Chapter 3
Green Algae (Chlorophyta and Streptophyta) in Rivers

Alison R. Sherwood

Abstract The green algae represent one of the most diverse and abundant algal lineages in river systems around the world, and their evolutionary diversification led to two major lineages, the Chlorophyta and Streptophyta (with the latter including the land plants). Macroscopic and microscopic forms of green algae are common in streams, as are those living on hard substrata, epiphytically on aquatic plants or other algae, and a few free-floating forms. This chapter treats the most common genera from stream habitats, with an emphasis on the benthic forms, the macroscopic taxa, and those that are widespread in distribution. Basic descriptions of 42 genera are provided, along with illustrations and information on the habitat and phylogeny of each genus, where known.

Keywords Algae • Benthic • Biodiversity • Charophytes • Chlorophyta • Green algae • River • Streptophyta • Viridiplantae

Introduction

Phylogenetic Scope and Features of the Green Algae

The green algae (Divisions Chlorophyta and Streptophyta) comprise the green lineage, or Viridiplantae, which also includes the land plants, and represents one of the major evolutionary lines of oxygenic photosynthetic organisms. The green algae include organisms that have successfully established in marine, freshwater, and some terrestrial environments and which have led to the evolution of land plants and the subsequent development of terrestrial ecosystems. Approximately

A.R. Sherwood (✉)
Department of Botany, University of Hawaii, 3190 Maile Way, Honolulu, HI 96822, USA
e-mail: asherwoo@hawaii.edu

O. Necchi Jr. (ed.), *River Algae*, DOI 10.1007/978-3-319-31984-1_3

14,000 species of green algae have been described to date, and an estimated 21,000 species may exist (Guiry 2012). The green algae are distinguished from the other algal lineages by having chlorophyll *a* and *b* within a double membrane-bound chloroplast, an organelle that resulted from a primary endosymbiotic event. The primary photosynthetic storage product is true starch, which is stored in the chloroplast. The green algal cell wall is most commonly composed of cellulose, although a number of variations on this theme are known (Graham et al. 2009).

Current research supports an early divergence of the green algae into two main clades, whose ancestor was likely a flagellated green alga (Leliaert et al. 2012). The Chlorophyta (one of the two clades) consists of a series of early diverging prasinophyte lineages as well as the "core" chlorophytes—the classes Ulvophyceae, Trebouxiophyceae, Chlorodendrophyceae, and Chlorophyceae. The second main clade includes both the land plants and their closest green algal relatives, the charophyte green algae from which they have evolved. Green algae in stream ecosystems are represented by both of these main clades, and belong predominantly to the classes Ulvophyceae, Trebouxiophyceae, and Chlorophyceae in the Chlorophyta, and classes Charophyceae, Coleochaetophyceae, Klebsormidiophyceae, and Zygnematophyceae of the Streptophyta.

Features of Taxonomic Importance

The higher level taxonomic scheme adopted in this chapter is based on a combination of ultrastructural characters—i.e., cell division and flagellar apparatus patterns—and molecular data analyses—i.e., phylogenetic reconstruction based on nuclear, chloroplast, and mitochondrial markers—as well as, more recently, genomic analyses (Pröschold and Leliaert 2007; Friedl and Rybalka 2012; Leliaert et al. 2012). However, the features of greatest importance for genus- and species-level identification are visible at the light microscope level and pertain to cellular characteristics and the organization of the thallus. The thallus construction can be discerned by eye, with a dissecting microscope, compound light microscope, or some combination of those. Of critical importance is whether the alga is single-celled or multicellular, whether it is flagellated or nonflagellated (generally for single-celled forms), colonial or free-living, and if multicellular, whether it is filamentous, parenchymatous, or coenocytic/siphonous in organization. Taxa inhabiting streams are more often than not attached, and few unicellular flagellated forms are common. Multicellular thalli may be branched or unbranched. The number, shape, and position of the chloroplast are diagnostic for many taxa, as is the presence/absence of pyrenoids and their number and position in the chloroplast (Prescott 1951; Hall and McCourt 2015; John and Rindi 2015; Nakada and Nozaki 2015; Shubert and Gärtner 2015; John et al. 2011).

Collecting and Preserving Samples

Large growths of benthic green algae or floating mats can be easily seen unaided in stream systems, but many forms are sufficiently small that additional help is needed—this can be accomplished by using a view box, constructed of plastic or plexiglass sides with a glass bottom (Sheath and Vis 2015). Benthic macroalgal individuals, colonies, and mats are most easily collected using long-handled forceps (for robust taxa) or suction devices such as a turkey baster (for more delicate taxa). Microscopic periphyton can be collected by removing the entire community with a toothbrush or scraping with a razor blade, knife, or the edge of a metal spoon. Epiphytic taxa (e.g., those attached to macrophytes and some species of *Coleochaete*) are best sampled by collecting the substratum along with the alga of interest, which allows closer examination of the material at the microscopic level in the laboratory (Lowe and LaLiberte 2007). How the collections are further processed depends on the scope of analysis techniques to be used. For example, if only light microscope examination is anticipated, samples should be placed into vials or small bags and either immediately fixed (2.5 % $CaCO_3$-buffered glutaraldehyde is an excellent fixative because it retains the color of the algae for some years, but samples stored in this fixative must be refrigerated; Sheath and Vis 2015) or kept cool in a small amount of stream water for 1–2 days before fixation. Samples for molecular characterization (not covered further in this chapter) should be examined and cleaned, if necessary, while viewing with a dissecting microscope prior to DNA extraction (samples can also be either frozen or desiccated in silica gel if not immediately extracted). Artificial surfaces such as plastic or glass bottles can also be excellent substrata for attached stream algae and are often a good source of unialgal material and yield easily removed samples.

Classification Followed in this Chapter

Stream-inhabiting green algae of the Phyla Chlorophyta and Streptophyta are treated in this chapter, with the former represented by three classes (Chlorophyceae, Trebouxiophyceae, and Ulvophyceae) and the latter by four (Charophyceae, Coleochaetophyceae, Klebsormidiophyceae, and Zygnematophyceae). Of the classes within the Chlorophyta, the Chlorophyceae contains the greatest number of genera in stream systems, while within the Streptophyta the Zygnematophyceae is treated in most detail. Genera are arranged alphabetically within each order. Taxonomy, for the most part, follows that presented in AlgaeBase as of the time of this writing (Guiry and Guiry 2015).

