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Robert Edward Lee
Excerpt
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Part I

Introduction

Chapter I

Basic characteristics of the algae

Phycology or algology is the study of the algae. The word **phycology** is derived from the Greek word *phykos*, which means “seaweed.” The term **algology**, described in Webster’s dictionary as the study of the algae, has fallen out of favor because it resembles the term *algogenic* which means “producing pain.” The algae are **thallophytes** (plants lacking roots, stems, and leaves) that have chlorophyll *a* as their primary photosynthetic pigment and lack a sterile covering of cells around the reproductive cells. This definition encompasses a number of plant forms that are not necessarily closely related, for example, the cyanobacteria which are closer in evolution to the bacteria than to the rest of the algae.

Algae most commonly occur in water, be it freshwater, marine, or brackish. However, they can also be found in almost every other environment on earth, from the algae growing in the snow of some American mountains to algae living in lichen associations on bare rocks, to unicellular algae in desert soils, to algae living in hot springs. In most habitats they function as the primary producers in the food chain, producing organic material from sunlight, carbon dioxide, and water. Besides forming the basic food source for these food chains, they also form the oxygen necessary for the metabolism of the consumer organisms. In such cases humans rarely directly consume the algae as such, but harvest organisms higher up in the food chain (i.e., fish, crustaceans, shellfish). Some algae, particularly the reds and browns, are harvested and eaten as a vegetable, or the mucilages are extracted from the thallus for use as gelling and thickening agents.

Structure of the algal cell

There are two basic types of cells in the algae, **prokaryotic** and **eukaryotic**. Prokaryotic cells lack membrane-bounded organelles (plastids, mitochondria, nuclei, Golgi bodies, and flagella) and occur in the cyanobacteria (Fig. 2.11). The remainder of the algae are eukaryotic and have organelles.

A eukaryotic cell (Fig. 1.1) is often surrounded by a cell wall composed of polysaccharides that are partially produced and secreted by the Golgi body. The plasma membrane (plasmalemma) surrounds the remaining part of the cell; this membrane is a living structure responsible for controlling the influx and outflow of substances in the protoplasm. Locomotory organs, the flagella, propel the cell through the medium by their beating. The flagella are enclosed in the plasma membrane and have a specific number and orientation of microtubules. The nucleus, which contains the genetic material of the cell, is surrounded by a double membrane with pores in it. The contents of the nucleus are a nucleolus, chromosomes, and the background material or karyolymph. The chloroplasts have membrane sacs called thylakoids that carry out the light reactions of photosynthesis. The thylakoids are embedded in the stroma where the dark reactions of carbon fixation take place. The stroma has small 70S ribosomes, DNA, and in some cases the storage product. Chloroplasts are surrounded by the two membranes of the chloroplast envelope. Sometimes chloroplasts have a dense proteinaceous area, the pyrenoid, which is associated with storage-product formation.

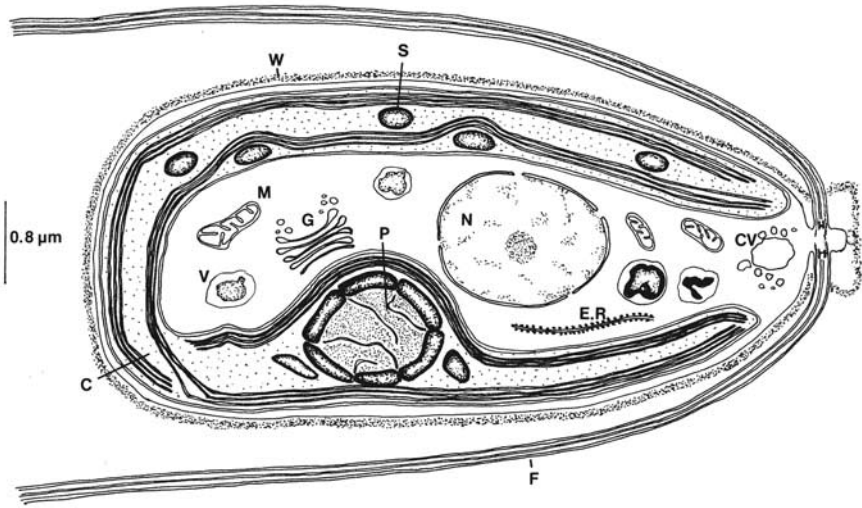


Fig. 1.1 Drawing of a cell of the green alga *Chlamydomonas* showing the organelles present in a eukaryotic algal cell. (C) Chloroplast; (CV) contractile vacuole; (E.R.) endoplasmic reticulum; (F) flagella; (G) Golgi body; (M) mitochondrion; (N) nucleus; (P) pyrenoid; (S) starch; (V) vacuole; (W) wall.

