Chlorophyta

Members of this phylum are common inhabitants of marine, freshwater, and terrestrial environments; within the phylum, a great range of somatic differentiation occurs, ranging from flagellates to complex multicellular thalli differentiated into macroscopic organs. The different level of thallus organization (unicellular, colonial, filamentous, siphonous, and parenchimatous) has traditionally served as the basis of classification of this division. 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). All members of the chlorophytes have motile stages with two or four anterior isokont flagella (i.e., flagella are of equal length and possess equivalent function), although algae with two flagella of slightly unequal lengths have been described. Flagella are characterized by a "stellate structure"-type flagellar transition region. Within the cell, the flagellar basal bodies are associated with four microtubular rootlets, cruciately arranged, which alternate between two and higher numbers of microtubules, according to the formula X-2-X-2. When viewed from above the cell, the basal bodies and rootlets can have a perfect cruciate pattern, with the basal bodies directly opposed (DO) or they can be offset in a clockwise (CW) or counterclockwise (CCW) position.

According to the most recent classifications, Chlorophyta comprises the early-diverging prasinophytes, which gave rise to the core chlorophytes (including the early diverging Chloredendrophycae with the three major classes of Ulvophyceae, Trebouxiophyceae, and Chlorophyceae), to the Pedinophyceae, sister class to the core chlorophytes, and the recently proposed group Palmophyllales.

The prasinophytes, as presently conceived, include a heterogeneous assemblage of unicellular motile algae, either naked or covered on their cell body and flagella by nonmineralized organic scales (Figures 1.1l and 1.39). They are predominantly marine planktonic, but also include several freshwater representatives. At present, nine prasinophyte clades are recognized, two of which have been recently accommodated into the two classes of Mamiellophyceae and Nephroselmidophyceae. Mamiellophyceae (Figure 1.1m) are typically solitary cells, with one or two chloroplasts, mono- or biflagellate, with isokont or anisokont flagella. They may be scale-covered or naked. Nephroselmidophyceae (Figure 1.1n) are laterally compressed, scale-covered cells, with laterally inserted anisokont flagella, and possess a single cup-shaped chloroplast. Pedinophyceae (Figure 1.1o) are unicellular, monoflagellate asymmetrical algae, with CCW basal body orientation. Rigid or thin hair-like appendages are present on the flagellum. Chloredendrophyceae (Figure 1.1p) possess a pair of flagella inserted in a pit; basal body orientation is CCW. These algae are covered by organic scales, the outer layer of which is fused to form a theca. The class Chlorophyceae (Figure 1.1q) comprises mainly swimming cells with one or two pair of flagella, without mastigonemes. Cells can be naked or covered by a cell wall more or less calcified (Figure 1.40). Either DO or CW arrangements are present in the members of this class. Ulvophyceae morphologies range from microscopic unicellular to macroscopic multicellular plants and giant-celled organisms (Figures 1.1r, 1.41, and 1.42). Four main cytomorphological types can be distinguished: nonmotile uninucleate unicells; multicellular filaments or blades composed of multinucleate cells; multicellular bodies composed of multinucleate cells with nuclei organized in regularly spaced cytoplasmic domains; siphonous thalli consisting of a single giant tubular cell containing thousands to millions of nuclei. In some species, siphonous thalli are encrusted with calcium carbonate. The majority of Ulvophyceae are marine, but several members also occur in freshwater or damp subaerial habitats. All the algae of

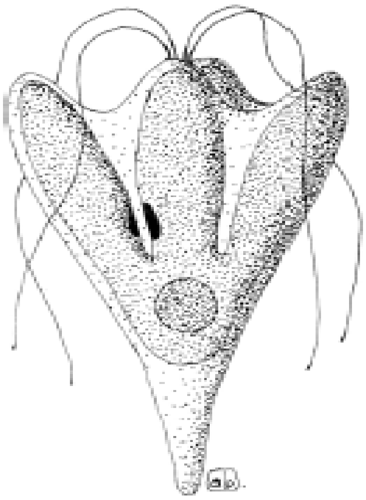

FIGURE 1.39 Unicell of *Pyramimonas longicauda*.

