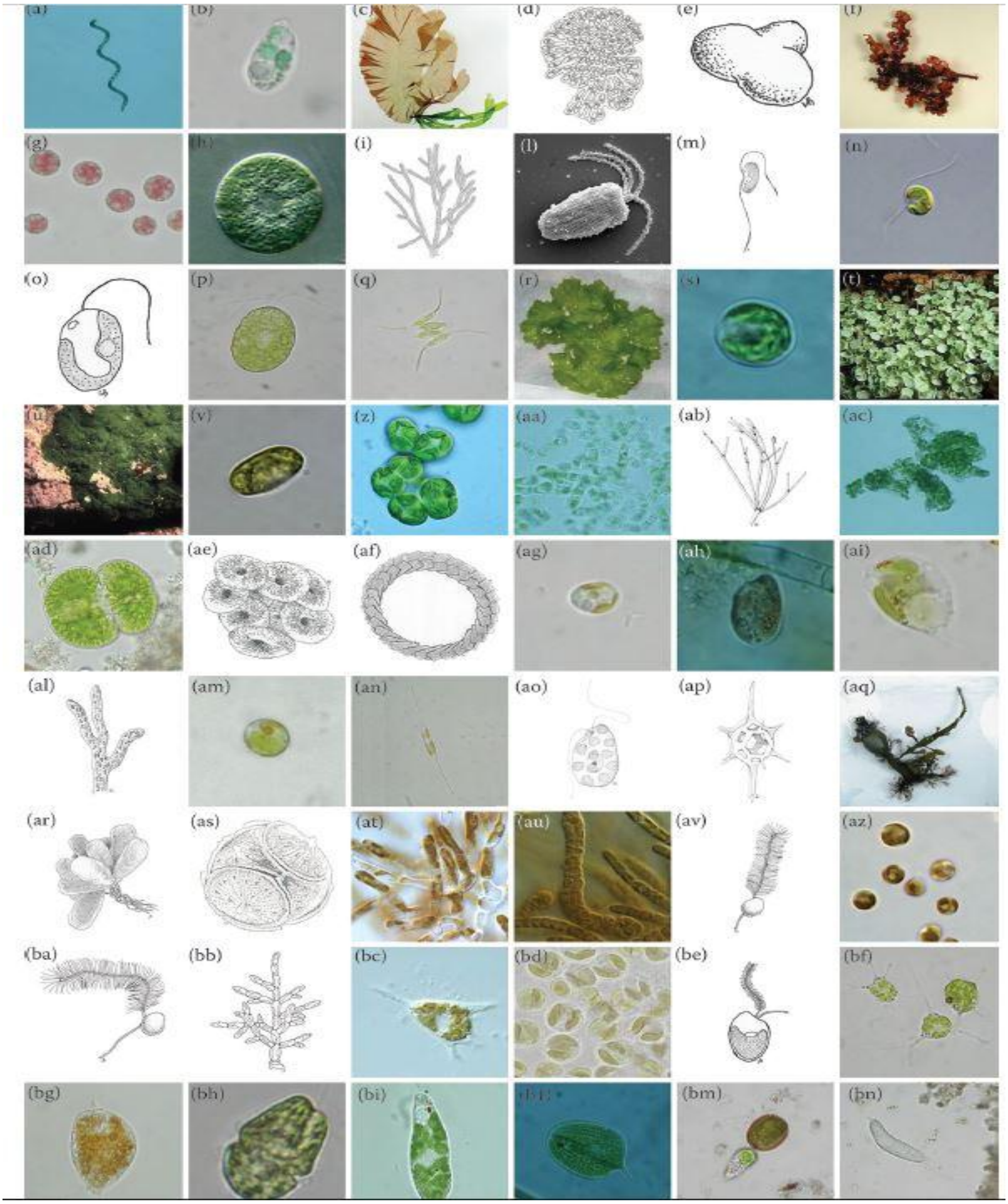

FIGURE 1.1 Examples of representatives of the different algal classes. See Table 1.1 for details. (Figures 1.1c, 1.1t, 1.1u—courtesy of Prof. Gianfranco Sartoni.)