Double-membrane-bounded mitochondria have 70S ribosomes and DNA, and contain the respiratory apparatus. The Golgi body consists of a number of membrane sacs, called cisternae, stacked on top of one another. The Golgi body functions in the production and secretion of polysaccharides. The cytoplasm also contains large 80S ribosomes and lipid bodies.

Flagella

The flagella of the green alga *Chlamydomonas* have been used as a model of flagellar structure. Flagella structure has been highly conserved throughout evolution, images from *Chlamydomonas* are virtually indistinguishable from flagella (or cilia – a term for a short flagellum) of mammalian cells including human sperm and certain epithelia (Johnson, 1995). *Chlamydomonas* has been chosen because of the ease of growing the organism and because the flagella can be detached from the cells by pH shock or blending. Since the flagella are not essential for viability of the cell, it is relatively easy to isolate mutations affecting flagella synthesis by the cells.

A flagellum consists of an axoneme of nine doublet microtubules that surround two central

microtubules, with all of the microtubules encased in the plasma membrane (Figs. 1.2, 1.3). On entering the cell body, the two central microtubules end at a dense plate, whereas the nine peripheral doublets continue into the cell, usually picking up an additional structure that transforms them into triplets. The flagellum passes through a tunnel in the cell wall called the flagellar collar.

The central pair of microtubules are single microtubules with 13 protofilaments while the outer microtubules are doublets with the A-tubule consisting of 13 protofilaments and the B-tubule having 11 protofilaments. The central-pair microtubules resemble cytoplasmic microtubules, in that they are more labile than the outer doublet microtubules. The axoneme microtubules are composed of α - and β -tubulin which make up 70% of the protein mass of the axoneme (Dutcher, 1995). Radial spokes, each consisting of a thin stalk and head, project from the A-tubule of the outer microtubule doublets (Figs. 1.2, 1.3).

Inner and outer dynein arms attach to the A-tubule of the outer microtubule doublet and extend to the B-tubule of the adjacent outer microtubule doublet. Dynein is a mechanoenzyme that hydrolyzes ATP with the resulting energy used by dynein to move along the B-tubule of the adjacent outer microtubule doublet (Fig. 1.3). In this action, the B-tubule is called the track while the A-tubule is called the cargo. The resulting displacement of outer microtubule

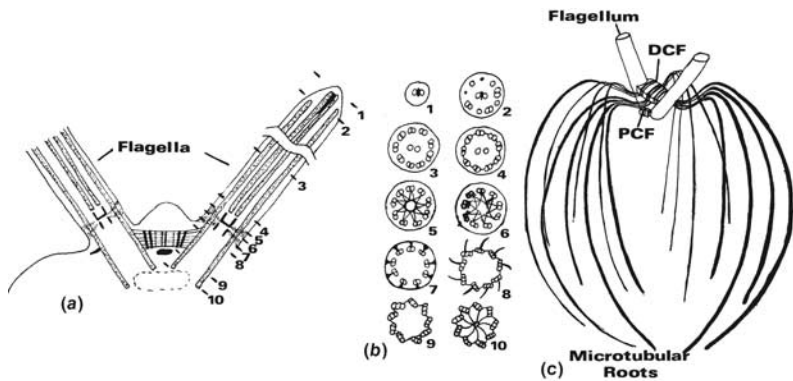


Fig. 1.2 The flagellar system in the green alga *Chlamydomonas*. (a) A diagrammatic drawing of a section of the flagellar system. The numbers refer to cross sections of the flagellar system in (b). (c) Diagrammatic drawing of the whole flagellar apparatus. The two flagella are joined by the proximal connecting fiber (PCF) and distal connecting fiber (DCF). (After Ringo, 1967.)