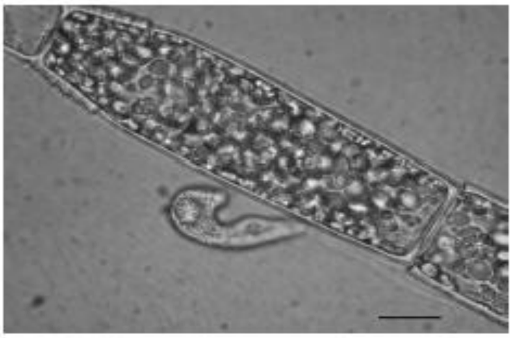

FIGURE 1.40 Filament of *Oedogonium* sp., with a *Peranema* sp. cell. Scale bar: 20 μm.

FIGURE 1.41 Thallus of *Codium* sp. Scale bar: 2 cm.

the class possess a CCW basal body orientation. The class Trebouxiophyceae (Figures 1.1s and 1.43) encompasses motile and nonmotile unicells, colonies, and multicellular filaments or blades from freshwater or terrestrial habitats, with some species present also in brackish or marine water. Several species are either symbiotic with fungi to form lichens or endosymbiotic with freshwater and marine protists, invertebrates, and plants. Swimming cells can have one or two pair of flagella without mastigonemes. All the algae of the class possess a CCW basal body orientation. The class Dasycladophyceae (Figures 1.1t and 1.19) contains algae characterized by a siphounous organization of the thallus, with numerous chloroplasts. This class is entirely marine.

As already stated, Palmophyllales (Figure 1.1u) are an early-diverging chlorophytic lineage; these algae are restricted to dimly lit habitats and deep water. They possess a unique type of multicellularity, forming well-defined macroscopic bodies composed of small spherical cells embedded in a firm gelatinous matrix.

Chlorophyta possess chlorophylls *a* and *b*, β- and γ-carotene, and several xantophylls as accessory pigments. Chloroplasts are surrounded by a two-membrane envelope without any ER membrane. Within the chloroplasts, thylakoids are stacked to form grana. Pyrenoids, where present,

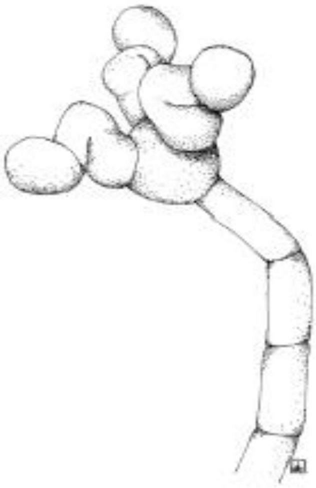

FIGURE 1.42 Thallus of *Trentepohlia arborum*.

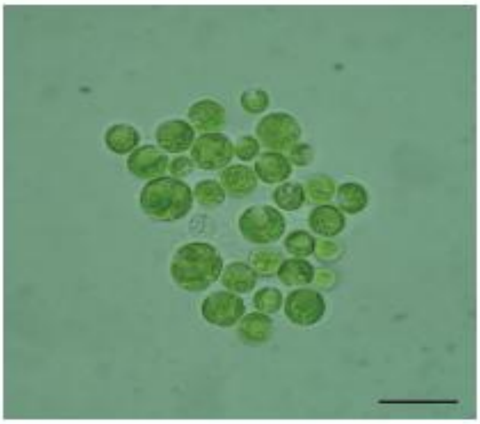

FIGURE 1.43 Group of *Chlorella* sp. cells. Scale bar: 10 µm.

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 grains inside the chloroplasts; glucan or β-1,4 mannan can be present in the cell wall of some Ulvophyceae. 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.

Charophyta

Charophytes are the organisms most closely related to land plants. The six groups of the phylum have been distinctly recognized on the basis of ultrastructural, biochemical, and molecular data. Mesostigmatophyceae (Figure 1.1v) and Chlorokybophyceae form the earliest branching

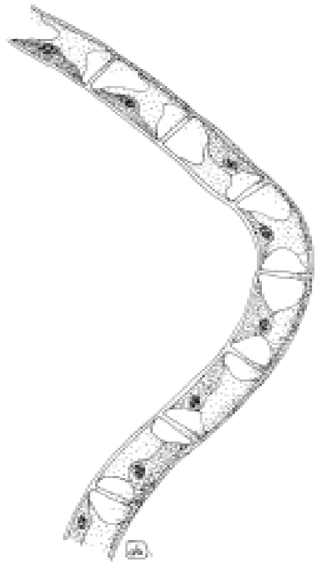

FIGURE 1.44 Filament of *Klebsormidium* sp.

