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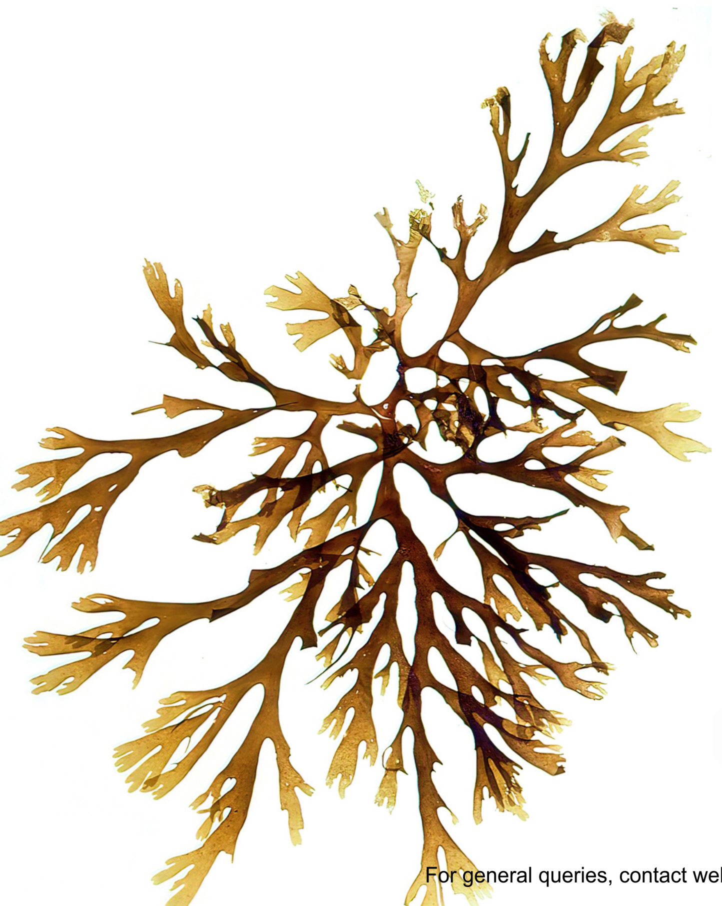
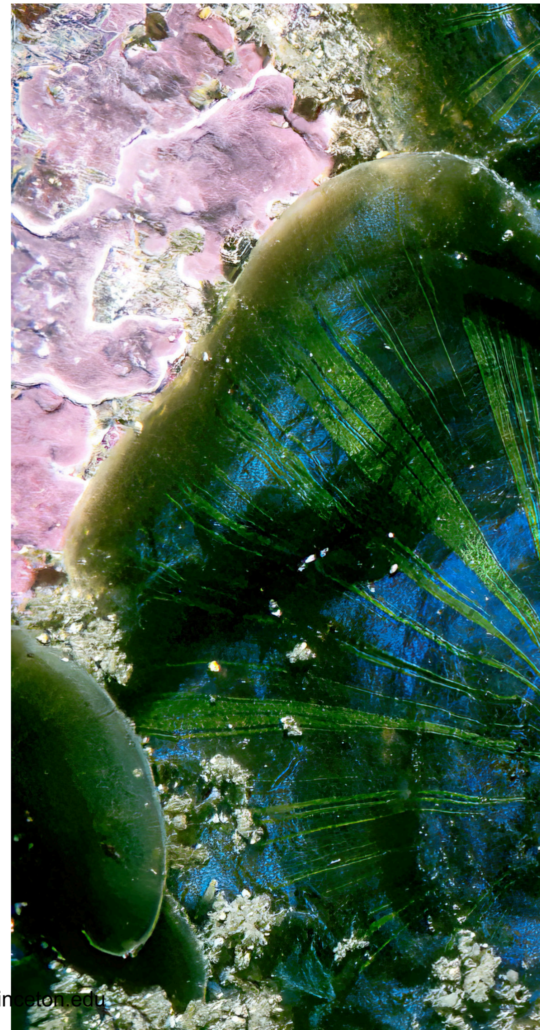


Algal classification in the twenty-first century

The realization in the 1970s that plastids originated by endosymbiosis was a major turning point in understanding algal evolution. Using extant species and the fossil record to unravel events that have occurred across 3.5 billion years is challenging. Nevertheless, evidence based on morphology, anatomy, biochemistry, fossils, ultrastructure, and molecular DNA studies has produced a six-kingdom classification for life on Earth.

RECONCILING CLASSIFICATION SCHEMES

Today, there is more than one biological classification scheme for all species on Earth, which largely reflects different approaches using a variety of techniques. Molecular biologists, for example, construct phylogenetic trees and deal with groups of organisms. One such phylogenetic tree divides all life into five super groups, including Plantae and Unikonts (which contains the fungi and animals, among other groups). However, reconciling phylogenetic trees with the traditional binomial classification system can sometimes prove difficult. This book follows the classification scheme devised by Professor T. Cavalier-Smith that is widely accepted by the majority of phycologists and which provides a comprehensive classification at all levels from kingdom to species.

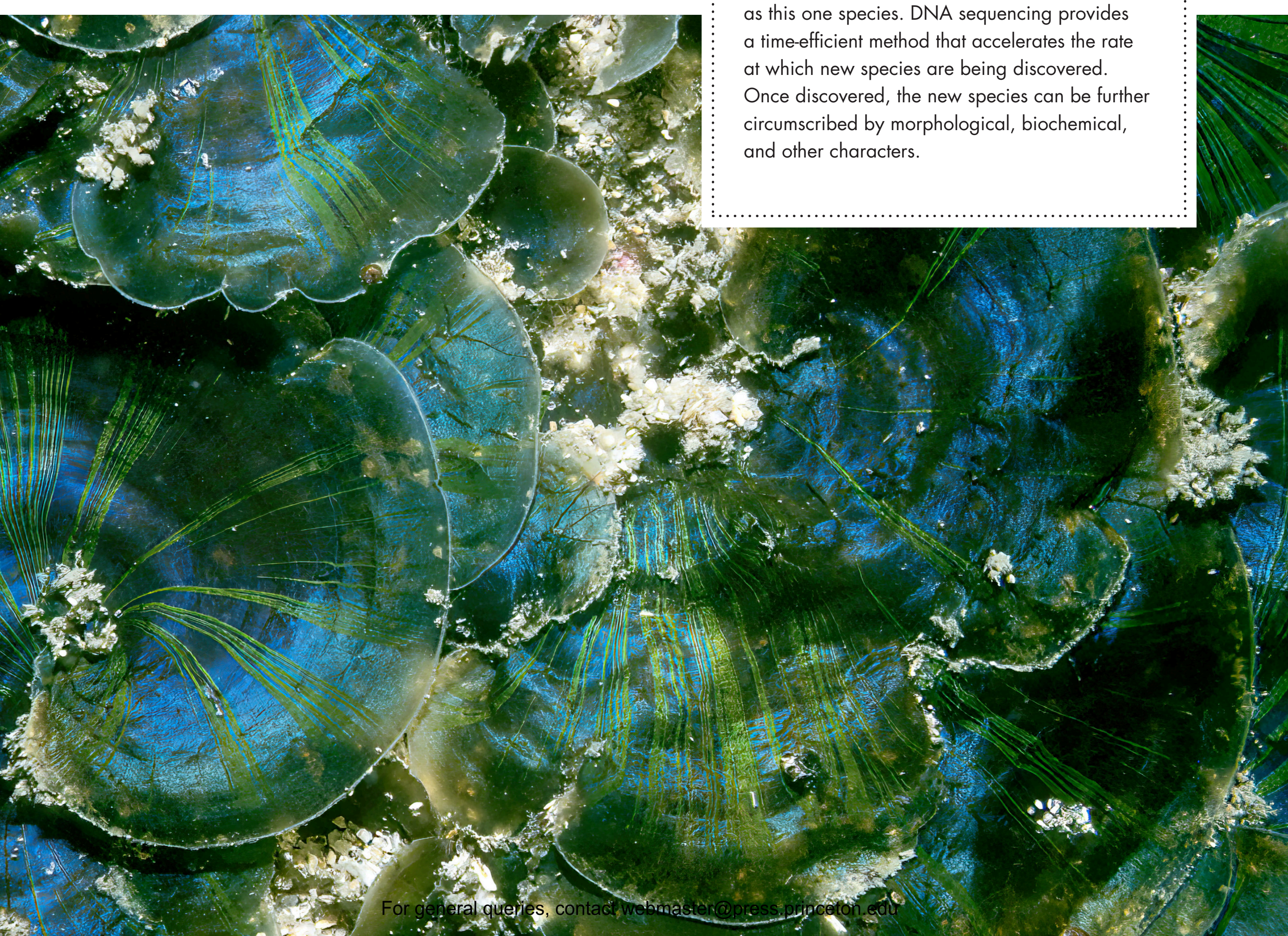


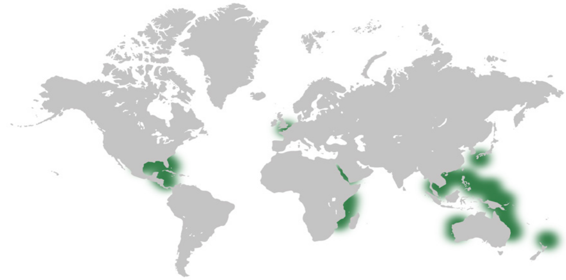
→ Widely distributed in tropical to warm temperate seas worldwide, the stunning iridescent brown seaweed *Lobophora variegata* was once recognized as a single species but is now known to comprise at least 15 morphologically similar species.