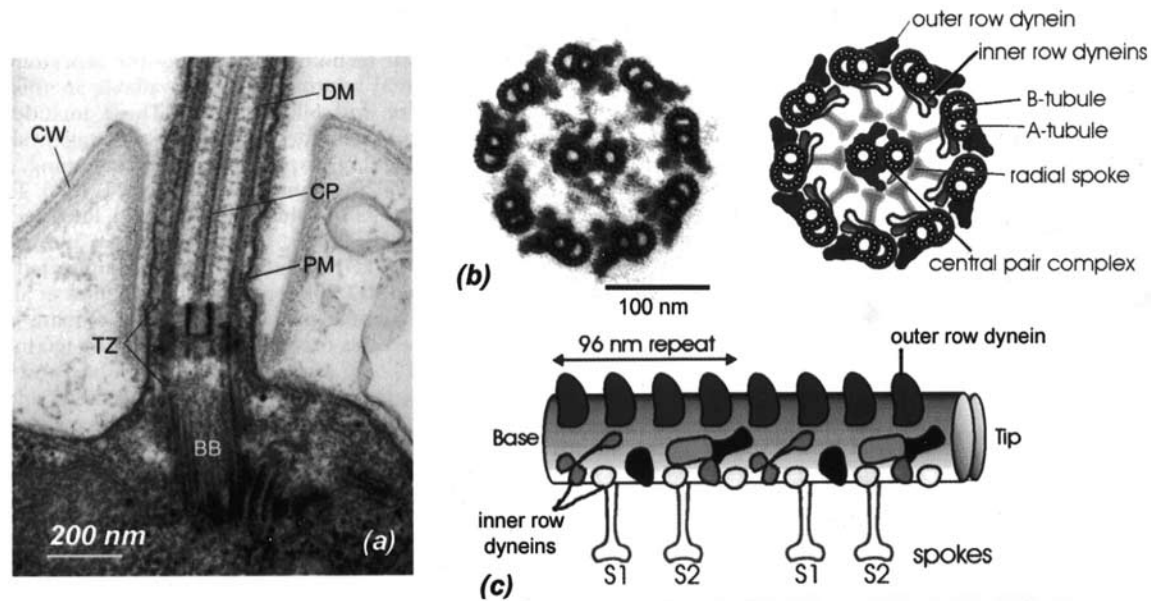


Fig. 1.3 *Chlamydomonas* flagella. (a) Transmission electron micrograph through the anterior region of a *Chlamydomonas reinhardtii* cell including the cell wall (CW), double microtubules (DM), central pair microtubules (CP), plasma membrane (PM), transition zone (TZ), and basal body (BB). (b) Thin section through an isolated demembranated flagellar axoneme showing the main components. (c) Diagrams of dyneins and related structures seen along the A-tubule of each doublet. (From Mitchell, 2000.)

doublets in relation to each other causes bending of the flagellum (Mitchell, 2000). Kinesin proteins cause the central pair of microtubules to rotate within the axoneme (Fig. 1.4). As the central pair of microtubules rotates, the microtubules interact with the individual radial spokes inducing sliding between adjacent microtubule doublets,

asymmetric bending of the flagellum and propagation of flagellar waves (Johnson, 1995). There are also other structures between the microtubules in the basal region of the flagellum (**basal body**). Attached to the basal body there can be either microtubular roots or striated fibrillar roots. The former type of root consists of a group of microtubules running from the basal body into the protoplasm (Figs. 1.2, 1.4), whereas the latter consists of groups of fibers that have striations along their length (Figs. 1.4, 1.6) The gamete of the green seaweed *Ulva lactuca* (sea lettuce) has both types of flagellar roots (Fig. 1.5) (Melkonian, 1980; Andersen et al., 1991). There are four **microtubular roots** composed of microtubules arranged in a cruciate pattern, and **fibrous roots (rhizoplasts)** composed of a bundle

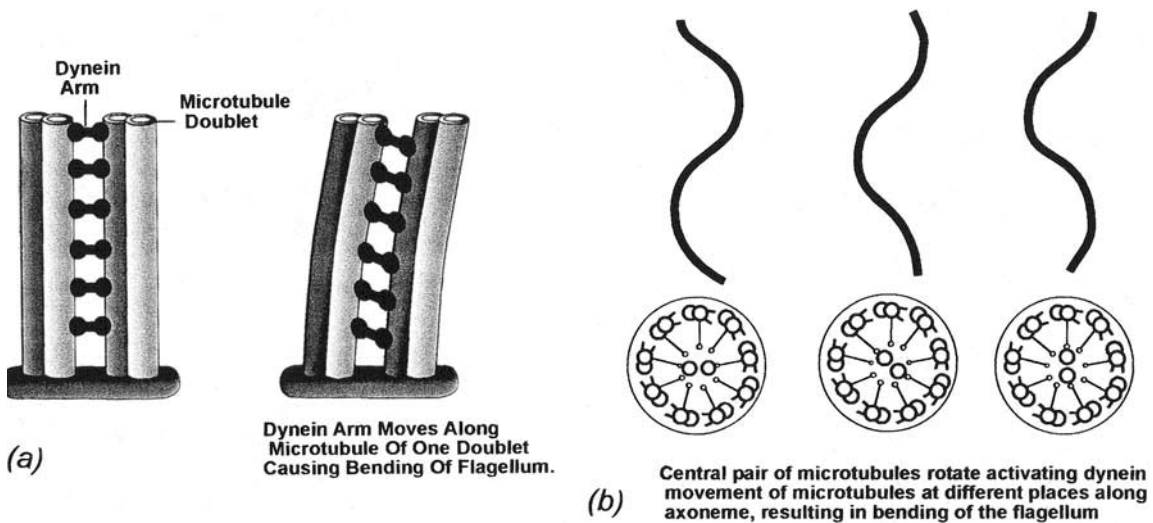


Fig. 1.4 Bending of flagella occurs by the rotating central pair of microtubules activating dynein movement of specific outer doublet microtubules.