streptophytes; the only genus of Mesostigmatophyceae is *Mesotigma* with two species, *M. viride* and *M. grande*. These isogamous algae are freshwater, scaly, asymmetrical, and unicellular biflagellate, and unlike other charophytes, possess two multilayered structures and an eyespot. Chlorokybophyceae (Figure 1.1z) consists of a sole representative, *Chlorokybus atmophyticus*, occurring in moist terrestrial habitats where it forms sarcinoid packets of a few cells enveloped in a common mucilaginous matrix, which reproduce asexually by asymmetrical motile spores possessing a single multilayered structure. Klebsormidiophyceae (Figure 1.1aa) represent the common ancestor of the remaining streptophytes, in which multicellularity evolved in the form of unbranched filaments (Figure 1.44). These freshwater or terrestrial algae, which can also form sarcinoid packets, reproduce by filament fragmentation and release of motile spores. Charophyceae (Figures 1.1ab and 1.45) are the most plant-like in appearance among the charophytes, because of the independent evolution of macrophytic forms. Thalli consist of a central stalk of large, elongated multinucleate cells and whorls of branches at nodes. All species are oogamous with motile sperm produced in complex antheridia. Coleochaetophyceae (Figure 1.1ac) range in morphology from branched filamentous algae to relatively complex discoid parenchymatous thalli. They may be epiphytic, endophytic, or loosely attached to submerged vascular plants or other substrates. They are oogamous, with biflagellate zoospore and sperm. The Zygnematophyceae (Figure 1.1ad) are the most species-rich clade of the Charophyta and the most morphologycally diverse. Thalli include nonmotile unicells, filaments, and small colonial forms (Figure 1.11). They possess an unusual mode of sexual reproduction by fusion of nonflagellate gametes. A very recent comprehensive genome scale analysis of 160 nuclear genes drawn from species distributed across all the charophyte groups supported the Zygnematophyceae as the closest living relative to land plants.

Haptophyta

This phylum contains only two classes: Coccolitophyceae (Prymnesiophyceae; Figures 1.1ae, 1.1af, and 1.46) and Pavlovophyceae (Figure 1.1ag). The great majority of these algae are unicellular, motile, palmelloid, or coccoid, 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

FIGURE 1.45 Thallus of *Nitella* sp.

FIGURE 1.46 Unicell of *Helicosphaera carteri*.

environments. Flagellate cells bear two naked flagella, inserted either laterally or apically, which may have different lengths. A structure apparently found only in algae of this division is the haptonema, typically a long thin organelle reminiscent of a flagellum but with a different ultrastructure. The chloroplast contains only chlorophyll *a*, *c*1, and *c*2. The golden yellowish-brown appearance of chloroplast is due to the accessory pigments such as fucoxanthin, β-carotene, and other xanthins. Each chloroplast is enclosed within a fold of ER, 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* (Figure 1.1ag), 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. Phagothropy 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 flagellate belonging to the division Cryptophyta are asymmetric cells dorsiventrally constructed (Figure 1.47). They are mostly biflagellated, with 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 ciliate.

These algae possess only chlorophyll *a* and *c*2. Phycobilins are present in the thylakoid lumen rather than in phycobilisomes. The chloroplasts, one or two per cell, are bounded by four membranes. The outermost membrane is continuous with the nuclear envelope and its surface is studded with ribosomes. Between the inner and outer membrane pairs is the periplastidial compartment, which contains the nucleomorph, the relict nucleus of the eukaryotic endosymbiont. 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 periplastidial 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 by polygonal plates. Most forms are photosynthetic, but there are some colorless, heterotrophic. The primary method of reproduction is simply by longitudinal cell division, but sexual reproduction has also been documented.

Ochrophyta

One of the defining features of the members of this division is that when two flagella are present, they are different. Flagellate stages, when present, are therefore termed heterokont, that is, they possess a long mastigonemate flagellum, which is directed forward during the swimming, and a

FIGURE 1.47 Unicell of *Cryptomonas* sp. Scale bar: 6 µm.