TABLE 1.2
Distribution of Algal Divisions

Phylum	Common Name	Habitat			
		Marine	Freshwater	Terrestrial	Symbiotic
Cyanobacteria	Blue-green algae	Yes	Yes	Yes	Yes
Glaucophyta	n.a.	n.d.	Yes	Yes	Yes
Rhodophyta	Red algae	Yes	Yes	Yes	Yes
Chlorophyta	Green algae	Yes	Yes	Yes	Yes
Charophyta	n.a.	Yes	Yes	Yes	n.d.
Haptophyta	Coccolithophorids	Yes	Yes	Yes	Yes
Cryptophyta	Cryptomonads	Yes	Yes	n.d.	Yes
Ochrophyta	Golden algae Yellow-green algae Diatoms Brown algae	Yes	Yes	Yes	Yes
Cercozoa (Chlorarachniophyceae)	n.a.	Yes	n.d.	n.d.	Yes
Myzozoa (Dynophyceae)	Dinoflagellates	Yes	Yes	n.d.	Yes
Euglenozoa (Euglenophyceae)	Euglenoids	Yes	Yes	Yes	Yes

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

STRUCTURE OF THALLUS—CYTOMORPHOLOGICAL TYPES

An unrivalled diversity of morphological and cytological designs has evolved within algae, from microscopic unicells to macroscopic multicellular organisms, from simple filaments to giant-celled algae. Examples of the distinctive morphological characteristics within different groups are set forth in Table 1.3.

TABLE 1.3

Thallus Morphology in the Different Algal Divisions

Phylum	Unicellular and Nonmotile	Unicellular and Motile	Colonial and Nonmotile	Colonial and Motile	Filamentous	Siphonous	Parenchimatous
Cyanobacteria	*Synechococcus* *Prochloron*	n.d.	*Anacystis*	n.d.	*Calothrix* *Prochlorothrix*	n.d.	*Pleurocapsa*
Glaucophyta	*Glaucocystis*	*Cyanophora*	n.d.	n.d.	n.d.	n.d.	n.d.
Rhodophyta	*Phorphyridium*	n.d.	*Cyanoderma*	n.d.	*Goniotricum*	n.d.	*Palmaria*
Chlorophyta	*Chlorella*	*Dunaliella*	*Pseudo-sphaerocystis*	*Volvox*	*Ulothrix*	*Bryopsis*	*Ulva*
Charophyta							
Haptophyta	n.d.	*Chrysochromulina*	n.d.	*Corymbellus*	n.d.	n.d.	n.d.
Cryptophyta	n.d.	*Cryptomonas*	n.d.	n.d.	*Bjornbergiella*	n.d.	n.d.
Ochrophyta	*Triceratium*	*Ochromonas*	*Chlorobotrys*	*Synura*	*Ectocarpus*	*Vaucheria*	*Fucus*
Cercozoa (Chlorarachniophyceae)	n.d.	*Chlorarachnion*	n.d.	n.d.	n.d.	n.d.	n.d.
Myzozoa (Dynophyceae)	*Dinococcus*	*Gonyaulax*	*Gloeodinium*	n.d.	*Dinoclonium*	n.d.	n.d.
Euglenozoa (Euglenophyceae)	*Ascoglena*	*Phacus*	*Colacium*	n.d.	n.d.	n.d.	n.d.

Note: n.d., not detected.

Unicells and Unicell Colonial Type

Many algae are solitary cells, the unicell, with or without flagella, hence motile or nonmotile. *Nannochloropsis* (Ochrophyta) (Figures 1.1am and 1.2) is an example of a nonmotile unicell, while *Ochromonas* (Ochrophyta) (Figures 1.1ai and 1.3) is an example of a motile unicell. Other algae exist as aggregates of few or many single cells held together loosely or in a highly organized fashion, the colony. In this type of aggregate, 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* (Ochrophyta) (Figure 1.4) forms long and bushy nonmotile colonies with cells evenly distributed throughout a gelatinous matrix, while *Synura* (Ochrophyta) (Figures 1.1bd and 1.5) forms free-swimming colonies composed of cells held together by their elongated posterior ends. Another quite unusual example of colony is *Tetraflagellochloris mauritanica* (Chlorophyta) (Figure 1.6a and 1.6b): up to 12 cells can be arranged in groups, which are connected by intercellular diaphragms and cytoplasmic bridges, without sharing any common colonial boundary. When the number and arrangement of cells are determined at the time of origin of the colony and remain constant during the lifespan period of the individual colony, the colony is termed coenobium. *Volvox* (Chlorophyta) (Figure 1.7) with its spherical colonies composed of up to 50,000 flagellated cells interconnected by cytoplasmic bridges is an example of a motile coenobium, as well as *Eudorina* (Chlorophyta) (Figure 1.8). *Hydrodictyon* (Chlorophyta) with its flat plat-like networks of several thousand cells and *Pediastrum* (Chlorophyta) (Figure 1.9) with its flat colonies of cells characterized by spiny protuberances are examples of nonmotile coenobia.