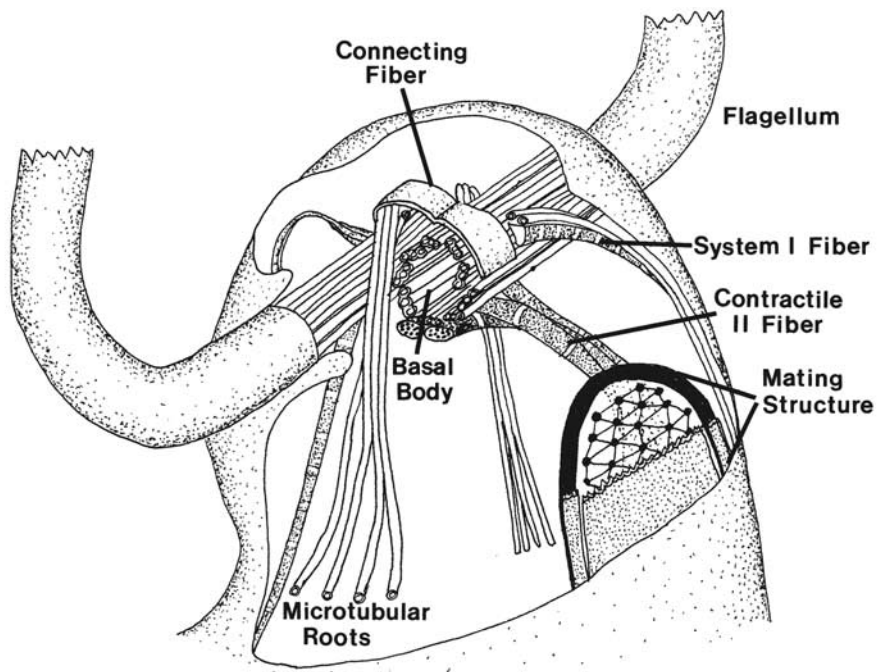


Fig. 1.5 Schematic three-dimensional reconstruction of the flagellar apparatus of a female gamete of *Ulva lactuca* showing the four cruciately arranged microtubular roots and the fibrous contractile roots. (Adapted from Melkonian, 1980.)

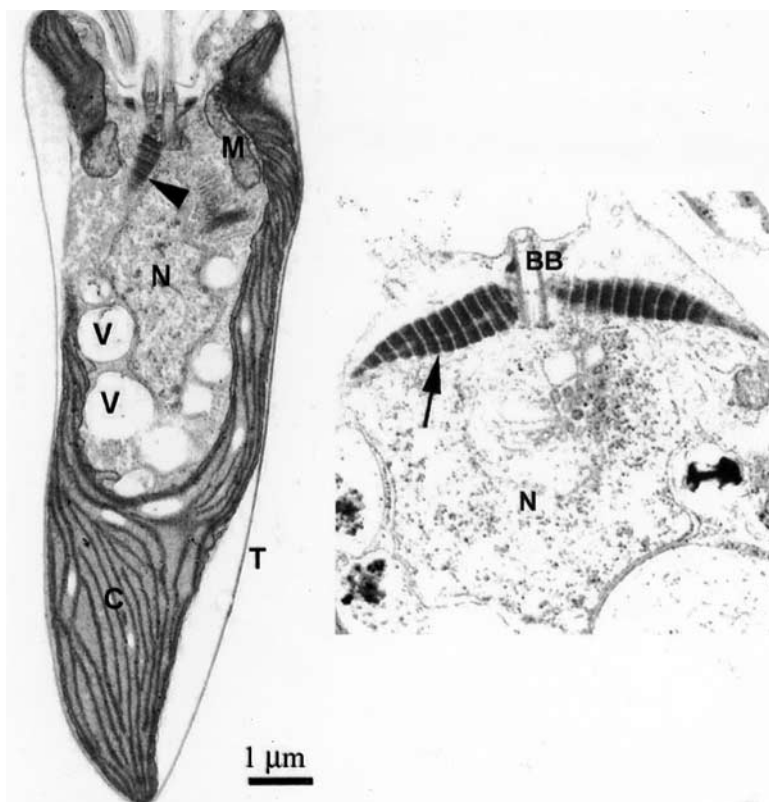


Fig. 1.6 Transmission electron micrographs of striated roots (rhizoplasts) in the green alga *Scherffelia dubia* (Chlorophyta). Arrow and arrowhead point to a striated root. (BB) Basal body; (C) chloroplast; (M) mitochondrion; (N) nucleus; (V) vacuole. (From Vierkotten et al., 2004.)

of filaments (Fig. 1.6). There are two types of fibrous roots: (1) **system I fibrous roots** composed of 2 nm filaments cross-striated with a periodicity of approximately 30 nm and (2) **system II fibrous roots** composed of 4–8 nm filaments usually cross-striated with a periodicity greater than 80 nm. System I fibrous roots are non-contractile while system II fibrous roots are contractile when appropriately stimulated (Moestrup, 2000; Brugerolle and Mignot, 2003).