After five decades of intensive investigation, the classification of the algae is still a work in progress, with many taxa requiring far more research. There are many instances where a formal classification at the level of phylum or class is not designated and the algal group is referred to informally. For example, there is little agreement as to whether the close relatives of the land plants should be recognized as the phylum Charophyta or the class Charophyceae, meaning these organisms are often referred to as an informal group—the charophytes or charophyceans. This dilemma also needs resolving in the phylum Ochrophyta, which has 18 classes. Many of these had previously been recognized at phylum level, but are now widely recognized informally, reflecting the confusion.

CRYPTIC SPECIES

An area that has been yielding amazing results in describing algal biodiversity is the discovery of not only undescribed species in poorly surveyed habitats and geographical regions but also of cryptic species in well-known floras. Cryptic species are seemingly one species, often morphologically indistinguishable, but in reality they are two or more and sometimes many species masquerading as one. There are many examples of cryptic algal species. This hidden diversity was revealed in the brown seaweed *Lobophora variegata*, which had been regarded for 200 years as a single species widely distributed in tropical to warm temperate seas worldwide. Recent DNA studies have revealed that at least 15 species from different geographical regions had been recognized as this one species. DNA sequencing provides a time-efficient method that accelerates the rate at which new species are being discovered. Once discovered, the new species can be further circumscribed by morphological, biochemical, and other characters.





PHYLUM CYANOBACTERIA

Lyngbya majuscula

Mermaid's hair

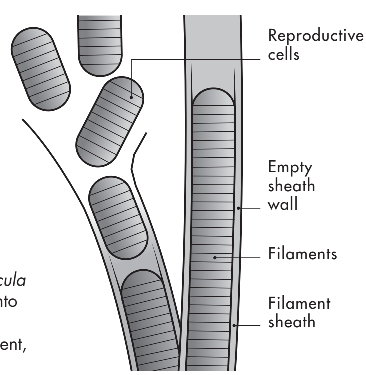
KINGDOM	Eubacteria
PHYLUM	Cyanobacteria
CLASS	Cyanophyceae
ORDER	Oscillatoriales
GENUS	*Lyngbya*
SIZE	Filament diameter 40 microns
HABITAT	A marine species of estuaries, sheltered bays, and coral reefs

Cyanobacterial species are usually microscopic unicellular, colonial, or filamentous organisms that can become visible to the unaided eye when they form large, luxuriant growths. Their cells contain chlorophyll *a* that is masked by phycobilin pigments—the blue-green phycocyanin and the red phycoerythrin.

The Cyanobacteria have two unique features: they are the only bacterial organisms included in the algae, and they are the only group of bacteria that photosynthesize and release oxygen.

Approximately 5,000 cyanobacterial species are estimated to exist on Earth. They occur most frequently as minor components in most marine, freshwater, and terrestrial habitats. Cyanobacteria often become ecologically dominant in harsh environments that are similar to those in which they evolved billions of years ago, or in those that have been damaged by human activities.

Lyngbya majuscula is a filamentous species, with each microscopic unbranched filament composed of a row of cells enclosed in a mucilage sheath. The species is a common inhabitant of estuarine mudflats and seagrass communities worldwide, particularly in tropical to warm temperate seas, although it also occurs on some coral reefs and in other marine habitats. It grows as a small group of filaments, as a mat covering the mud, or as a loosely entangled mass of filaments that are attached onto seagrass leaves. In shaded habitats the filaments are often bright red, due to the red photosynthetic pigment phycoerythrin, while in sunlit seagrass communities, the filaments of *Lyngbya majuscula* are brown, as the light-sensitive red pigment is degraded by the sunlight. Luxuriant growths of *Lyngbya majuscula* billow from seagrasses in long tresses that are reminiscent of human hair, hence its common name, "mermaid's hair."



Reproduction in *Lyngbya majuscula*

Filaments of *Lyngbya majuscula* reproduce by fragmenting into short sections of cells that, once free of the parent filament, grow into new filaments.

→ Light microscope image of the entangled filaments of *Lyngbya majuscula*. Enclosed in a colorless mucilaginous sheath, the filaments are composed of very narrow cells, whose longer dimension stretches across the filament. Many empty mucilaginous sheaths are visible in the background of the image.

PHYLUM RHODOPHYTA

Delesseria sanguinea

Sea beech

KINGDOM	Plantae
PHYLUM	Rhodophyta
CLASS	Florideophyceae
ORDER	Ceramiales
GENUS	*Delesseria*
SIZE	Individual blades 2–10 in (5–25 cm) long, 1.2–4 in (3–10 cm) wide
HABITAT	A marine species of rocky subtidal habitats

The phylum Rhodophyta (red algae) is a large, diverse group of approximately 7,000 known species, of which 95 percent are marine macroalgae (seaweeds). Red seaweeds are typically small- to medium-sized plants that are less than 12 in (30 cm) tall, although a few species grow much larger.

The red seaweeds grow in intertidal to deep subtidal habitats. The remaining 5 percent of Rhodophyta are either unicellular species, freshwater macroalgal species that live primarily in rivers and streams, or inhabitants of atypical environments, such as hot springs, soils, caves, and even sloth hair.

The Rhodophyta are classified in the kingdom Plantae based on the presence of the photosynthetic pigment chlorophyll *a* and the two-membrane plastid envelope. The Rhodophyta are also defined by the presence of floridean starch (the storage carbohydrate found only in the red algae); phycobilin photosynthetic pigments (particularly the red phycoerythrin); a cell wall of three carbohydrates (cellulose and the mucilaginous agar, or carrageenan); and the lack of flagellated cells. Agar and carrageenan, which are only found in the cell walls of the red seaweeds, have a multitude of uses in the food industry and medicine. Several species of red algae are farmed for their agar and carrageenan.

The elegant sea beech (*Delesseria sanguinea)* is a common perennial species that inhabits subtidal rocks on the Atlantic coasts of Europe. The species grows in the deep shade of lower intertidal rock pools, or more commonly as an understory species under the canopy of kelp forests and in open rock communities to depths of 100 ft (30 m). The plants attach to the rocks with a strong, disklike structure (holdfast), from which arise one to many stalked, flat, leaflike structures called blades. The blades are narrow to broad and taper to the blade tip; they have a prominent midrib from which arise visible lateral veins. The blade is delicate, membranous, and only one cell thick except for the well-developed tough midrib that is many cells thick. The blade margins are often ruffled. The plants of sea beech vary from blood red, as indicated by the species name, to rose in color. Victorian ladies favored this beautiful species for their seaweed albums.

→ A beautiful red seaweed. The delicate membranous blades of the sea beech are wrinkled, have ruffled margins, and are one cell thick except for the prominent midrib and lateral veins.

PHYLUM CHLOROPHYTA

Anadyomene lacerata

Green alga

KINGDOM	Plantae
PHYLUM	Chlorophyta
CLASS	Ulvophyceae
ORDER	Cladophorales
GENUS	*Anadyomene*
SIZE	Plants to 2.4 in (6 cm) tall
HABITAT	A deep sea species restricted to depths of 49–197 ft (15–60 m)

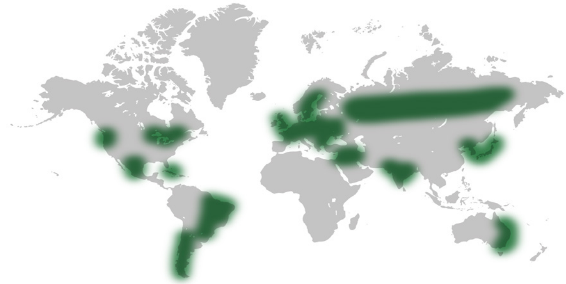
The phylum Chlorophyta (green algae) include unicellular, colonial, and macroalgal species that inhabit freshwater, marine, and terrestrial environments. Freshwater species live in lakes, rivers, streams, ponds, bogs, wetlands, and even garden birdbaths, while marine species inhabit rocky shores, estuaries, bays, coral reefs, and the world's oceans.