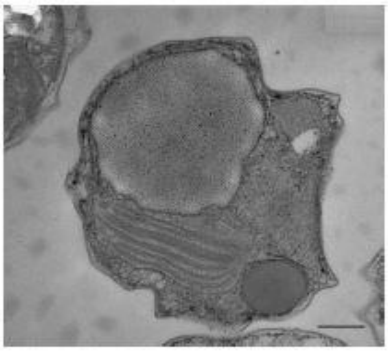

FIGURE 1.2 Transmission electron micrograph of a *Nannochloropsis* sp. nonmotile unicell. Scale bar: 0.5 µm.

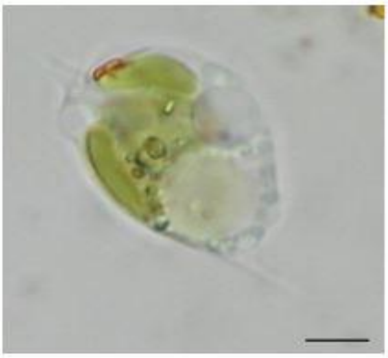

FIGURE 1.3 *Ochromonas* sp. motile unicell. Scale bar: 4 µm.

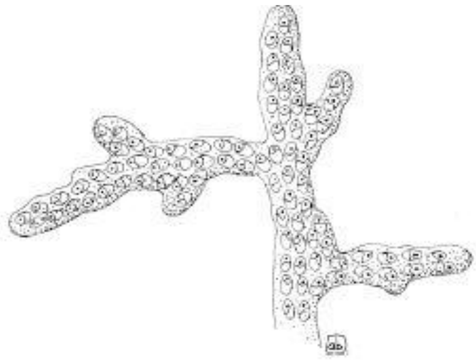

FIGURE 1.4 Nonmotile colony of *Hydrurus foetidus*.

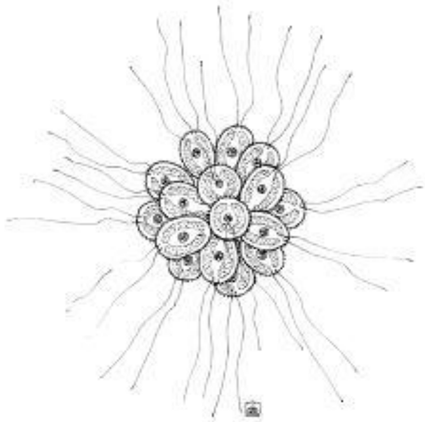

FIGURE 1.5 Free-swimming colony of *Synura uvella*.

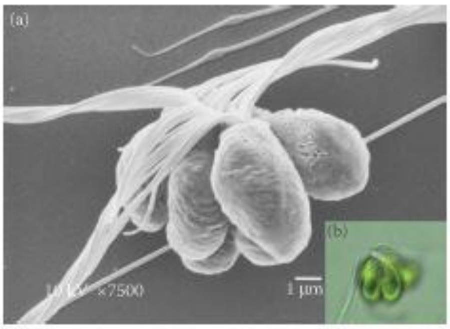

FIGURE 1.6 Free-swimming colony of *Tetraflagellochloris mauritanica*: (a) SEM image and (b) wide-field optical microscope image.

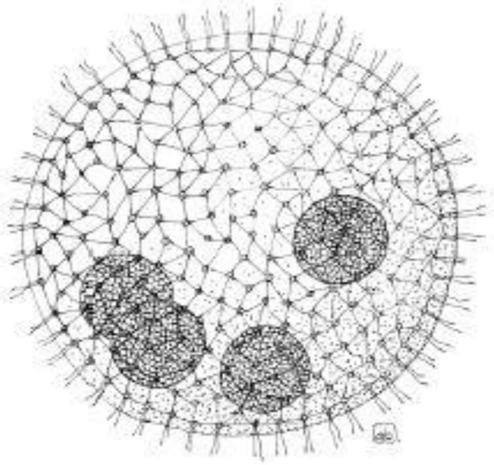

FIGURE 1.7 Motile coenobium of *Volvox aureus*.