Given the large number of green algal genera known from streams, not all could be treated in this chapter. Thus, emphasis is given to the more common taxa, the larger green algae, and the attached forms, and the reader is referred to some of the excellent recent and classic literature on freshwater green algae for additional information on some of the less widespread and less commonly encountered taxa (e.g., Prescott 1951; Wehr et al. 2015; John et al. 2011). Some examples of recent literature applying molecular methodologies to green algal systematics are cited under the descriptions of individual genera.

Distribution of Green Algae in Streams

Most stream-inhabiting green algae, by virtue of living in unidirectional flow, are attached to hard surfaces, including rocks, plant material (aquatic vegetation as well as decaying trees and other plant material that has fallen into the stream), animals (e.g., turtles and mollusk shells), and artificial surfaces (e.g., glass, plastic, or other man-made materials). Occasionally, algal growth can be seen on sand or mud surfaces, but these are typically too unstructured for prolific algal growth in streams, and these surfaces also tend to be rare habitat in flowing waters. The ecology of green algae in stream habitats is covered elsewhere in the literature (e.g., Allan 1995; Stevenson et al. 1996; Dodds 2002; Wehr et al. 2015), and the reader is referred to these sources for detailed information on the seasonality of algal communities as well as the effects of abiotic factors (such as light, temperature, nutrients, and flow) and biotic factors (such as grazing and competition) on the diversity and biomass of green algae.

Taxonomic key to the green algae of streams

1a	Alga microscopic	2
1b	Alga forming a macroscopic thallus	10
2a	Alga attached to benthic substratum, or living epiphytically or endophytically in algal or plant tissue	3
2b	Alga free floating	7
3a	Thallus composed of solitary cells or clusters of cells, or parenchyma/pseudoparenchyma	4
3b	Thallus filamentous, branched or unbranched	6
4a	At least some cells of the thallus with basally sheathed hairs	5
4b	Cells usually solitary, grouped in a mucilaginous matrix (occasionally in short filaments)	*Cylindrocystis*
5a	Thallus composed of individual cells or clusters of cells connected by long, gelatinous tubes	*Chaetosphaeridium*
5b	Thallus pseudoparenchymatous or parenchymatous, but usually with long, basally sheathed hairs	*Coleochaete* (in part)
6a	Thallus epiphytic, formed of prostrate and creeping filaments that can be branched or unbranched	*Aphanochaete*
6b	Thallus epi- or endophytic, composed of irregularly branched filaments	*Chaetonema*
7a	Alga unicellular, composed of needle-like cells with sharply tapered apices	*Closteriopsis*

(continued)

7b	Alga colonial, composed of multiple cells	8
8a	Thallus a sphaerical or irregularly shaped colony composed of radiating clusters of four cells	*Dictyosphaerium*
8b	Thallus not composed of radiating clusters of cells	9
9a	Thallus composed of a colony of cells in a monostromatic layer that is circular or oval in shape	*Pediastrum*
9b	Thallus composed of a colony of cells (4–32) laterally joined in a linear or alternating series	*Scenedesmus*
10a	Thallus filamentous, although may be plant-like in form	14
10b	Thallus sheet-like, parenchymatous or a gelatinous or reticulate colony (or otherwise), but not fundamentally filamentous	11
11a	Thallus sheet like and with cells in regular groupings	*Prasiola*
11b	Thallus not sheet like	12
12a	Thallus composed of sphaerical or oval-shaped cells embedded in a gelatinous matrix	*Tetraspora*
12b	Thallus parenchymatous or composed of a net-like colony of cells	13
13a	Thallus linear, elongated and “filament-like,” uniseriate at the base but becoming parenchymatous above	*Schizomeris*
13b	Thallus composed of a net-like mesh of five- and six-sided polygons of cells	*Hydrodictyon*
14a	Thallus filamentous (may be plant like) and typically branched	15
14b	Thallus filamentous and typically unbranched	29
15a	Branched thallus consisting of both an upright and prostrate system of uniseriate filaments, appearing cushion-like macroscopically	*Gongrosira*
15b	Thallus not appearing cushion-like macroscopically	16
16a	Thallus large and “plant like” (not flimsy), with main axis and branches clearly visible without magnification (the “stoneworts”)	17
16b	Thallus clearly “alga like” (soft, flexible, not stiff), with thallus construction not clearly visible without magnification	19
17a	Branches with cortication (more rarely with partial or complete lack of cortication), with undivided branchlets, and with bract cells at nodes	*Chara*
17b	Branches usually lacking cortication, and with branchlets divided	18
18a	Branchlets forked at least once, with resulting unicellular rays of equal length	*Nitella*
18b	Branchlets forked into multicellular rays of unequal length, resulting in bushy or “untidy” appearance	*Tolypella*
19a	Cells of thallus typically broader at the anterior end or cylindrical in shape, with “apical rings” visible at the ends of some cells	20
19b	Cells of thallus broader at the anterior end or not, but lacking “apical rings” at ends of cells	21
20a	Thallus heterotrichous	*Oedocladium*
20b	Thallus not heterotrichous, consisting only of upright filaments	*Bulbochaete*
21a	Cells with a single parietal chloroplast	22
21b	Cells with one or more reticulate parietal chloroplasts	26
22a	Cells of branches markedly smaller than those of the main axis	23
22b	Cells of branches slightly, but not markedly, smaller than those of the main axis	24

(continued)