Still other green algal species have moved from aquatic to terrestrial environments, where they have adapted to the rigors of life on soils, tree trunks, leaves, fences, and snow. A very diverse, species-rich group, the Chlorophyta comprise approximately 8,000 described species, the majority of which live in freshwater habitats rather than in marine and terrestrial habitats. Interestingly, the main lineages in the Chlorophyta gave rise to either freshwater or marine species, unlike the Rhodophyta and Phaeophyceae, which consist predominantly of seaweeds.

Although red and green algae are both classified in the kingdom Plantae and possess plastids with a two-membrane envelope, the green algae have diverged more widely from their cyanobacterial ancestor. The green algae have lost the phycobilin pigments and acquired chlorophyll *b*. They have developed a more complex plastid with stacks of two to six to sometimes many thylakoid membranes and have starch as their storage carbohydrate.

The stiff, erect, shield-shaped thalli of *Anadyomene lacerata* grow as scattered plants attached by numerous thick-walled rhizoids to pebbles and rubble on subtidal sand plains. The thallus is composed of one layer of large multinucleate cells, which are organized into a beautiful lacy pattern of veins, fanned branches, and smaller cells. Veins are composed of one to three long, tubular, inflated club-shaped cells that radiate from the base to the upper edges of the plant body. In the middle of the thallus, these long cells can attain lengths of 0.14 in (3.44 mm) and widths of 0.01 in (0.31 mm). Each vein cell has, at its summit, two to six large cells that form fingerlike fanned branches. The spaces between the veins are filled with smaller cells that, being perpendicular to the veins, have a featherlike branching pattern.

→ The elaborate lacy thallus of the green seaweed *Anadyomene lacerata* is constructed from one layer of large cells organized into fan-shaped patterns of veins and parallel cells infilling the spaces between the veins.



PHYLUM EUGLENOZOA

Euglena deses

Unicellular alga

KINGDOM	Protozoa
PHYLUM	Euglenozoa
CLASS	Euglenophyceae
ORDER	Euglenida
GENUS	*Euglena*
SIZE	83–163 microns long, 10–24 microns wide
HABITAT	Fresh and brackish waters

Historically claimed by botanists as plants and by zoologists as animals, euglenoids are elongate, spindle-shaped, spherical, cylindrical, flattened, or twisted unicells that most commonly bear two flagella, inserted into the anterior pocket in the cell. They are classified in the unicellular kingdom Protozoa.

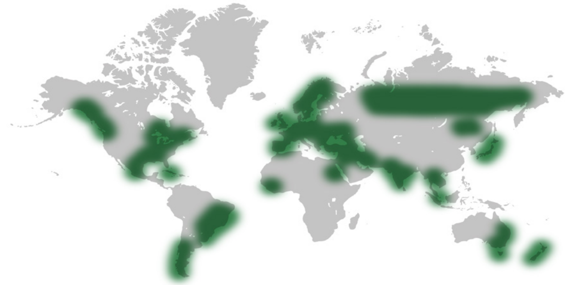
In comparison to other unicellular algae, some *Euglena* species have large cells, reaching lengths of 200–500 microns. Approximately 2,000 euglenoid species have been described, the majority of which live in freshwater and brackish habitats, although a few species are members of the marine phytoplankton. Curiously, some *Euglena* species live among wet sand grains and color the sand green in areas of freshwater seepage on ocean beaches.

Around one half of euglenoid species lack plastids and are colorless, while the other half typically have many green plastids (known as chloroplasts) in their cells. This affects their mode of nutrition. The colorless euglenoids feed by absorbing dissolved organic compounds or by ingesting bacteria and unicellular prey. Photosynthetic euglenoids acquired their chloroplasts from a green algal cell through secondary endosymbiosis, which is evident from the three-membrane envelope bounding the chlorophyll *a*- and *b*-containing chloroplasts. The storage carbohydrate paramylon is unique to the euglenoids, as is the pellicle lying under the cell membrane.

The pellicle, which can be rigid or flexible, is composed of parallel interlocking protein strips wound helically around the cell. In species with a flexible pellicle, the cell changes shape when the protein strips flex and slide relative to each another. This causes a cytoplasmic bulge to flow from the posterior to the anterior end of the cell, propelling the cell backward. These curious squirming backward movements—often referred to as euglenoid movements—occur when the cells are not using their flagella to swim.

Cells of *Euglena deses* contain numerous lens-shaped chloroplasts and a large red-orange eyespot that directs the cell to swim toward light; its flexible pellicle permits a violent, twisting, and continuously turning snakelike movement. The species has one short flagellum that is often retracted into the anterior pocket. *Euglena deses* is widely distributed in freshwater and brackish puddles, swamps, ponds, lakes, and bogs, where it is an indicator of moderate to heavy organic pollution.

→ Light microscope image of *Euglena deses*. The numerous snakelike cells, with many chloroplasts and a red-orange eyespot, are easily distinguished from the brown cell of another euglenoid species, *Lepocinclis spirogyroides*, which has rows of shining beadlike projections on its cell surface.



CLASS DINOPHYCEAE

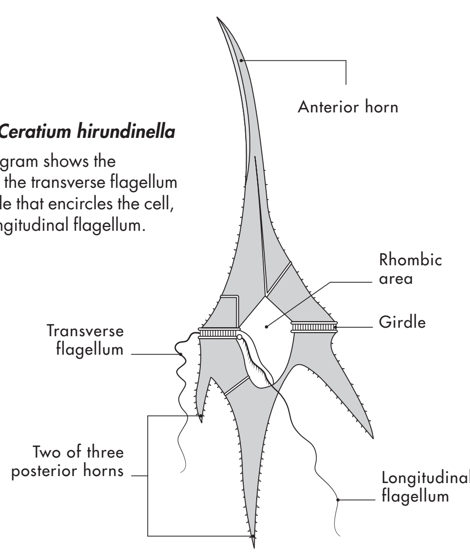
Ceratium hirundinella

Dinoflagellate

KINGDOM	Chromista
PHYLUM	Miozoa
CLASS	Dinophyceae
ORDER	Gonyaulacales
GENUS	*Ceratium*
SIZE	Cells 40–450 microns long
HABITAT	Freshwater lakes and ponds

Dinoflagellates are microscopic unicellular or colonial flagellates. Only half of the 2,500 described species possess plastids, which usually contain the red pigment peridinin and are bounded by a three-membrane envelope. Dinoflagellate plastids usually are derived from a red alga.

The plastid-bearing dinoflagellates are capable of photosynthesis, and may have either a phototrophic or a mixotrophic mode of nutrition (some mixotrophic dinoflagellates are osmotrophs, which absorb organic compounds from the surrounding water, while others are predators on other unicellular organisms).

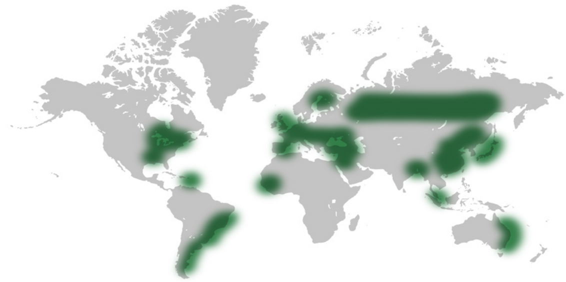


Cell structure in *Ceratium hirundinella*
This schematic diagram shows the spectacular horns, the transverse flagellum located in the girdle that encircles the cell, and the trailing longitudinal flagellum.

Dinoflagellates are common to abundant in marine, estuarine, and freshwater environments, although only 10 percent—approximately 250 species—occur in freshwater habitats. Although they range in length from 2 to 2000 microns, the majority are less than 100 microns long, but they all share a unique cell covering, flagellar orientation, and nuclear organization. The cells are covered by flattened thecal vesicles lying under the cell membrane, which appear empty in unarmored species or contain thecal plates (the armor) in armored species. Dinoflagellate cells have two flagella, one in a girdle encircling the cell and the other in the longitudinal groove or sulcus. In the nucleus of the dinoflagellates, the chromosomes are visible in nondividing cells, unlike in other eukaryotes in which the chromosomes are only visible during cell division.

The broad to narrow spindle-shaped cells of *Ceratium hirundinella,* which measure from 40 to 450 microns in length, are large for a dinoflagellate species. The species is easily recognized by its distinctive morphology. The epitheca (the anterior half of the cell) is drawn out into a single hollow apical horn, while the hypotheca (the posterior half) bears two or three hollow posterior horns, one horn being considerably longer than the other one or two. The cell is armored, covered by relatively thick thecal plates. This mixotrophic species is common in nutrient poor to nutrient enriched freshwater ponds and lakes.