short smooth one that points backwards along the cell. These algae are mostly marine, but they can also be found 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 division. The members of this division possess chlorophylls *a*, *c*1, *c*2, and *c*3 with the exception of the Eustigmatophyceae, Aurearenophyceae, and *Ochromonas* (Chrysophyceae) that have only chlorophyll *a*. The principal accessory pigments are β-carotene, fucoxantin, and vaucheriaxanthin. The chloroplast is surrounded by four membranes: the normal plastidial double-membrane envelope, surrounded by a periplastidial membrane and by rough ER, which may be continuous with the outer membrane of the nuclear envelope. The periplastidial membrane is considered to be the remnants of the eukaryotic endosymbiont's (a red alga) plasmalemma. The chloroplast interior is occupied by thylakoids, which are grouped into stacks of three, called lamellae. One lamella usually runs along the whole periphery of the chloroplast, and is termed girdle lamella, absent only in the Eustigmatophyceae. 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 chrysol-aminarin, 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 member of this phylum can grow photoautrophycally, but can also combine different nutritional strategy such as heterotrophy (phagotrophy). The Ochrophyta species that reproduce sexually have a haplontic (e.g., Chrysophyceae), diplontic (e.g., Bacillariophyceae), or diplohaplontic (e.g., Phaeophyceae) life cycles. Chrysophyceae are predominantly single-celled flagellate individuals, but also coccoid, filamentous, and parenchymatous (Figures 1.1ai and 1.3). Most of these algae lack cell walls and have flagella inserted apically or slightly subapically. Cell coverings, when present, include organic scales, organic lorica, and cellulose cell wall. Xanthophyceae can be unicellular coccoids or flagellate, ameboid, or filamentous, but the most distinctive species are siphonous (Figures 1.1al and 1.18). Most Xanthophyceae are freshwater or soil algae, but a few are marine. All known species of Eustigmatophyceae are green coccoid unicells either single, in pairs or in colonies, which exhibit little morphological diversity (Figures 1.1am and 1.2). They are found in fresh, brackish, and seawater, as well as soil environments. Bacillariophyceae or diatoms 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 (Figures 1.1an, 1.48, and 1.49). They are both marine and freshwater. Raphidopyceae are all unicellular autotrophic cells (Figures 1.1ao and 1.50), relatively big in size (30–80 μm), and globoid to ovoidal elongated shaped. Sometimes, they show a more sharpened point with a curved dorsal side and a flat ventral

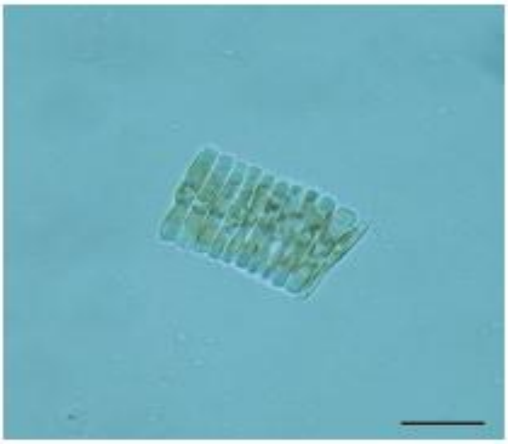

FIGURE 1.48 Marine diatom. Scale bar: 10 μm.

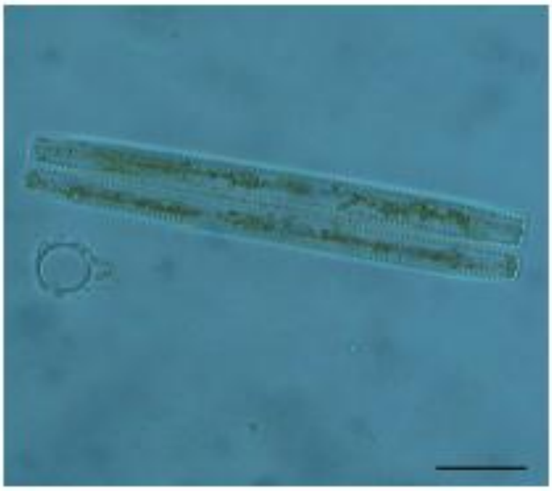

FIGURE 1.49 Freshwater diatom. Scale bar: 20 μm.