23a	Secondary branching irregular	*Cloniophora*
23b	Secondary branches borne oppositely, alternately or in whorls, in clusters or tufts	*Draparnaldia*
24a	Chloroplasts lacking pyrenoids	*Microthamnion*
24b	Chloroplasts with pyrenoids	25
25a	Thallus macroscopically appears as a tuft or mat	*Stigeoclonium*
25b	Thallus macroscopically appears globose, arbuscular or tubercular, often enveloped in mucilage	*Chaetophora*
26a	Filaments with solitary, paired or short chains of akinetes	*Pithophora*
26b	Filaments lacking akinetes	27
27a	Angle of branching typically approaching 90°, filaments stiff and irregularly branched	*Aegagropila*
27b	Angle of branching typically much less than 90°	28
28a	Thallus heterotrichous with a prostrate layer of coalescing filaments and an upright portion of stiff filaments	*Arnoldiella*
28b	Thallus consisting of sparsely to abundantly branched uniseriate filaments, not heterotrichous	*Cladophora*
29a	Asexual, or if sexually reproducing, not by conjugation	30
29b	Sexual reproduction via conjugation	36
30a	Thallus consisting of unbranched filaments with one or more reticulate chloroplasts	31
30b	Thallus consisting of unbranched filaments with a band-shaped or plate-like chloroplast, but not reticulate	33
31a	Cells of thallus typically broader at the anterior end, with "apical rings" visible at the ends of some cells	*Oedogonium*
31b	Cell ends lacking "apical rings"	32
32a	Cells of filaments constructed of "H-walls," having a bipartite structure, chloroplasts lacking pyrenoids	*Microspora*
32b	Cells of filaments not having a bipartite structure, pyrenoids present in chloroplasts	*Rhizoclonium*
33a	Filaments surrounded by a thick, mucilaginous sheath	34
33b	Filaments not surrounded by a mucilaginous sheath	35
34a	Cells of filaments separated from one another but in a linear arrangement, cells equidistant or in pairs, but not forming "H-shaped" sections	*Geminella*
34b	Cells of filaments separated from one another but in a linear arrangement, cells equidistant or in pairs, forming "H-shaped" sections	*Binuclearia*
35a	Unbranched, uniseriate filaments attached by a basal cell	*Ulothrix*
35b	Unbranched, uniseriate filaments lacking apical/basal differentiation	*Klebsormidium*
36a	Cell wall lacking a median constriction	37
36b	Cell wall with a median constriction, thallus usually surrounded by a thick mucilaginous sheath	41
37a	Chloroplast nearly ribbon like and straight to spiraled, parietal, 1–16 per cell	38
37b	Chloroplast plate like or stellate	39

(continued)

38a	Chloroplast spiraling more than one-half a turn per cell, distinct conjugation tube formed during sexual reproduction	*Spirogyra*
38b	Chloroplast straight or nearly so, not spiraling more than one-half a turn per cell, no conjugation tube formed during sexual reproduction	*Sirogonium*
39a	Chloroplast(s) plate like	40
39b	Chloroplasts stellate, two per cell	*Zygnema*
40a	One or two axial, plate-like chloroplasts per cell, with one to several pyrenoids	*Mougeotia*
40b	One axial, plate-like chloroplast per cell, lacking pyrenoids	*Mougeotiopsis*
41a	Thallus with or without a thick mucilaginous sheath, median constriction shallow but discernable	*Desmidium*
41b	Thallus almost always with a thick mucilaginous sheath, median constriction not discernable or only slightly so	*Hyalotheca*

Descriptions of Common Genera of Green Algae in Rivers

Phylum Chlorophyta

Class Chlorophyceae: Order Chaetophorales

Aphanochaete A. Braun (Fig. 3.1a)

Thalli grow epiphytically on submerged aquatic plants and filamentous algae. Uniseriate filaments of *Aphanochaete* can be branched or unbranched, but prostrate and creeping. Cells are cylindrical or inflated, with a parietal, disk-shaped chloroplast and one to several pyrenoids. Upper surfaces of cells sometimes possess setae, one to several per cell, which can be swollen at the base. Either quadriflagellate zoospores or aplanospores can be asexually produced, while sexual reproduction is oogamous.

Remarks: *Aphanochaete* is cosmopolitan in distribution and most commonly found in hard or eutrophic waters. Caisová et al. (2011, 2013) used molecular data to characterize several strains of *Aphanochaete*, which were recovered as monophyletic toward the base of the Chaetophorales, but with high divergence from one another.

Chaetonema Nowakowski (Fig. 3.1b)

Chaetonema grows on or in the mucilaginous sheath of some freshwater macroalgae, including *Batrachospermum*, *Chaetophora*, *Draparnaldia*, and *Tetraspora*. Filaments are irregularly branched, with some cells forming short side branches arising at right angles to the main filament and others attenuating to a hair. Main