→ The light microscope image of the distinctive cell of *Ceratium hirundinella.*



PHYLUM CRYPTOPHYTA

Cryptomonas ovata

Unicellular alga

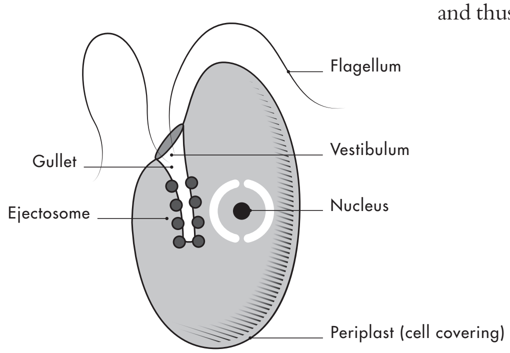
KINGDOM	Chromista
PHYLUM	Cryptophyta
CLASS	Cryptophyceae
ORDER	Cryptomonadales
GENUS	*Cryptomonas*
SIZE	Cells 14–80 microns long, 5–20 microns wide
HABITAT	Freshwater planktonic species

The phylum Cryptophyta are microscopic unicellular flagellates that can be colorless, blue-green, reddish, red-brown, olive-green, or brown. The photosynthetic cryptophytes have retained the blue-green and red phycobilin pigments of their red algal ancestor.

The presence of the phycobilin pigments distinguishes the cryptophytes from the other algal groups that have also acquired their plastids from a red alga but have lost these pigments. The cryptophytes are also characterized by their cell covering (the periplast), which is a series of proteinaceous plates below the cell membrane, and an anteriorly located furrow-gullet system from which two hairy flagella emerge.

Cell structure of *Cryptomonas ovata*

The two flagella are inserted into the vestibulum, below the opening of a groove that runs longitudinally through the cell and terminates in the saclike gullet. The gullet is lined with longitudinal rows of ejectosomes, organelles that eject fine threads.

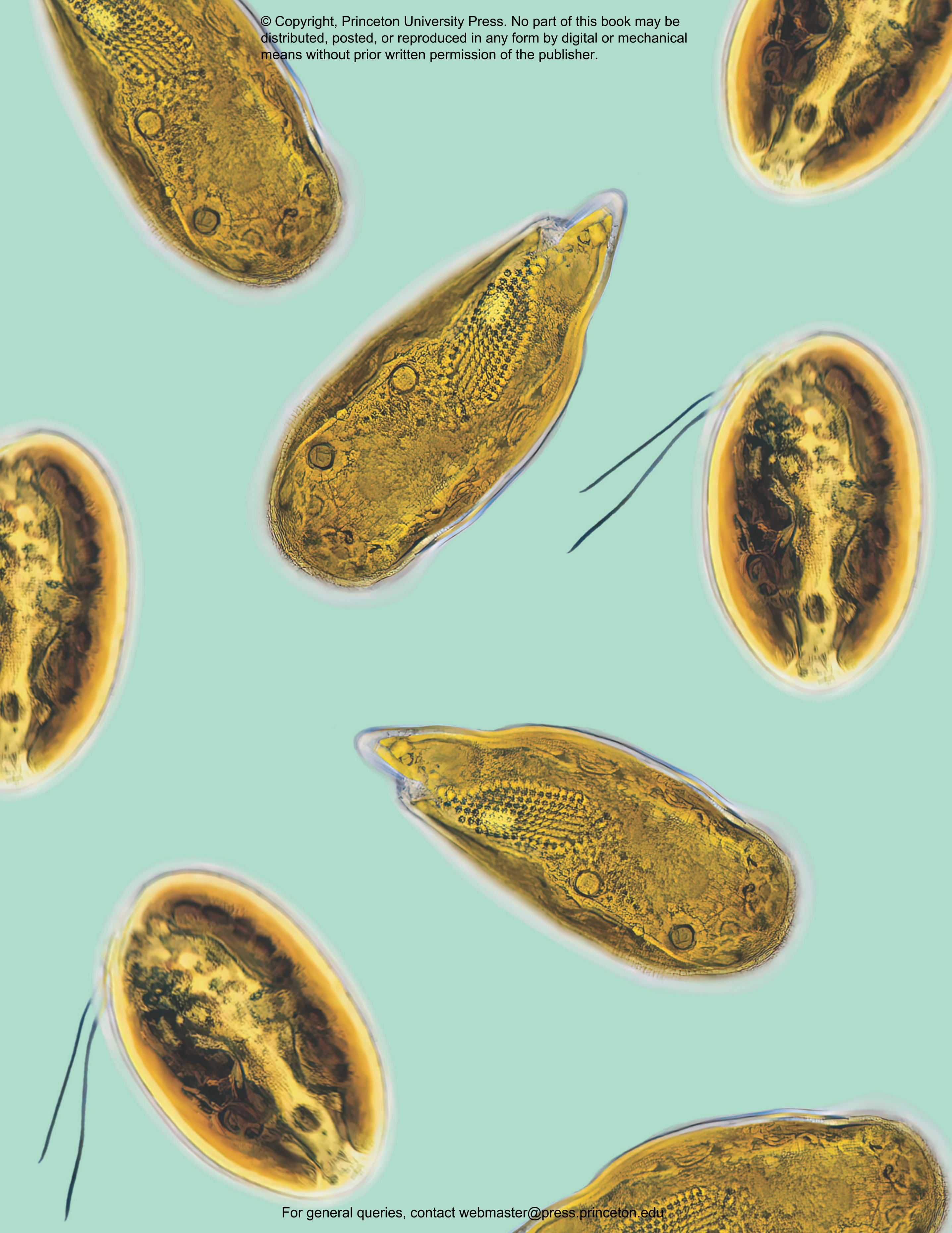


Around 200 species of cryptophytes have been described from marine, estuarine, and freshwater habitats. They are important components of phytoplankton communities worldwide and often increase in abundance when other phytoplankton groups are declining, particularly during periods of environmental disturbance. Pulses of cryptophytes commonly occur following the environmental disturbances caused by major rain events.

Cryptophytes are often prolific in aquatic ecosystems, and are common food organisms for many unicellular organisms. Containing high levels of polyunsaturated fatty acids (among other nutrients), cryptophytes are generally regarded as a high-quality food for aquatic herbivorous unicellular species, including dinoflagellates and ciliates.

Cryptomonas ovata is a common species that inhabits the plankton of freshwater habitats, where it forms blooms. As the species name implies, the cells are oval in shape and have two plastids. *Cryptomonas ovata* supplements the energy it produces by photosynthesis by ingesting bacteria in low-light environments and thus has a mixotrophic mode of nutrition.

→ Rare light microscope images of *Cryptomonas* (Latin, meaning "hidden individual"). The oval cells (front view) have two brown plastids and two whiplike flagella, while the gullet lined with rows of ejectosomes is visible in the conical cells (side view).



PHYLUM BACILLARIOPHYTA

Planktoniella sol

Centric diatom

KINGDOM	Chromista
PHYLUM	Bacillariophyta
CLASS	Mediophyceae
ORDER	Thalassiosirales
GENUS	*Thalassiosira*
SIZE	Cells 10–60 microns in diameter
HABITAT	Planktonic in coastal seas

The microscopic unicellular and colonial species of the phylum Bacillariophyta are the best-known and most abundant group of the planktonic algae. Commonly called diatoms, they are defined by their unique cell wall, the frustule, which is composed of silica and organic material.