The flagellar membrane may have no **hairs** (**mastigonemes**) on its surface (**whiplash** or **acronematic flagellum**) or it may have hairs on its surface (**tinsel** or **hairy** or **pantonematic** or **Flimmergeissel**). There are two types of flagellar hair (Fig. 1.7):

1 Non-tubular flagellar hairs made up of solid fibrils 5–10 nm wide and 1–3 μm long that are composed of glycoproteins. These hairs are flexible and wrap around the flagellum increasing the surface area and efficiency of propulsion.

2 Tubular flagellar hairs about 2 μm long composed of three regions: (1) a tapering basal region 200 nm long attached to the flagellar membrane, (2) a microtubular shaft 1 μm long, and (3) a few 0.52 μm-long terminal filaments (Andersen et al., 1991).

The bases of the hairs do not penetrate the flagellar membrane but are stuck to it. Development of the tubular hairs begins in the space between the inner and outer membrane of the nuclear envelope (perinuclear continuum) where the basal and microtubular regions are assembled. These then pass to the Golgi apparatus, where the terminal filaments are added. Finally the hairs are carried to the plasma membrane in Golgi vesicles, where they are discharged and attached to the flagellar membrane. Tripartite tubular hairs occur in the Heterokontophyta. The term **stramenopile** (straw hair) has been used to include all protists with tubular hairs (van der Auwera and deWachter, 1997). In addition to the algae in the Heterokontophyta, the

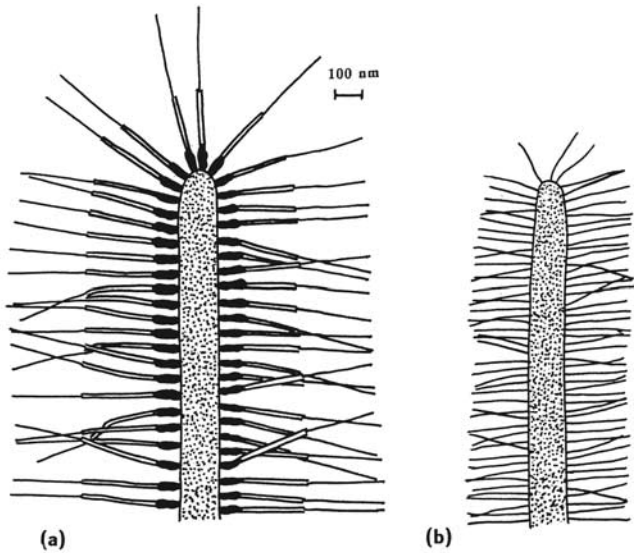


Fig. 1.7 Drawings of the types of hairs on algal flagella. (a) Tripartite hairs (example *Ascophyllum* sperm). Each hair is composed of a basal region attached to the flagellar membrane, the microtubular shaft, and a terminal hair. (b) Non-tubular hairs (example *Chlamydomonas* gamete). ((a) adapted from Bouck, 1969; (b) from Snell, 1976.)

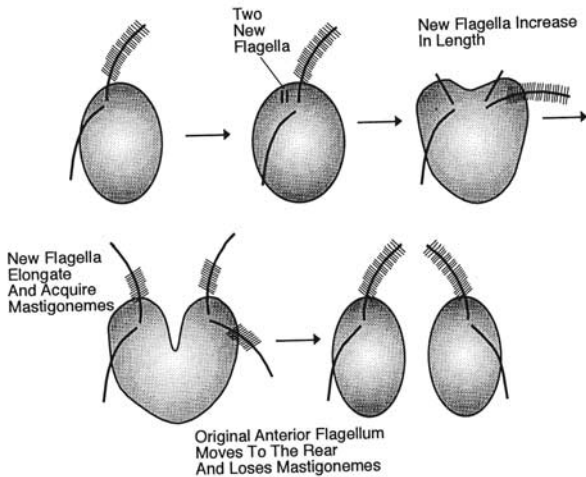


Fig. 1.8 The sequence of flagellar transformation during cell division.

stramenopiles include the fungal oomycetes, hyphochytridomycetes, thraustochytrids, and the bicosoecids and labyrinthulids.

The remainder of the algae have non-tubular hairs if hairs occur on the flagella (Moestrup, 1982). In addition to hairs, a number of different scale types occur on the surface of the flagella. These will be discussed in the chapters on the individual algal groups.