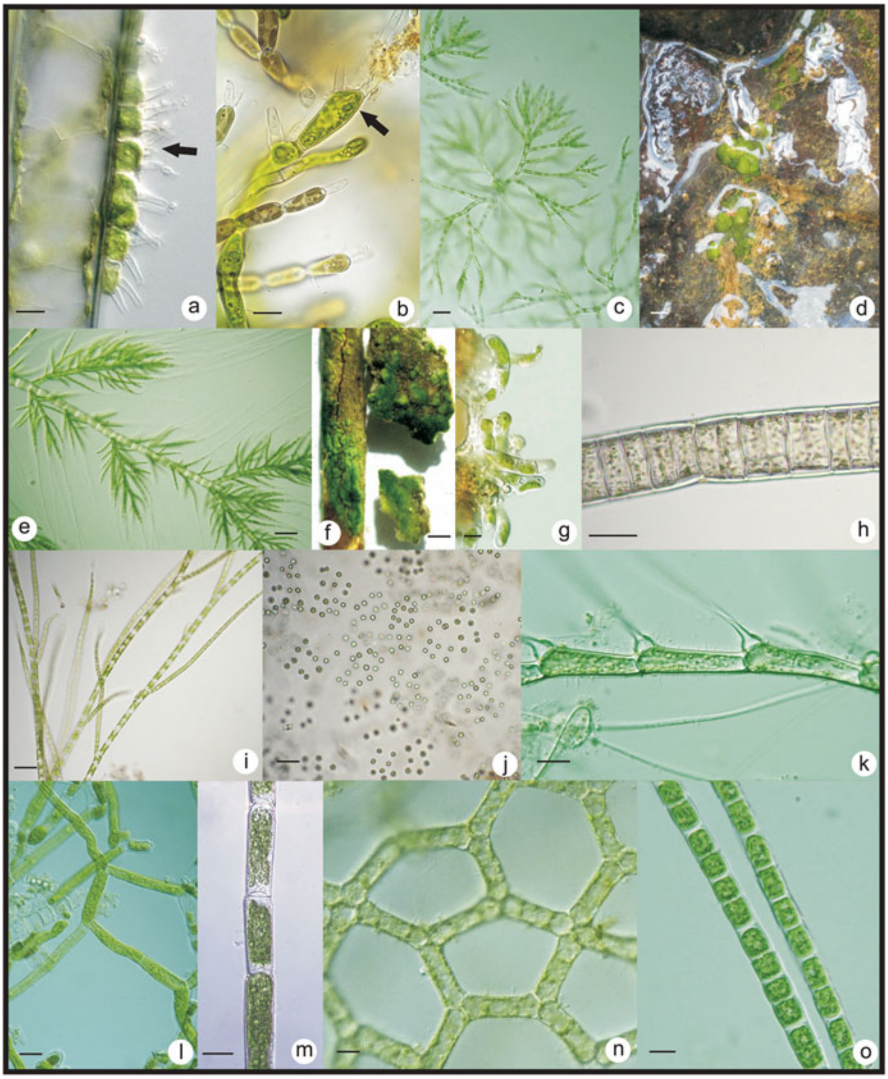

Fig. 3.1 (**a**) *Aphanochaete*, growing on a larger filamentous alga. (**b**) *Chaetonema*, growing on the freshwater red alga *Batrachospermum*. (**c**, **d**) *Chaetophora*: (**c**) filaments; (**d**) macroscopic colonies in a stream. (**e**) *Draparnaldia*. (**f**, **g**) *Gongrosira*: (**f**) Macroscopic colonies; (**g**) filaments. (**h**) *Schizomeris*. (**i**) *Stigeoclonium*. (**j**) *Tetraspora*. (**k**) *Bulbochaete*. (**l**) *Oedocladium*. (**m**) *Oedogonium*. (**n**) *Hydrodictyon*. (**o**) *Microspora*. Scale bars: (**f**) = 2 cm; (**d**) = 1 cm; (**e**) = 100 μm; (**h**) = 75 μm; (**i**, **j**, **m**, **n**) = 30 μm; (**c**, **k**, **l**, **o**) = 20 μm; (**a**, **b**, **g**) = 10 μm. Image authors: (**a**) W. Bourland; (**b**) C. Carter; (**f**) D. John; (**c**, **e**, **k**, **l**, **n**, and **o**) Y. Tsukii; (**g**) P. York

cells of the thallus are cylindrical in shape, with a parietal, plate-like chloroplast and one to two pyrenoids. Asexual reproduction occurs by production of two quadriflagellate zoospores per cell, and sexual reproduction is oogamous, with male gametes biflagellate and formed in groups of 8.

Chaetophora Schrank (Fig. 3.1c, d)

A number of thallus shapes are known for the macroscopic genus *Chaetophora*, including globose, arbuscular, or tubercular, and the thallus can be enveloped in soft or firm mucilage. Thalli consist of uniseriate filaments and possess an underdeveloped prostrate system and a highly branched erect system. Filaments terminate in a blunt point or an elongated, multicellular hair. Cells contain a single, parietal chloroplast, and one to several pyrenoids. Motile cells are produced at the tips of branches. Asexual reproduction occurs via production of quadriflagellate zoospores; sexual reproduction is isogamous and occurs following the production of biflagellate gametes.

Remarks: *Chaetophora* occurs on a wide variety of substrata and is common in fast-flowing streams. Abundance peaks during the colder months of the year, at least in temperate areas. *Chaetophora* has been demonstrated to be a polyphyletic genus in need of much further systematic work (Caisová et al. 2011, 2013).

Draparnaldia Bory de Saint-Vincent (Fig. 3.1e)

Thalli are embedded in a soft, mucilaginous matrix. The erect system is uniseriate and consists of barrel-shaped or cylindrical cells on the main axis; secondary branches in clusters or tufts with much smaller cells. Secondary branches are borne oppositely, alternatively or in whorls, and each terminates in a blunt cell or a multicellular hair. Cells of the main axis possess a single large, band-shaped parietal chloroplast that can vary in degree of entirety of its edges; cells of secondary branches have a single laminate parietal chloroplast with one to three pyrenoids. Reproductive cells are produced in the secondary branches. Asexual reproduction occurs by aplanospores and biflagellate zoospores; sexual reproduction is isogamous with quadriflagellate gametes.

Remarks: *Draparnaldia* is common in cool, clean waters and is frequently encountered in higher elevation streams and springs. Like *Stigeoclonium*, members of the genus can exhibit substantial morphological plasticity, and molecular phylogenetic assessment of the genus in the context of other members of the Chaetophorales is needed. The limited molecular data thus far suggest that the genus is monophyletic (e.g., Caisová et al. 2011).

Gongrosira Kützing (Fig. 3.1f, g)

Thalli composed of both a prostrate (uniseriate) and erect system of filaments, appearing cushion-like macroscopically. There can be considerable variation in the prostrate system, but it is usually pseudoparenchymatous in mature specimens. The erect system consists of short branches terminating in blunt tips. Cells are cylindrical in shape or sometimes clavate and can have thick and lamellated walls. Cells possess a single parietal chloroplast and one or more pyrenoids. Asexual reproduction can occur by aplanospores, zoospores, or akinetes; sexual reproduction is unknown.

Remarks: *Gongrosira* can occur on a variety of substrata.

Schizomeris Kützing (Fig. 3.1h)

Schizomeris is an unbranched, tube-like green alga with a macroscopic growth form. The alga is typically uniseriate at the base, but becoming multiseriate, such that a solid parenchyma is formed above the base. Thalli can be constricted at multiple points along their length. Cell shape tends to be elongated toward the base of the thallus but quadrate in the upper portions. Cells possess a single band-like, parietal chloroplast that encircles much of the cell. Thalli reproduce through the production of zoospores, which are quadriflagellate, and tend to be produced in the more mature sections of the thallus; sexual reproduction is unknown.