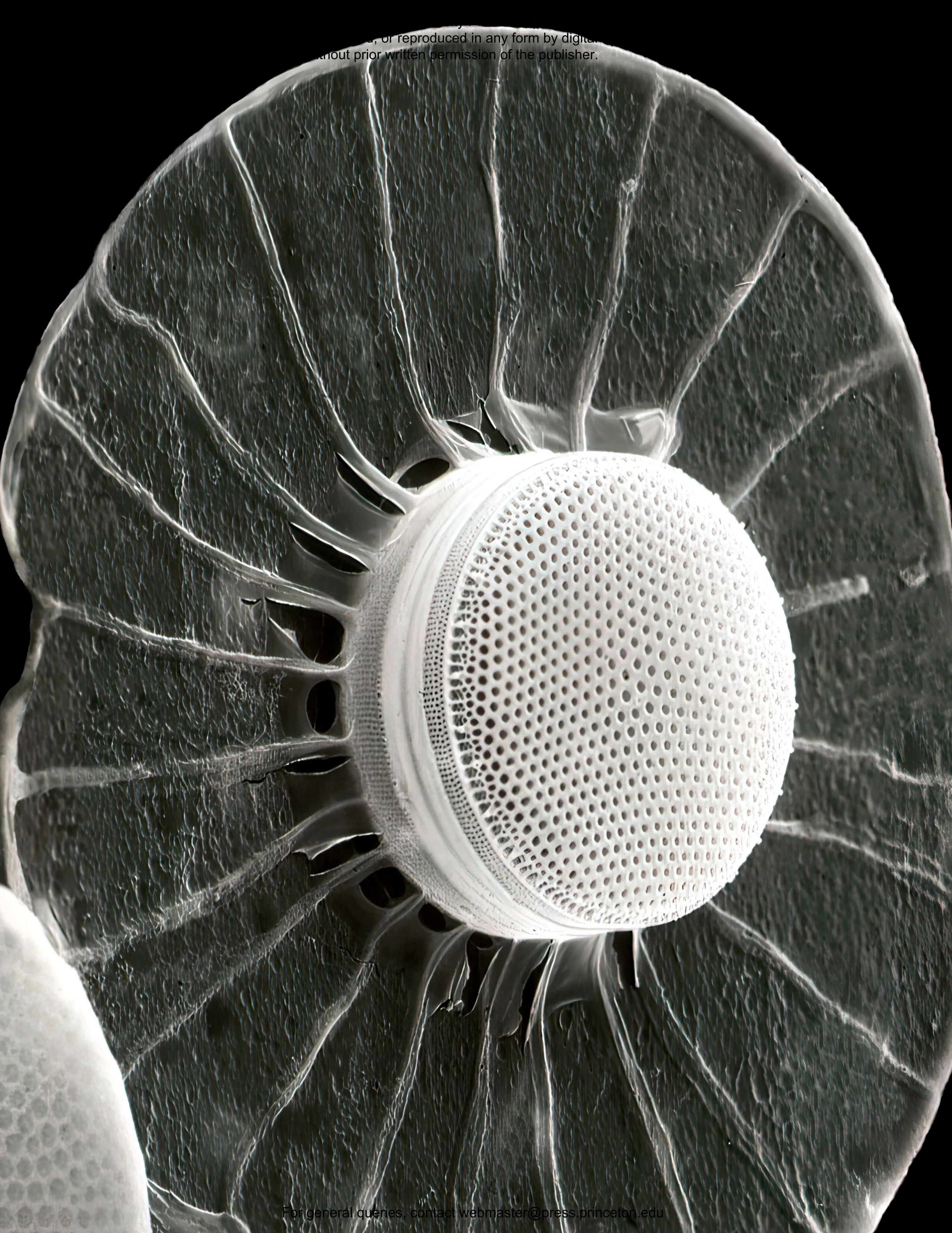
The diatoms' boxlike frustule, which ranges in size from 2 to 200 microns, is exquisitely ornamented with patterns of pores, ribs, and spines that radiate in spectacular geometric symmetry across the surfaces of the cells.

The lack of flagella on the diatom vegetative cell is another character that distinguishes the diatoms from the majority of algal phyla. Species of diatoms are either planktonic and float in the water column or live attached to various surfaces in oceans, seas, rivers, lakes, and many other habitats. Although they lack flagella, some diatom species can glide relatively rapidly on surfaces onto which they have secreted a layer of mucilage. The male gametes of one group (centric diatoms) are the only flagellate cells in the diatoms. These male gametes have one hairy flagellum that is directed forward when swimming. They lack the smooth posterior flagellum typical of the other heterokont algae (algae that have one hairy flagellum and one smooth flagellum).

The number of diatom species occurring on Earth is not known, but they are nevertheless a species-rich group that has been wildly successful in terms of evolutionary diversification. Estimates vary widely, with a current conservative estimate of 20,000 species, significantly less than 100,000 species proposed by some diatom specialists. Yet regardless of the actual number, diatoms are important primary producers in aquatic ecosystems worldwide, underpinning the food webs that support highly productive natural ecosystems and commercial fisheries.

The pillbox-shaped cell of *Planktoniella sol* sits in the center of a prominent flaplike membranous wing, a structure that is uncommon in the diatoms. This winglike ribbed extension of organic material is extruded from and remains attached to the side of the cell. It is thought to function as a flotation device aimed at keeping the cells of *Planktoniella* in the sunlit surface waters of the sea. Diatoms that lack flagella, and therefore cannot swim, possess a variety of structures that maintain the buoyancy of their cells. The boxlike frustule covering the diatom cell consists of two valves that are held together by girdle bands, with the smaller valve fitting into the larger one. Diatom cells look different when viewed from the top or bottom (valve view) compared to when viewed from their sides (girdle view). The top or bottom view of the *Planktoniella* frustule reveals an elegantly ornamented valve face covered with rows of pore-like depressions radiating from the center, whereas in the side view the rows of smaller pores are separated by girdle bands that lack ornamentation.

→ Electron microscope image of the pillbox-shaped cell of *Planktoniella sol* surrounded by the organic wing.



CLASS PHAEOPHYCEAE

Fucus vesiculosus

Bladder wrack

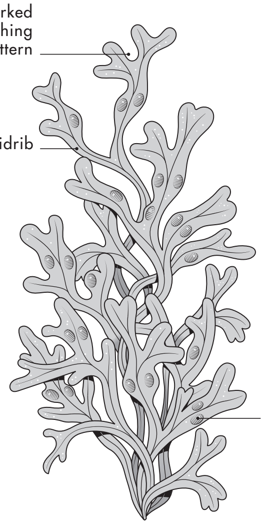
KINGDOM	Chromista
PHYLUM	Ochrophyta
CLASS	Phaeophyceae
ORDER	Fucales
GENUS	*Fucus*
SIZE	Blades usually 7.9–27.5 in (20–70 cm) long, 0.2–1.6 in (0.5–4 cm) wide
HABITAT	Mid intertidal zone on seashores

The class Phaeophyceae (brown algae) is loosely assigned with 17 other classes to the phylum Ochrophyta, based on their dissimilar flagella comprising a hairy anterior flagellum and a smooth posterior flagellum.

The brown seaweeds are distinguished from other algae by the possession of chlorophyll *a* and *c*; a cell wall composed of cellulose, alginic acid, and fucoidan; the storage carbohydrate laminarian; and their complex multicellularity. Approximately 1,792 species of the brown algae have been described worldwide, most of which are marine species, although a few species have invaded freshwater habitats from the sea. They range in appearance and size from microscopic filaments to large leathery kelps up to 100 ft (30 m) long. There are no unicellular brown algal species. Carpeting the rocky intertidal shores in cool temperate regions and forming complex subtidal forests from the tropics to polar regions, the brown seaweeds function as ecosystem engineers, providing a habitat and food for diverse assemblages of other algae and marine animals.

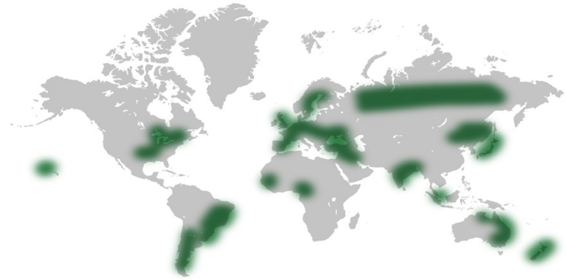
On European shores, species of *Fucus* are common intertidal seaweeds that often form wide bands across the rocks in the upper intertidal (*Fucus spiralis*), mid-intertidal (*Fucus vesiculosus*), and lower intertidal (*Fucus serratus*) zones.

Fucus vesiculosus derives its name from the vesicles or air bladders that float thalli into the sunlit waters of the sea. The flat, leathery, straplike thallus of this species repeatedly branches into two equal branches. Each branch has pairs of bladders, which are generally (but not always) present either side of the prominent midrib, except at the branching point where there is only one. The bladders are almost spherical, protruding equally on both sides of the thallus surface.



Thallus structure of the bladder wrack
The thallus branches into two equal branches and generally has paired vesicles (air bladders for flotation) either side of the conspicuous midrib.

→ The leathery, flat, straplike thallus of the bladder wrack is distinguished from other brown seaweeds by its forked branching pattern, the presence of a prominent midrib, and usually paired vesicles.



CLASS CHRYSOPHYCEAE

Dinobryon sertularia

Golden-brown alga

KINGDOM	Chromista
PHYLUM	Ochrophyta
CLASS	Chrysophyceae
ORDER	Chromulinales
GENUS	*Dinobryon*
SIZE	Individual lorica 30–40 microns long, 10–14 microns wide
HABITAT	Planktonic in freshwater habitats

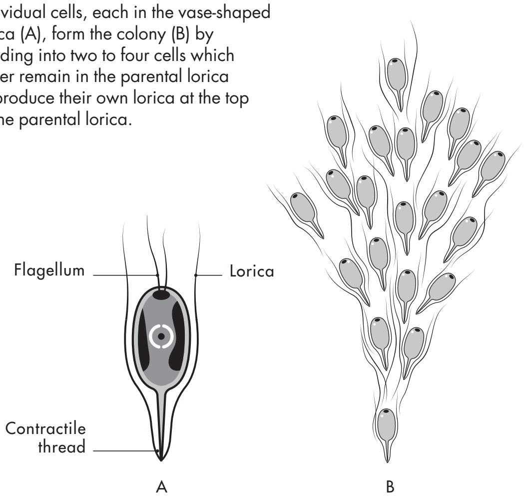
The class Chrysophyceae (golden-brown algae) range in form from unicellular flagellates and colonies to filaments. Around 430 chrysophycean species have been described, most of which occur in freshwater habitats, with a few species found in estuarine and marine waters.