FIGURE 1.50 Unicell of *Heterosigma akashiwo*.

side. All the species lack a cell wall and they have no covering outside the cell membrane; consequently, the shape of the cell can vary with external conditions. They possess both trycocysts and mucocysts. Dictyochophyceae are naked unicells that bear a single flagellum, anteriorly directed, with mastigonemes (Figures 1.1ap and 1.51). The class includes the silicoflagellates, a group characterized by formation of a silicified skeleton, and organically scaled members. Phaeophyceae are multicellular, from branched filaments to massive, and complex parenchymatous kelp (Figures 1.1aq and 1.52). Flagellated stages possess two flagella usually laterally inserted, one anteriorly and one posteriorly directed. Cells show an alginate and cellulose wall. Pelagophyceae includes ciliated and coccoid members; cells can bear a single flagellum anteriorly directed, or two flagella, the second posteriorly directed (Figure 1.1ar). Bolidophyceae are flagellated picoplanktonic algae, considered as the closest, although separated lineage to diatoms (Figure 1.1as). Schizocladophyceae contains

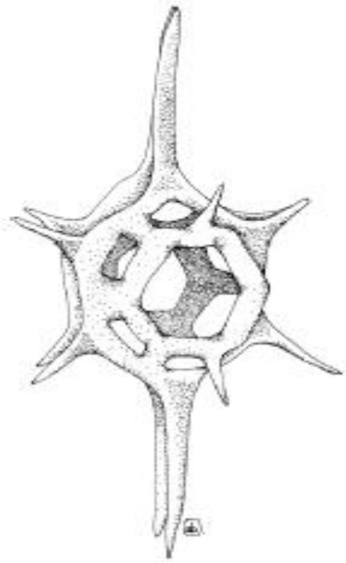

FIGURE 1.51 The silicoflagellate *Disthepanus speculum*.

FIGURE 1.52 Frond of *Bellotia eriophorum*. Scale bar: 5 cm.

a single species, a marine filamentous alga isolated from the Tirrenian Sea; the cells possess a wall containing alginates but lacking cellulose (Figure 1.1at). Chrysomerophyceae are filamentous marine or brackish algae, epiphytic on halophytes, or algae (Figure 1.1au). Picophagophyceae contains both photosynthetic and nonphotosynthetic phagothrophs with filopodia or reticulopodia; the status of these algae as a distinct class has been questioned (Figure 1.1av). Pinguiophyceae are all single-celled microalgae from picoplankton size to over 40 µm (Figure 1.1az). They deserve mentioning because of the unusually high percentage of polyunsaturated fatty acids, especially eicosapentanoic acid (20:5, *n*-3); this peculiarity is the basis for the choice of the Latin noun *pingue* (adj. fat) as the root for the class name. Placidiophyceae are kidney-shaped unicell with two flagella arising from a subapical region of the flattened ventral side. Cells that are usually attached to the substratum can glide or swim freely. They ingest prey particles on the posterior ventral side (Figure 1.1ba). Phaeothanmniophyceae can be filamentous (Figure 1.1bb), palmelloid, or coccoid; the vegetative cells are surrounded by a distinct cell wall of varying thickness. During cell division, an entirely new cell wall is formed inside the parent cell wall, that is, the new walls are formed by eleutheroschisis. Swimming stages have flagella inserted laterally. Synchromophyceae cell types can be sessile, migrating, and floating amoebae, surrounded by a lorica usually with one ostiole, through which reticulopodia protrude and fuse with neighboring cell to build up a meroplasmodium (Figure 1.1bc). The most striking and unique morphological feature of these algae is the aggregation of chloroplasts, each with two membranes, into groups of up to eight enclosed in a common periplastidial membrane and epiplastid rough ER. Synurophyceae are unicellular and colonial algae, important components of the species composition and biomass in freshwater environment worldwide (Figures 1.1bd and 1.5). A well-organized cell covering of siliceous, overlapping scales is characteristic of the class. These scales are morphologically unique for each species, and observations made with electron microscopy usually are required for species-level identification. They differ from closely related Chrysophyceae in the presence of only chlorophyll *c*1, the parallel basal body orientation and the lack of eyespot. Aurearenophyceae (Figure 1.1be), a recently established class, are nonmotile algae, surrounded by a cell wall, with two unequal flagella lying inside the cell wall, or cells naked, motile, and biflagellate.

Cercozoa—Chlorarachniophyceae

Chlorarachniphyceae are naked, uninucleate cells that form a net-like plasmodium via filopodia (Figures 1.1bf, 1.53a, and 1.53b). The basic life cycle of these algae comprises ameboid, coccoid, and flagellate cell stages. The ovoid zoospores bear a single flagellum that during the swimming wraps around the cell. Chlorachniophytes are marine. They possess chlorophyll *a* and *b*. Each chloroplast has a prominent projecting pyrenoid and is surrounded by four envelope membranes. Thylakoids are grouped in stacks of 1–3. 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 cryptophyte nucleomorph, since the chlorachniophytes came from a green algal endosymbiont. Paramylon (β-1,3-glucan) is the storage carbohydrate. They can 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.