Remarks: *Schizomeris* is typically collected from slow-flowing regions of streams, but may occasionally be found near waterfalls. The genus is widespread, but not commonly reported. A single species is recognized in the genus (*S. leibleinii* Kützing), and recent molecular analyses of collections from widespread locations support the monotypic status of this genus (Caisová et al. 2011). Several studies have found phylogenetic evidence for *Schizomeris* as sister to the remainder of the order Chaetophorales (Buchheim et al. 2011; Tippery et al. 2012). It has also been reported that *Schizomeris* and *Stigeoclonium* chloroplast genomes share a number of features that support a close phylogenetic relationship between the genera (Brouard et al. 2011).

Stigeoclonium Kützing (Fig. 3.1i)

Thalli are heterotrichous with prostrate and erect systems that are developed to various degrees, depending on the species and the conditions under which they grow. The filamentous thalli are uniseriate, and upright portions can be branched alternately, oppositely, or dichotomously, or irregularly (rarely). Apices of the upright filaments are attenuated, narrowly obtuse, or with a multicellular hyaline hair; prostrate sections of the thallus are typically rhizoidal or sometimes pseudoparenchymatous. Cells of *Stigeoclonium* are either cylindrical or inflated in shape and can be either thin or thick walled. Each cell contains one parietal chloroplast and one or more pyrenoids. Asexual reproduction via quadriflagellate zoospores can be by micro- or macrozoospores; sexual reproduction occurs via production of isogametes that are bi- or quadriflagellate.

Remarks: *Stigeoclonium* is a common component of stream algal floras and appears as tufts or mats on a variety of surfaces. Members of the genus are renowned for being polymorphic and identification based on morphology of the upright thallus portion is unreliable. Culture-based analyses suggest that far fewer species should be recognized than are indicated, and molecular analyses illustrate that much more work needs to be completed on members of *Stigeoclonium*, within the context of analyses of the order Chaetophorales, before the taxonomy can be resolved. Caisová et al. (2011) recovered the genus as polyphyletic in their molecular analyses. As mentioned for *Schizomeris*, *Stigeoclonium* and that genus share a number of features of their chloroplast genomes that support their close phylogenetic relationship (Brouard et al. 2011).

Class Chlorophyceae: Order Chlamydomonadales

Tetraspora Link ex Desvaux (Fig. 3.1j)

Tetraspora is a colonial macroalga consisting of spherical or oval-shaped cells embedded in a gelatinous matrix; cells may be grouped in 2's or 4's, especially at the periphery. Colonies are spherical, elongated, or amorphous in shape. Each cell possesses a cup-shaped chloroplast with a single pyrenoid and a pair of anterior pseudoflagella that project toward the colony edge. Asexual reproduction occurs by zoospores, akinetes, and colony fragmentation; sexual reproduction via isogamous gametes has been reported for two species.

Remarks: *Tetraspora* is typically attached in stream systems and is a common and widespread genus.

Class Chlorophyceae: Order Oedogoniales

Bulbochaete C. Agardh (Fig. 3.1k)

Bulbochaete consists of uniseriate filaments that are unilaterally branched and usually attached by holdfast cells. Cells of the filaments are typically broader at the anterior end and many bear a colorless, elongated terminal hair cell with a swollen base (one of the most distinctive features of the genus). Cells each contain a parietal, reticulate chloroplast with several pyrenoids. Asexual reproduction occurs by akinetes, fragmentation of filaments or by zoospores with a distinctive, apical ring of flagella; sexual reproduction is oogamous, with female cells dividing to form the oogonium and two supporting (suffultory) cells, with dwarf male filaments produced in some species (nannandrous) and others directly producing antheridia. Cell division like for *Oedogonium* and resulting in "apical rings."

Remarks: *Bulbochaete* is a common genus that is most often found growing epiphytically and usually in slower-flowing waters. Much research remains to be completed to clarify the systematics of the Oedogoniales using molecular data; published studies thus far suggest that *Bulbochaete* is indeed a distinct genus from the other members of the order (Buchheim et al. 2001; Mei et al. 2007).

Oedocladium Stahl (Fig. 3.1l)

Oedocladium is a heterotrichous alga with branching on all sides of the filament. Cells are cylindrical in shape and have a single, parietal, reticulate chloroplast, and several pyrenoids. Cell division occurs most commonly in the apical cells and is of the same type as reported for *Bulbochaete* and *Oedogonium*. Asexual reproduction by multiflagellate zoospores, akinetes or fragmentation of the filament; sexual reproduction as for *Oedogonium*.

Remarks: *Oedocladium* can be either terrestrial or freshwater; thalli in the former have colorless and hyaline cells growing subterraneously. Molecular analyses suggest that *Oedocladium* may not be a distinct genus from *Oedogonium* (Mei et al. 2007), but further research is necessary for confirmation.

Oedogonium Link ex Hirn (Fig. 3.1m)

Oedogonium consists of unbranched filaments of cylindrical cells (which may be slightly broader at the anterior end), and are usually attached. Cells are characterized by one-to-many ring-like caps directly adjacent to the cross-wall, and possess a reticulate and parietal chloroplast that can have one or more pyrenoids. Asexual reproduction occurs by the production of zoospores (one per cell, and distinctive in having an apical ring of flagella), aplanospores, akinetes, and fragmentation of filaments; sexual reproduction is oogamous with female cells forming oogonia after division to separate the supporting (or suffultory) cell, and males as short, disk-like antheridia. Sexual reproduction is termed either nannandrous (with dwarf males—short antheridium-producing filaments attached near oogonia) or macrandrous (lacking dwarf males).

Remarks: *Oedogonium* is a very common green alga that can be attached to various substrata, including macrophytic vegetation, or free-living. The ~250 species are usually discerned based on characters pertaining to sexual reproduction, which can be rare. Molecular research thus far suggests a separation of the dioecious nannandrous taxa from the monoecious taxa (Mei et al. 2007).