The Chrysophyceae are one of the 18 classes of the phylum Ochrophyta of the much larger group, the heterokont algae. The chrysophyceans contain the pigments chlorophyll *a* and *c*, and the brown pigment fucoxanthin, as well as possessing two dissimilar or heterokont flagella (an anterior hairy flagellum and a posterior smooth flagellum). However, unlike most other heterokonts, cells of these golden-brown algae are either naked (lacking cell walls) or covered by a silica exoskeleton, silica scales, or a cellulose lorica (a protective covering surrounding the cell).

Species of *Dinobyron* are either solitary or colonial, with cells surrounded by a cellulose, vaselike lorica. *Dinobryon sertularia* is a colonial species that forms dense, branched, treelike colonies. These grow when a newly divided cell settles and builds a lorica on the edge of an existing lorica. Inside each lorica, a thin cytoplasmic thread attaches the cells to the lorica's base. The cells have two flagella (the longer flagellum extends into the water beyond its lorica), two plastids, and, at the cell's apex, a light-sensitive red eyespot that directs the cell to swim toward light. Each cell's flagella beat, enabling the colony to swim in a graceful—albeit rather slow—manner. Although it is photosynthetic, *Dinobryon sertularia* also engages in substantial rates of bacterivory. This is an adaptation to life in slightly alkaline, relatively nutrient-poor lakes and pools. This strategy, which supplements the uptake of carbon and other nutrients, enables it to maintain its abundance in the plankton during periods where poor light and nutrient conditions are less suited to growth.

A colony of *Dinobyron sertularia*

Individual cells, each in the vase-shaped lorica (A), form the colony (B) by dividing into two to four cells which either remain in the parental lorica or produce their own lorica at the top of the parental lorica.



→ A swimming colony of the planktonic golden-brown alga *Dinobryon sertularia* is composed of many flagellate cells, each located in a translucent cellulose vase-shaped protective covering (lorica).

MORPHOLOGY

The megadiverse algae

Algae are curious living organisms that exist in every conceivable shape and size. The algal body—called the thallus—ranges from the relative simplicity of a microscopic single cell measuring just 1 micron in diameter, to the complexity of giant leathery kelps that can grow more than 160 ft (50 m) in length. The external form and structure—termed morphology—are important characteristics used to describe algal species.

AN AMAZING ARRAY OF FORMS

The morphological diversity encompassed by the algae is enormous. Single algal cells are not just simple red, green, or yellow-brown spheres; they have evolved into the shapes of spindles, crescents, pyramids, stars, cubes, cones, and even more complicated configurations, with their cell margins bearing horns, lobes, ridges, spines, and winglike extensions. One group of freshwater green algae, the desmids (order Desmidiales), are remarkable for the amazing array of their morphology, the often extraordinary complexity of their cell outlines, and their marked symmetry.

The seaweeds are equally diverse, with thalli (algal bodies) that form delicate or robust filaments, sheets, tubes, blades, fronds, crusts, sacs, cushions, and large, leathery straps. Yet despite this enormous morphological variation, there are five key, basic body plans that are used to describe the different levels of thallus organization in the various lineages. These are unicellular, colonial, multicellular, siphonocladous, and siphonous.

The body plan of a unicellular species is a single cell. In the colonial body plan, many individual cells of similar form and function are loosely held together by a viscous secretion known as mucilage, or interlocking structures or by other means. The multicellular body plan is an advanced level of organization, with numerous closely adherent cells that have the capacity to communicate with each other and to specialize. In siphonocladous body plans, thalli are composed of large cells with numerous nuclei (called multinucleate cells). The siphonous multinucleate body plan takes the form of a long tube—the siphon.

Having evolved independently, these five basic body plans are found in the various algal lineages. For example, all five body plans are identifiable among species of the very diverse green algae (Chlorophyta) but only the multicellular body plan has evolved in brown algae (Phaeophyceae), almost all of which are seaweeds or marine macroalgae (algae that are visible to the unaided eye). Microscopic unicells and colonies are referred to as microalgae.

Although there are only five basic body plans, there are still plenty of variations in morphology within them. Unicellular and colonial species differ markedly in cell structure, and may be motile—capable of movement—or nonmotile—incapable of movement.

→ Phycologist David Williamson's poster collage illustrates a small proportion of desmid morphological diversity, which includes the multilobed circular cell of *Micrasterias* (top left corner).


2
4
5
3
1

MULTICELLULAR BODY PLAN

Multicellular thalli are composed of either filaments that consist of a row of cells joined end to end or tissues formed from three-dimensional arrays of cells. Protoplasts of these cells are interconnected to the adjoining cells by strands of cytoplasm. Some multicellular thalli that superficially appear to be composed of tissues are actually formed from tightly adherent branched filaments, a thallus construction that occurs in the majority of red seaweeds.

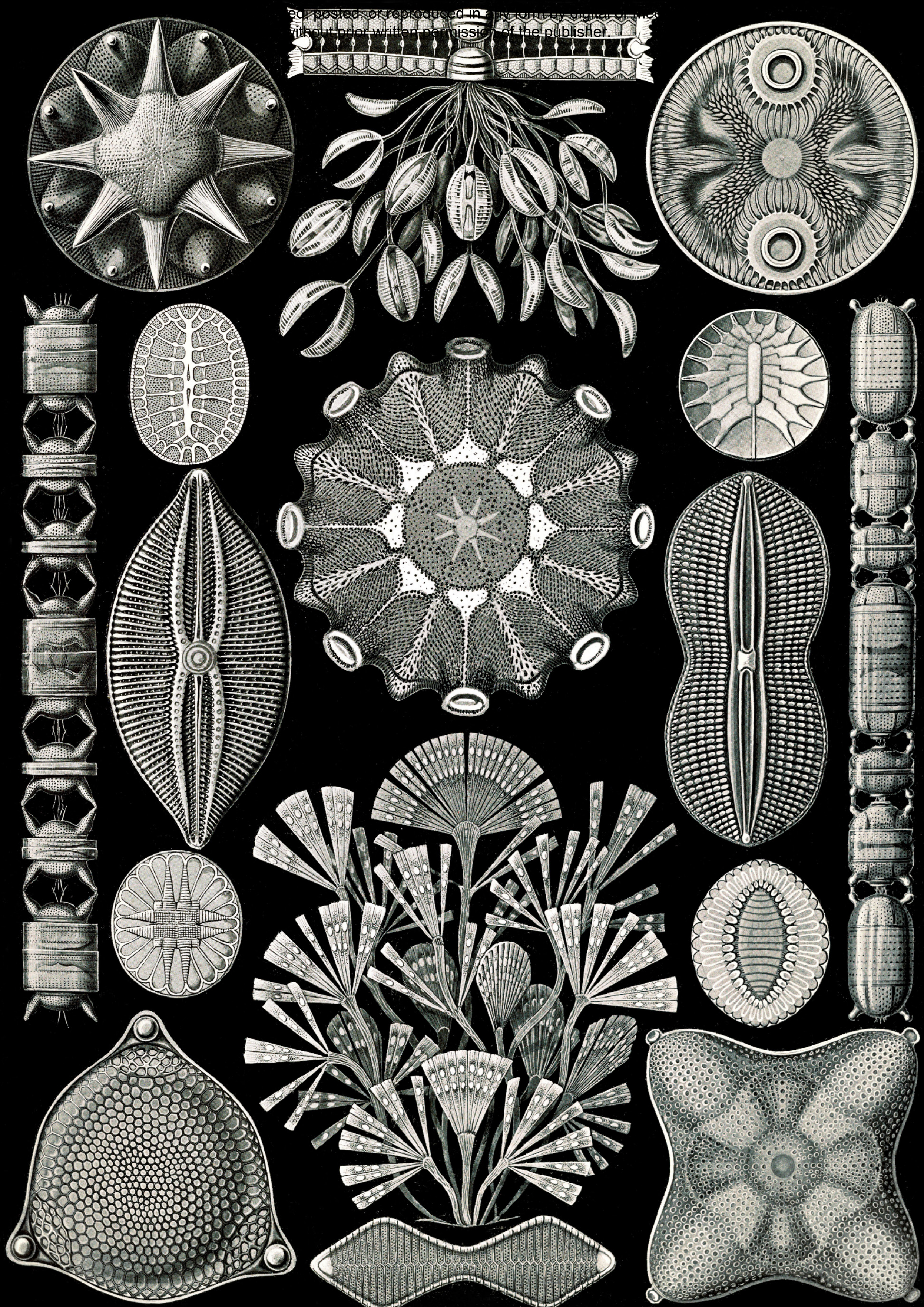
Most macroalgae, including *Laurencia brongniartii*, show no differentiation into specialized structures: all parts of the thallus look similar. However, some large brown seaweeds, particularly the brown algal genus *Sargassum*, display a level of body differentiation that is similar to the flowering plants, with rootlike holdfasts, stemlike stipes, and primary axes, leaflike lateral branches, and reproductive structures.