Flagella progress through a set of developmental cycles during cell division (Fig. 1.8). A biflagellate cell with an anterior flagellum covered with tubular hairs (insel flagellum), and a posterior smooth flagellum (whiplash flagellum), will be used as an example. Before the onset of cell

division, two new flagella appear next to the anterior flagellum. These two new flagella elongate while the original anterior flagellum moves toward the posterior of the cell and loses its tubular hairs, to become the posterior smooth flagellum of one of the daughter cells. The two new flagella at the anterior end of the cell acquire tubular hairs and become the insel flagella of the daughter cells. Thus, each daughter cell has one new anterior insel flagellum, and one posterior smooth whiplash flagellum that was originally a flagellum in the parent cell (Beech and Wetherbee, 1990; Melkonian et al., 1987).

Algal cells can have different arrangements of flagella (Fig. 1.9). If the flagella are of equal length,

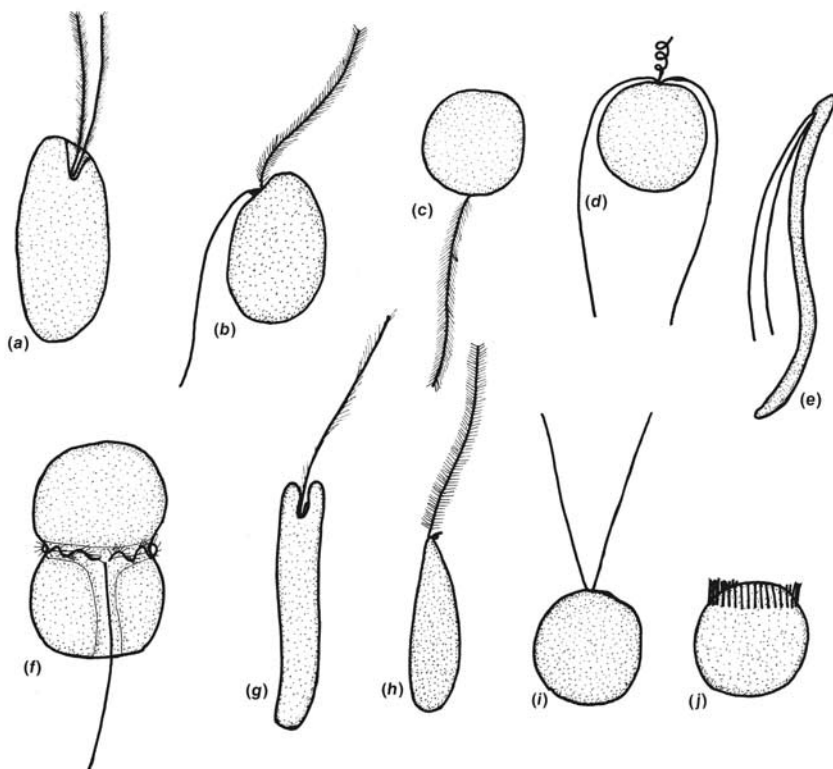


Fig. 1.9 The shape of eukaryotic motile algal cells and their flagella. The drawings represent the common arrangement of flagella in the groups. There are a number of modifications in structure that are not included here. (a) Cryptophyta; (b) most of the Heterokontophyta; (c) Bacillariophyceae of the Heterokontophyta; (d) Prymnesiophyta; (e) Chlorophyta; (f) Dinophyta; (g) Euglenophyta; (h) Eustigmatophyceae of the Heterokontophyta; (i, j) Chlorophyta.

they are called **isokont** flagella; if they are of unequal length, they are called **anisokont** flagella; and if they form a ring at one end of the cell, they are called **stephanokont** flagella. **Heterokont** refers to an organism with a hairy and a smooth flagellum (Moestrup, 1982).

Flagella can be of different length in the same cell. This is controlled by **intraflagellar transport**, defined as the *bi-directional movement of particles along the length of the flagellum between the axoneme and the flagellar membrane* (Beech, 2003). A mature flagellum that is not elongating has a steady disassembly of the flagellum that is countered by an equally steady assembly provided by intraflagellar transport (Fig. 1.10). A change in length of the

flagellum is produced by an imbalance in the assembly or disassembly of flagellar components (Rosenbaum and Witman, 2002). Thus, disassembly occurs faster than assembly in flagellar retraction. The opposite occurs during flagellar growth. The differences in length of flagella arise from the shorter flagellum being delayed in the initial stages of construction. The assembly rate of the shorter flagellum is the same as the longer flagellum. There may be a gate at the base of the flagellum that regulates the passage of flagellar precursors into the basal body and the flagellum (Schoppmeier and Lehtreck, 2003).

Cell walls and mucilages

In general, algal cell walls are made up of two components: (1) the fibrillar component, which forms the skeleton of the wall, and (2) the amorphous component, which forms a matrix within which the fibrillar component is embedded.