Class Chlorophyceae: Order Sphaeropleales

Hydrodictyon Roth (Fig. 3.1n)

Thallus consists of a macroscopic, coenobial reticulate mesh of five- or six-sided polygons with each cell attached to two others at its end walls. Cells are cylindrical or slightly inflated in shape. Cells are multinucleate and possess a single chloroplast that is parietal and plate like with a single pyrenoid in young cells, and reticulate with multiple pyrenoids in older cells, surrounding a central vacuole. Asexual reproduction occurs via production of biflagellated zoospores that align and elongate to form a new colony (autocolony formation); sexual reproduction occurs via isogamous, biflagellate gametes that unite to form a zygote; the zygote loses its flagella and becomes a zygospore, which undergoes meiosis to form a zoospore and eventually the polyhedral stage of the alga.

Remarks: *Hydrodictyon* is a common and sometimes abundant alga that can grow to nuisance levels and is distributed in tropical and temperate regions. Four species of *Hydrodictyon* are currently recognized; molecular data representing three of these supports their recognition as distinct species (Buchheim et al. 2005; McManus and Lewis 2011).

Microspora Thuret (Fig. 3.1o)

Plants either floating or attached basally, thallus filamentous and uniseriate. Filaments constructed of "H" walls; having a bipartite structure that can typically be discerned with the light microscope. Cell shape varies from cylindrical to quadrate and sometimes slightly inflated, cell walls can be slightly lamellate. Each cell with a single chloroplast, lacking pyrenoids, which can be finely or coarsely reticulate. Asexual reproduction by biflagellate zoospores, aplanospores, and akinetes; sexual reproduction via biflagellate isogametes.

Remarks: *Microspora* is a widely distributed alga in freshwater habitats, with some species abundant in low pH environments. The genus can be easily confused with the tribophyte genus *Tribonema* (see Chap. 7) which is similar in structure but distinguished by having two or more discoid chloroplasts and lacking true starch.

Pediastrum Meyen (Fig. 3.2a)

Thallus a coenobium, composed of 4–64 (–128) cells, arranged in a monostromatic circular to oval layer. Cell shape highly variable; interior cells typically polyhedral with four or more sides, peripheral cells similar to those of the interior or with one to two lobes or processes. Cells of the colony can be completely contiguous with each other, or with gaps. Cell walls can be either smooth or ornamented. The multinucleate cells possess a single, parietal chloroplast, with one or more pyrenoids. Asexual reproduction via coenobium production from biflagellate zoospores, or by thick-walled resting spores; sexual reproduction infrequently reported but by isogamous, biflagellate gametes.

Remarks: *Pediastrum* is planktonic, but is a widespread genus and can occur in streams. Recent molecular work has demonstrated that *Pediastrum* is composed of a series of evolutionary lineages (Buchheim et al. 2005; McManus and Lewis 2011), which are beginning to be recognized at the generic level based on molecular and morphometric analyses (*Monactinus*, *Parapediastrum*, *Pseudopediastrum*, *Sorastrum*, and *Stauridium*) (Buchheim et al. 2005; McManus et al. 2011).

Scenedesmus Meyen (Fig. 3.2b)

Thallus a coenobium, composed of 4–32 elongated cells laterally joined in a linear or alternating series. Cell shape varies from ellipsoid to ovoid, crescent-shaped or elongated and tapering. Cell walls of *Scenedesmus* are smooth and lacking in spines. Cells possess a single parietal chloroplast and usually one pyrenoid. Asexual reproduction occurs via autospore production (2–32 per sporangium and usually arranged as a single coenobium); sexual reproduction presumably rare, but occurs via isogamous biflagellate gametes.

Remarks: *Scenedesmus* is planktonic, but is a widespread genus and can occur in streams. Previously recognized subgenera (*Desmodesmus* and *Scenedesmus*) were demonstrated to represent monophyletic lineages with relatively high divergence,