Macroalgae are anchored to rocks or other firm surfaces by a holdfast. Rhizoids, the rootlike filaments in the holdfast, glue the macroalgae onto the rocks. The macroalgal thallus usually grows from a meristem—a cell or a group of closely associated cells that are capable of repeated cell divisions. Meristems are located at the tip (apical meristem) or in the middle of the thallus (intercalary meristem).

Many algal species secrete complex extracellular carbohydrates in the form of gels, mucilages, and slimes, such as the mucilaginous adhesive that fastens the holdfast onto a rock. These have many important functions in the algae, although the presence of these extracellular substances has led some people to unkindly refer to algae as "slimy" or "green slime."

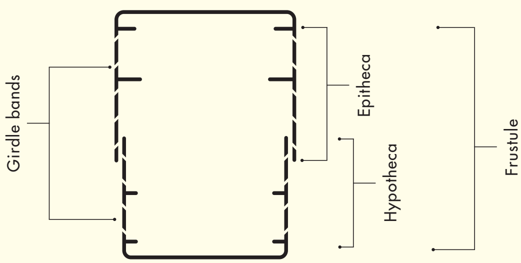
↑ All parts of the simple undifferentiated thallus of the red seaweed *Laurencia brongniartii* are similar in appearance.

← The thallus of the brown seaweed *Sargassum platycarpum* is differentiated into stemlike primary branches that are attached to rocks by a rootlike holdfast (1), fertile branches (2), leaflike lateral branches (3), reproductive structures (4), and gas-filled pneumatocysts (5).



Unicells

Unicellular algae exhibit an elaborate variety in their single-cell structure, which differs markedly in each algal lineage. They can be nonmotile or motile, with motile species (called algal flagellates) bearing flagella—whiplike appendages that beat to propel the cell through the water.



Life in glasshouses

The smaller posterior valve (hypotheca) of the boxlike frustule fits inside the larger anterior valve (epitheca), the two valves of the diatom cell held together by the girdle bands. Glass is made from silica.

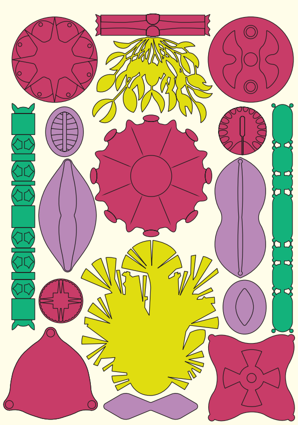
← A page from Ernst Haeckel's *Diatomeae* (1904) illustrates a small proportion of the morphological diversity encompassed by unicellular and colonial centric and pennate diatoms, including the pennate colonial *Licomorpha* (middle, bottom row).

Unicellular centric diatoms

Unicellular pennate diatoms

Colonial centric diatoms

Colonial pennate diatoms (includes the mucilaginous stalks that the diatoms secrete)

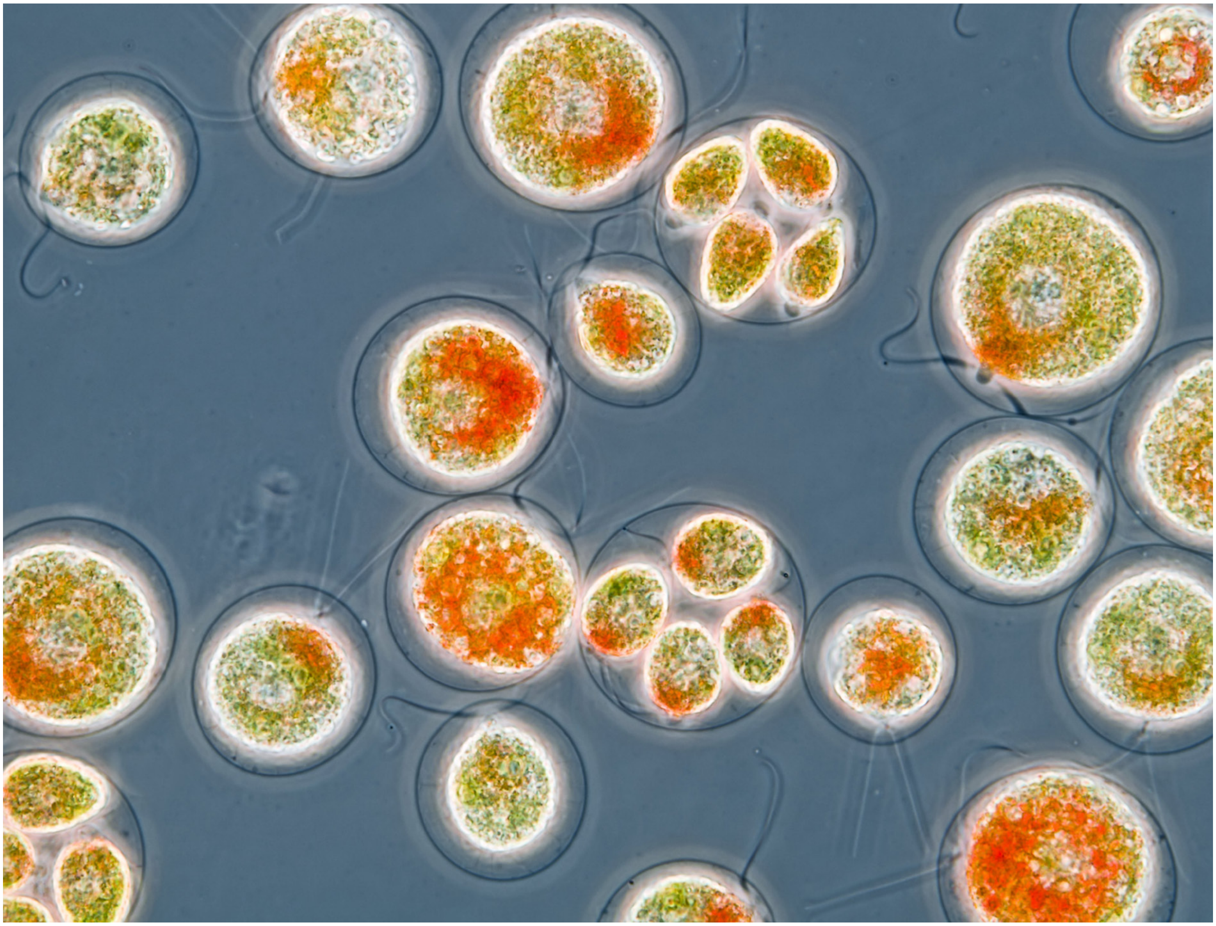


THE DIATOMS

The most diverse of the phytoplankton phyla are the diatoms (phylum Bacillariophyta). Their cells range in size from 5 to 200 microns. Unique in the algae, their distinctive, rigid, boxlike silica cell wall (the frustule) is composed of two halves that are known as valves. The smaller valve (the hypotheca) fits into the larger valve (the epitheca), with one or more girdle bands holding the two together.

Exquisitely ornamented, the pores, slits, tubes, ribs, and spines that radiate in spectacular geometry across the cell's surface aid buoyancy, lightening the heavy frustule and increasing the contact between the cell's cytoplasm (the protoplasm excluding the nucleus) and the external environment.

The diatoms comprise two groups of centric diatoms with radial symmetry, and a third group of pennate diatoms with bilateral symmetry. The vegetative (or nonreproductive) cells of the diatoms lack flagella, although some diatom cells are motile. Some pennate diatoms secrete mucilage onto the surface and rapidly glide on it. The male gametes of the centric diatoms are the only flagellate cells in the diatoms. They have one flagellum instead of the two flagella that are typical of algal species.



↑ The cell of *Haematococcus lacustris*, which is surrounded by a transparent extracellular matrix, has two whiplike flagella. Some cells have divided into four cells.

THE DESMIDS

The desmids (order Desmidiales) are a large group of freshwater green algae whose nonmotile unicells are renowned for their variety and the beauty of their shape and structure (see page 63). They are often much larger than other unicellular algae, as demonstrated by the cells of *Closterium acerosum*, which range in size from 300 to 600 microns in length and from 30 to 50 microns across. Species of *Closterium* can have simple, ellipsoidal, spindle-shaped, or cylindrical cells. The more intricate cells of *Micrasterias* are strongly compressed and almost circular (see page 63). They are divided into two halves by a prominent constriction and elaborately dissected into many leaflike or starlike lobes, with each half of the cell the mirror image of the other.