Myzozoa—Dinophyceae

Dinophyceae are typical unicellular flagellates, but can be also nonflagellate, ameboid, coccoid, palmelloid, or filamentous (Figures 1.1bg, 1.1bh, 1.54, and 1.55). Dinoflagellates have two flagella with independent beating pattern, one training, one girdling that confer characteristic rotatory swimming whirling motion. Flagella can be apically inserted (desmokont-type) or emerging 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 bipartite 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 1.55). A smaller groove, the sulcus, 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 dinoflagellates 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

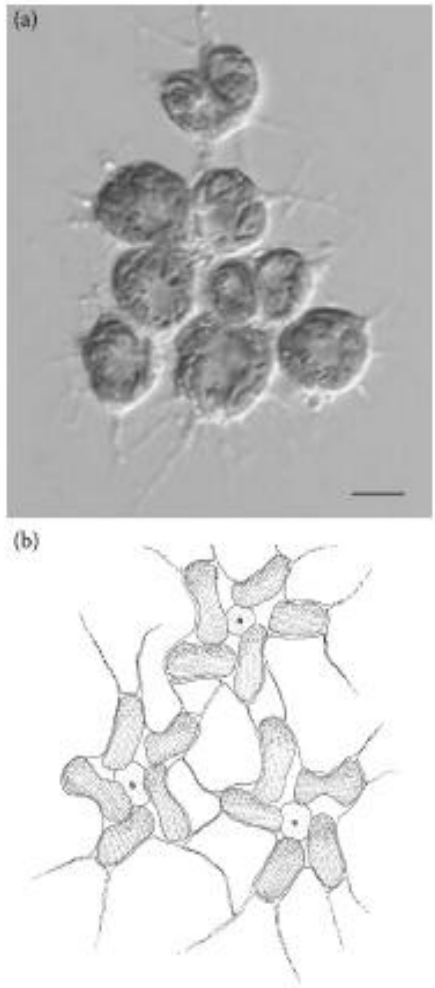

FIGURE 1.53 Plasmodial reticulum of *Chlorarachnion*: (a) bright-field microscope image and (b) schematic drawing. Scale bar: 4 µm.

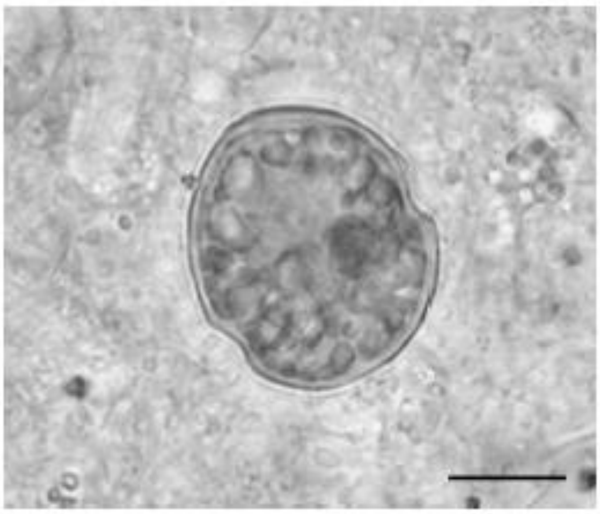

FIGURE 1.54 A marine dinoflagellate. Scale bar: 30 µm.

FIGURE 1.55 Dorsal view of *Gonyaulax* sp., a brackish water dinoflagellate.

fishes. Some dinoflagellates are invertebrate parasites, while others are endosymbionts (zooxanthellae) of tropical corals. Dinoflagellates possess chlorophylls *a*, *c*1, and *c*2, fucoxanthin, other carotenoids, and xanthophylls such as peridinin, gyroxanthin diester, dinoxanthin, diadinoxantin, and fucoxanthin. The chloroplasts, where present, are surrounded by three membranes. Within the chloroplasts typical pyrenoids are present, the thylakoids are for the most part united in a stack of 3. The chloroplast DNA is localized in small nodules scattered in the whole chloroplast. A really complex photoreceptive system is present in the dinophytes such as *Warnowia polyphemus*, *W. pulcra*, 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 that discharge explosively when stimulated. Besides photoautotrophy, dinoflagellates exhibit an amazing diversity of nutritional types since 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.