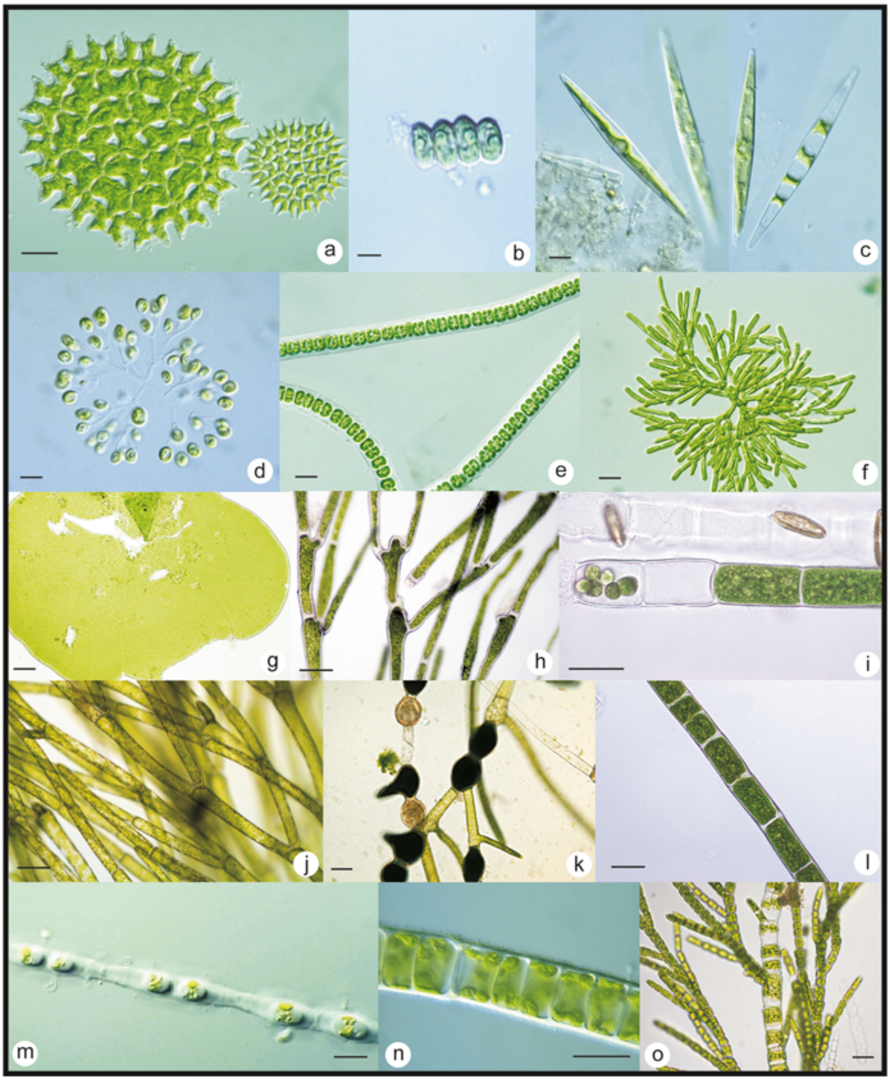

Fig. 3.2 (**a**) *Pediastrum*. (**b**) *Scenedesmus*. (**c**) *Closteriopsis*. (**d**) *Dictyosphaerium*. (**e**) *Geminella*. (**f**) *Microthamnion*. (**g**) *Prasiola*. (**h**) *Aegagropila*. (**i**) *Arnoldiella*. (**j**) *Cladophora*. (**k**) *Pithophora*. (**l**) *Rhizoclonium*. (**m**) *Binuclearia*. (**n**) *Ulothrix*. (**o**) *Cloniophora*. Scale bars: (**h**) = 150 μm; (**g**, **j**) = 100 μm; (**k**, **l**) = 80 μm; (**i**) = 60 μm; (**a**) = 25 μm; (**o**) = 20 μm; (**e**, **f**, **n**) = 15 μm; (**d**, **m**) = 10 μm; (**b**, **c**) = 8 μm. Image authors: (**a**, **c**–**f**, **n**) Y. Tsukii; (**g**) F. Rindi; (**h**) I. Bárbara; (**j**) C. Carter; (**k**) P. Škaloud; (**m**) P. York

and were proposed as separate genera (An et al. 1999). Paraphyly of *Scenedemus* (Hegewald and Wolf 2003) and the discovery of high molecular diversity within morphospecies (Vanormelingen et al. 2007) further illustrate the need for additional systematic research on this, and other related genera of coenobial green algae.

Class Trebouxiophyceae: Order Chlorellales

Closteriopsis Lemmermann (Fig. 3.2c)

Unicellular, needle-like algae with sharply tapered apices and lacking a mucilaginous envelope. Cells can be straight or curved. Cells possess a single chloroplast that can be parietal or axial in position, and ribbon-like, band-shaped or spirally twisted in shape, with multiple pyrenoids in a series. Asexual reproduction by autospores; sexual reproduction unknown.

Remarks: *Closteriopsis* is planktonic and widespread in distribution. Three species of *Closteriopsis* are currently recognized, and molecular data (nuclear 18S rDNA and chloroplast 16S rDNA) indicated the affinity of this genus with other members of the Chlorellales within the Trebouxiophyceae, rather than with the Chlorophyceae (Ustinova et al. 2001).

Dictyosphaerium Nägeli (Fig. 3.2d)

Thallus consists of unattached, spherical or irregularly shaped colonies that are formed by a series of clusters of four cells attached by cell wall material, and encased in a common mucilaginous envelope. Clusters of cells are attached via thin stalks and radiate from the center of the colony. Cells range in shape from spherical to ovoid, ellipsoid or cylindrical. Cells with one to two parietal, cup-shaped chloroplasts, each with a single pyrenoid. Asexual reproduction occurs via autospore production; sexual reproduction rarely reported but oogamous, with an elongated and biflagellate male gamete.

Remarks: *Dictyosphaerium* is planktonic or present in the metaphyton of freshwaters, and is very widely distributed. Paraphyly of the genus *Dictyosphaerium* was recently demonstrated (Krienitz et al. 2010), and several additional genera have been described in an effort to recognize monophyletic lineages (e.g., *Hindakia*—Bock et al. 2010; *Mucidosphaerium*—Bock et al. 2011).

Geminella Turpin (Fig. 3.2e)

Thallus consists of attached or free-floating uniseriate filaments (or, more accurately, pseudofilaments), with cells separated from one another but in a linear arrangement and surrounded by a thick mucilaginous sheath. Cells equidistant or in pairs, cylindrical, inflated, ellipsoidal, or ovoid in shape, each with a parietal band-shaped or laminate chloroplast (often restricted to the central section of the cell) and with a single pyrenoid. Asexual reproduction via fragmentation of filaments or thick-walled akinetes; sexual reproduction unknown.

Remarks: widespread in distribution and known from a variety of freshwater habitats; especially common in low pH habitats. DNA sequence analyses demonstrated a clear alliance of the genus with the Trebouxiophyceae rather than the Chlorophyceae, where it was previously classified (Durako 2007; Mikhailyuk et al. 2008).

Class Trebouxiophyceae: Order Microthamniales

Microthamnion Nägeli (Fig. 3.2f)

Thallus microscopic and consisting of an erect system of branched, uniseriate filaments that terminate in obtuse cells, attached by a mucilage pad. Branching pattern is characteristic of the genus with branches arising toward the distal end of cells. Cells are cylindrical in shape, with a single parietal chloroplast lacking pyrenoids. Asexual reproduction occurs via biflagellate zoospores; sexual reproduction and reproduction via akinetes and aplanospores are unconfirmed.

Remarks: *Microthamnion* occurs on a variety of benthic substrata.

Class Trebouxiophyceae: Order Prasiolales

Prasiola Meneghini (Fig. 3.2g)

Prasiola is a large and morphologically complex trebouxiophycean green alga that inhabits marine, freshwater and terrestrial environments. The freshwater species are found exclusively in clear, fast-flowing streams, often at high elevation. The thalli of the freshwater species are leafy, monostromic blades (rarely distromatic) that can be lobed or ruffled along their margins (typically 1–20 cm in length), occasionally ribbon like. The genus is readily recognizable by the cell arrangements of the thalli—cells are arranged in square or rectangular blocks of four or more; each cell has a single, stellate chloroplast with a central pyrenoid.