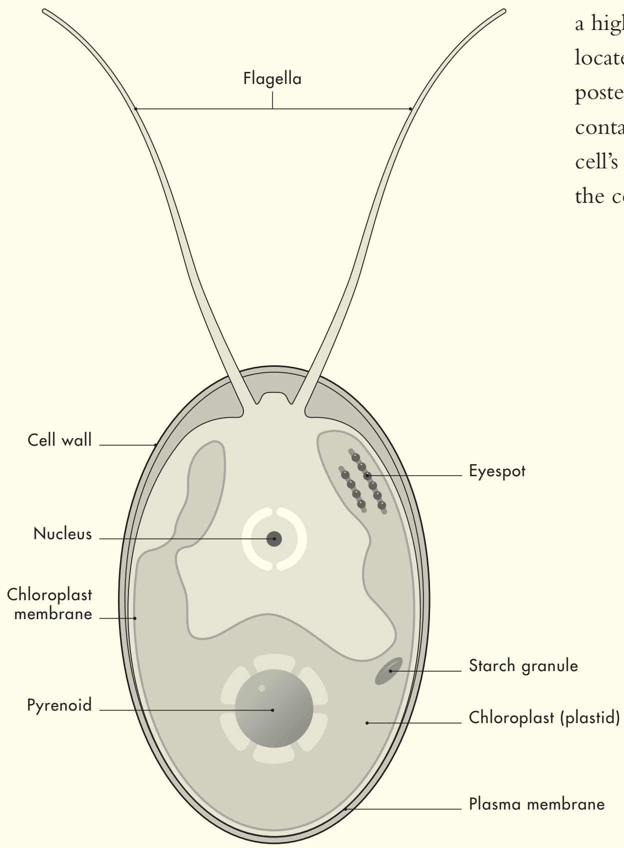
Desmids with cylindrical cells are similar when viewed from the front and side, but others appear different depending on the viewing angle. When the desmid *Staurastrum* is seen from its broad (front) side, each half-cell appears cup-shaped, with two long, armlike processes radiating at 45 degrees from each end of the two cups. However, in top view, the cell is triangular with three armlike processes; the fourth arm is either obscured by the cell or out of focus when the cell is viewed from its broadest side.

GREEN FLAGELLATES

There are numerous flagellate unicellular algal species. The green flagellates and the dinoflagellates are the best known and are both remarkably diverse. The green alga *Chlamydomonas* and its close relatives are flagellated unicells or colonies. The cells have two or four flagella and are usually covered by a thin glycoprotein layer that is external to the plasma membrane, which is thought to be "leaky." This cell covering would explain the unusual presence of two or more contractile vacuoles in the cytoplasm near the bases of the flagella in almost all species of the Volvocales—in unicellular organisms, the contractile vacuoles excrete excess water from the cell.

The cell covering of the biflagellate cells of *Haematococcus lacustris* is quite spectacular. These cells have radiating strands of cytoplasm that extend to the periphery of the wide and conspicuous watery and a sticky (mucilaginous) extracellular layer. In other volvocalean unicells the glycoprotein extracellular layer is less developed, and radiating cyptoplasmic strands are uncommon. *Haematococcus lacustris*, commonly known as the "blood-red alga," synthesizes and accumulates large amounts of carotenoids that are of great economic importance. There has been much study into the benefits of carotenoids in the prevention of a number of diseases in humans, including colon cancer.

The well-studied *Chlamydomonas reinhardtii* has been intensively researched by scientists for decades. The pear-shaped cell of this species measures from 20 to 30 microns in length and from 10 to 20 microns across. It is bounded by the plasma membrane, which is covered by a complex translucent three-layered extracellular matrix, with the outermost layer forming a highly organized capsule. The cell has a centrally located nucleus, many mitochondria, and—centered posteriorly in the cell—a large, cup-shaped chloroplast containing an eyespot. Two flagella are inserted at the cell's apex. The photosensitive eyespot apparatus directs the cell to swim toward light.



Chlamydomonas reinhardtii

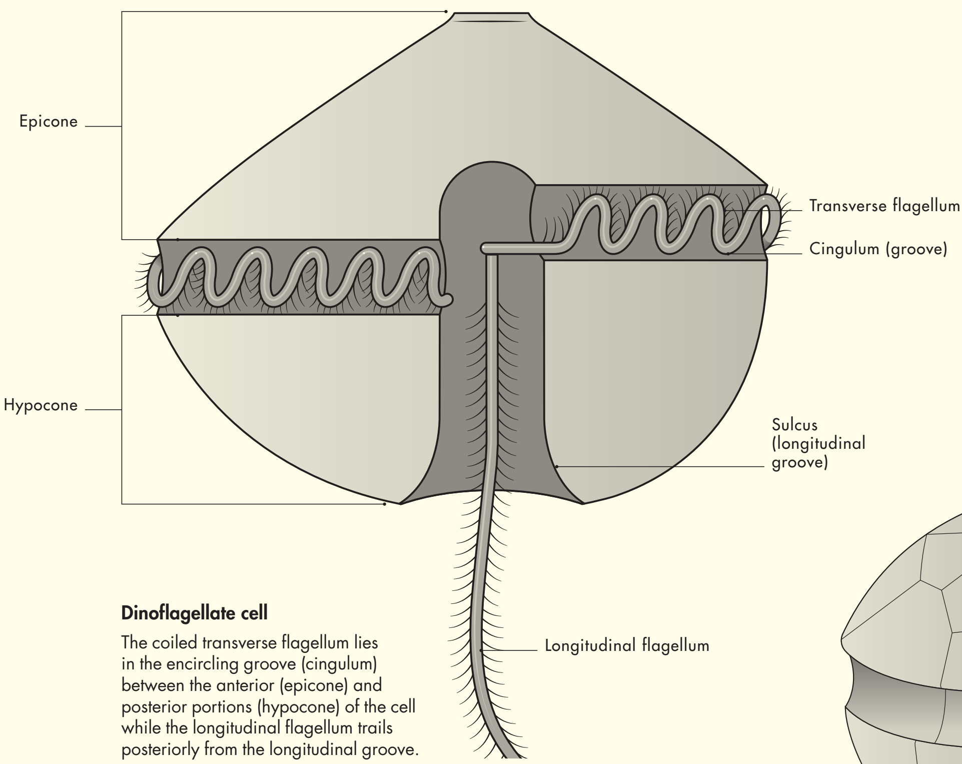
Considered the closest unicellular relative to and the basic unit of the colonies of *Gonium* and *Volvox*, cells of the green alga *Chlamydomonas reinhardtii* have two anterior flagella and a large, cup-shaped chloroplast with a pyrenoid (a starch storage body) and an eyespot.

THE DINOFLAGELLATES

The dinoflagellate cell usually consists of two parts: an anterior epicone and a posterior hypocone, which are separated by a groove (the cingulum) that encircles the cell. On the cell's ventral surface, a smaller groove (the sulcus) extends posteriorly from the cingulum and, in some species, anteriorly as well.

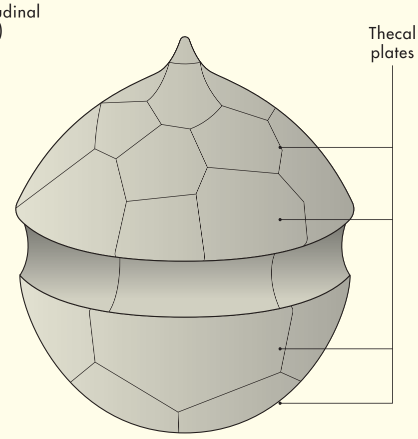
The two flagella on the dinoflagellate motile cells are also distinctive. They are inserted into the cell at the intersection of the two grooves. Both flagella are situated in the grooves. One flagellum—the transverse flagellum—is situated in the groove that encircles the cell, and the other flagellum—the longitudinal flagellum—is located in the smaller groove and trails behind the cell.

Dinoflagellate cells range in size from 5 to 200 microns, with some reaching 0.04 in (1 mm) in length (although this is rare). Another unique feature, a layer of flattened sacs (the thecal vesicles) lies under the plasma membrane of the dinoflagellate cell. These vesicles either appear empty or almost empty in the unarmored species, or they contain cellulose thecal plates of varying thickness in the armored species. The vesicles fit together tightly like jigsaw puzzle pieces



Dinoflagellate cell

The coiled transverse flagellum lies in the encircling groove (cingulum) between the anterior (epicone) and posterior portions (hypocone) of the cell while the longitudinal flagellum trails posteriorly from the longitudinal groove.



Armored or not

Armored dinoflagellate cells are covered by cellulose plates that fit together like jigsaw puzzle pieces to completely cover the cell.

(continued...)

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