The most common type of fibrillar component is **cellulose**, a polymer of 1,4 linked β -D-glucose. Cellulose is replaced by a **mannan**, a polymer of 1,4 linked β -D-mannose, in some siphonaceous

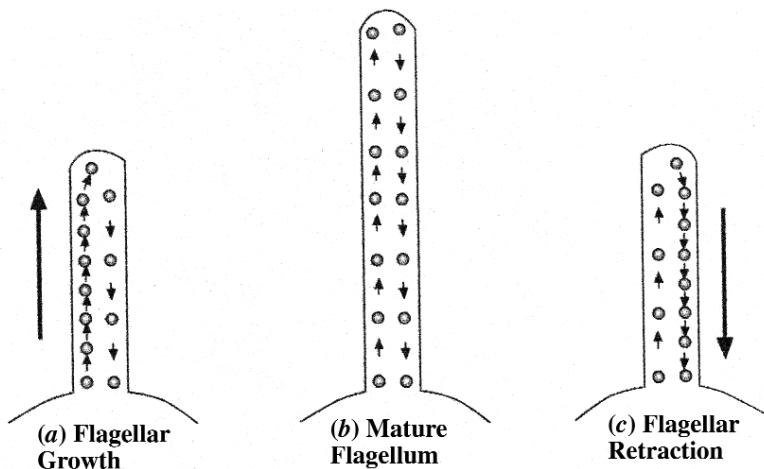


Fig. 1.10 (a) Intraflagellar transport results in more assembly of flagellar subunits than disassembly during flagellar growth. (b) A mature flagellum has an equal amount of assembly and disassembly of flagellar subunits. (c) There is more disassembly of flagellar subunits during flagellar retraction.

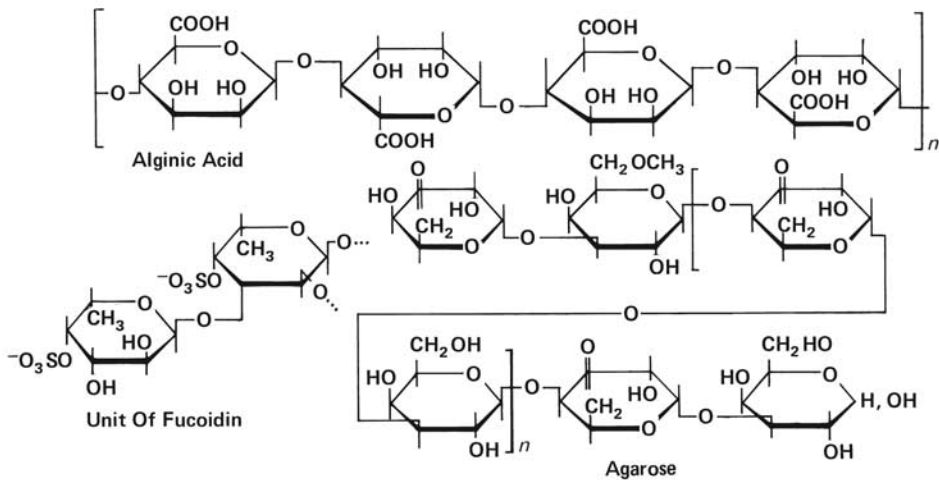


Fig. 1.11 Structural units of alginic acid, fucoidin, and agarose. (After Percival and McDowell, 1967.)

greens, and in *Porphyra* and *Bangia* in the Rhodophyta. In some siphonaceous green algae and some Rhodophyta (*Porphyra*, *Rhodochorton*, *Laurencia*, and *Rhodymenia*), fibrillar xylans of different polymers occur.

The amorphous mucilaginous components occur in the greatest amounts in the Phaeophyceae and Rhodophyta, the polysaccharides of which are commercially exploited. **Alginic acid** (Fig. 1.11) is a polymer composed mostly of β -1,4 linked D-mannuronic acid residues with variable amounts of L-guluronic acid. Alginic acid is present in the intercellular spaces and cell walls of the

Phaeophyceae. **Fucoidin** (Fig. 1.11) also occurs in the Phaeophyceae and is a polymer of α -1, 2, α -1, 3, and α -1, 4 linked residues of L-fucose sulfated at C-4. In the Rhodophyta the amorphous component of the wall is composed of galactans or polymers of galactose, which are alternatively β -1,3 and β -1,4 linked. These galactans include **agar** (made up of **agaropectin** and **agarose**, Fig. 1.11) and **carrageenan** (Fig. 4.15).

Plastids

The basic type of plastid in the algae is a **chloroplast**, a plastid capable of photosynthesis. **Chromoplast** is synonymous with chloroplast; in the older literature a chloroplast that has a color other than green is often called a chromoplast. A **proplastid** is a reduced plastid with few if any

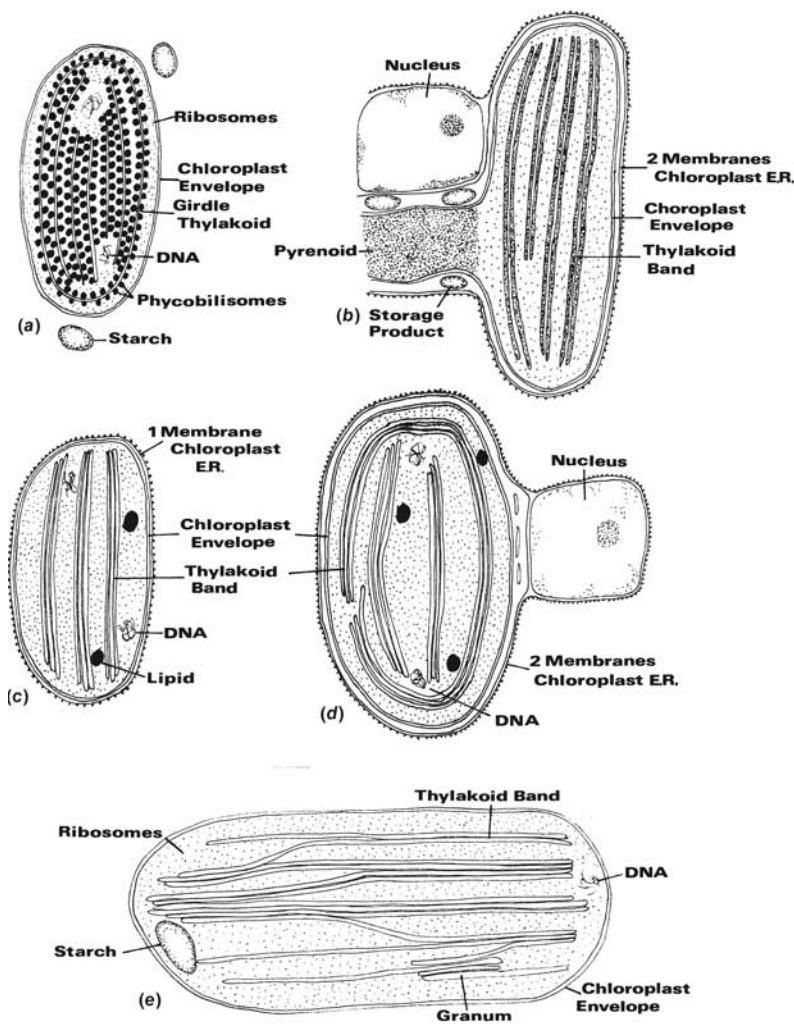


Fig. 1.12 Types of chloroplast structure in eukaryotic algae. (a) One thylakoid per band, no chloroplast endoplasmic reticulum (Rhodophyta). (b) Two thylakoids per band, two membranes of chloroplast E.R. (Cryptophyta). (c) Three thylakoids per band, one membrane of chloroplast E.R. (Dinophyta, Euglenophyta). (d) Three thylakoids per band, two membranes of chloroplast E.R. (Prymnesiophyta and Heterokontophyta). (e) Two to six thylakoids per band, no chloroplast E.R. (Chlorophyta).

thylakoids. A proplastid will usually develop into a chloroplast although in some heterotrophic algae it remains a proplastid. A **leucoplast** or **amyloplast** is a colorless plastid that has become adapted for the accumulation of storage product.

In the Rhodophyta and Chlorophyta, the chloroplasts are bounded by the double membrane of the chloroplast envelope (Fig. 1.12(a), (e)). In the other eukaryotic algae, the chloroplast envelope is surrounded by one of two membranes of **chloroplast endoplasmic reticulum** (chloroplast E.R.), which has ribosomes attached to the outer face of the membrane adjacent to the cytoplasm. The chloroplast E.R. is the remnant of the food vacuole membrane and/or the plasma membrane involved in the original endosymbiosis leading

to the chloroplasts in a secondary endosymbiosis. In the Euglenophyta and Dinophyta, there is one membrane of chloroplast E.R. (Fig. 1.12(c)). In the Cryptophyta, Prymnesiophyta, and Heterokontophyta, there are two membranes of chloroplast E.R., with the outer membrane of chloroplast E.R. usually continuous with the outer membrane of the nuclear envelope, especially if the chloroplast number is low (Fig. 1.12 (b), (d)).

The basic structure of the photosynthetic apparatus in a plastid consists of a series of flattened membranous vesicles called **thylakoids** or **discs**, and a surrounding matrix or **stroma**. The thylakoids contain the chlorophylls and are the sites of the photochemical reactions; carbon dioxide fixation occurs in the stroma. The thylakoids can