Remarks: freshwater species of *Prasiola* reproduce either by aplanospores, which are evident in thickened regions of the thallus, or by oogamous sexual reproduction in which the edges of the thallus develop patches of cells that produce either biflagellate male gametes or nonflagellated egg cells. Stream-inhabiting species of *Prasiola* are known from the Canadian Arctic to the tropics. Much research remains to be completed on the phylogeny of *Prasiola*, and especially the freshwater species (Rindi et al. 2007).

Class Ulvophyceae: Order Cladophorales

Aegagropila Kützing (Fig. 3.2h)

Thalli macroscopic and stiff, composed of irregularly branched filaments. Branching frequently lateral in angle and subterminal in origin, and more than one branch can originate from a cell. Rhizoidal branches sometimes produced from basal portions of cells. Cell division is primarily apical but sometimes intercalary. Numerous chloroplasts per cell form a parietal network, and contain pyrenoids. Asexual reproduction occurs through thallus fragmentation; sexual reproduction unknown. Remarks: *Aegagropila* is a widespread green alga that can form hemispherical clumps or dense mats of filaments; the range of morphological variation within the genus corresponds to only 0.1–0.5 % nucleotide variation for the nuclear ITS region (Boedeker et al. 2010). *Aegagropila* has been variously recognized as a distinct genus and as part of *Cladophora*, but 18S rDNA data established its position as a distinct entity (Hanyuda et al. 2002).

Arnoldiella V.V. Mill emend. Boedeker (=*Basicladia* W.E. Hoffmann and Tilden) (Fig. 3.2i)

Thallus heterotrichous with a prostrate layer of coalescing filaments and an upright portion of compact and rigid filaments. Degree of branching varies for the upright thallus portion, but becoming more abundant in apical regions. Branches arising subterminally or with a pseudodichotomous pattern. Cells becoming shorter and wider in the apical regions of the thallus. Numerous chloroplasts per cell form a parietal network, and contain pyrenoids. Asexual reproduction by flagellated zoospores that are produced in cells at the ends of filaments, and akinetes; sexual reproduction unknown.

Remarks: *Arnoldiella* is found growing on the shells of turtles or bivalves, or on *Cladophora* or hard substrata. *Arnoldiella* was recently emended and most species of *Basicladia* were transferred to this genus, based on a combination of molecular phylogenetic analyses and transmission electron microscopy (Boedeker et al. 2012).

Cladophora Kützing (Fig. 3.2j)

Thalli macroscopic, consisting of sparsely to abundantly branched uniseriate filaments, attached by a discoid or rhizoidal holdfast, or free-living, with primarily apical but sometimes intercalary cell divisions. Cells cylindrical or somewhat inflated, tending to be longer in sparsely branched forms. Branching irregular or pseudodichotomous. Chloroplasts parietal and reticulate with numerous pyrenoids. Asexual reproduction via bi- or quadriflagellate zoospores, rarely by akinetes; sexual reproduction by isogamous biflagellate gametes.

Remarks: *Cladophora* is largely a marine genus, but the freshwater species *C. glomerata* is one of the most cosmopolitan freshwater algal species worldwide. Members of the genus are recognized as "ecosystem engineers" for their role in hosting functional microflora (Zulkifly et al. 2013). Macroscopic growth forms vary widely, from small attached thalli, to large streaming mats. Some degree of tolerance to increased salinity has been demonstrated for *C. glomerata* specimens from Japan (Hayakawa et al. 2012).

Pithophora Wittrock (Fig. 3.2k)

Thallus macroscopic, consisting of uniseriate branched filaments that are free floating. Filaments freely branching, with branches arising subterminally at an almost right angle. Branches can be solitary or opposite. Filaments differ from *Cladophora* in having large akinetes (solitary, in pairs or in short chains) in terminal and intercalary positions, and in cells being longer at the ends of branches than at the base. Cells cylindrical, usually thick walled, each with a parietal reticulate chloroplast and multiple pyrenoids. Asexual reproduction via thallus fragmentation and production of akinetes; sexual reproduction unknown.

Remarks: *Pithophora* is widespread in the tropics and subtropics, and has recently been shown to consist of a single, broadly distributed species (*P. roettleri*) (Boedeker et al. 2012).

Rhizoclonium Kützing (Fig. 3.2l)

Thallus composed of uniseriate, mostly unbranched filaments (occasionally bearing short, rhizoidal branches). Each cell possesses a parietal reticulate chloroplast with several pyrenoids. Cells cylindrical, at least twice as long as broad, sometimes with thick and lamellate walls. Asexual reproduction occurs via thallus fragmentation, akinetes, or the production of biflagellate zoospores; sexual reproduction unknown in freshwater forms.

Remarks: *Rhizoclonium* is a widespread genus in freshwaters and frequently occurs in streams. Molecular phylogenetic work indicates that the genus is polyphyletic and in need of taxonomic revision (Hanyuda et al. 2002; Ichihara et al. 2013).

Class Ulvophyceae: Order Ulotrichales

Binuclearia Wittrock (Fig. 3.2m)

Thallus composed of uniseriate and unbranched filaments, surrounded by a thick mucilaginous sheath, attached or free living. Cells cylindrical to ellipsoid in shape and with rounded apices. Cells commonly in pairs following cytokinesis, and with their own mucilage envelope, separating more widely as they mature; older cross-walls becoming thick and lamellated and daughter cells giving rise to "H"-shaped sections. Each cell with a parietal, band-shaped chloroplast with a single, difficult to discern, pyrenoid. Asexual reproduction by fragmentation, akinetes, aplanospores, or quadriflagellate zoospores; sexual reproduction unknown.

Remarks: *Binuclearia* is widespread in low pH, soft waters.

Ulothrix Kützing (Fig. 3.2n)

Thallus composed of unbranched uniseriate filaments that are attached by a basal cell (which can be rhizoidal). Cells cylindrical or bead shaped, walls thin in young plants and thick in older plants. Each cell with a single parietal band-shaped chloroplast that can mostly or completely encircle the cell, and with a single pyrenoid. Asexual reproduction by fragmentation, akinetes, aplanospores, or quadriflagellate zoospores; sexual reproduction by isogamous biflagellate gametes. The multicellular filamentous gametophyte stage alternates with a unicellular sporophyte known as the *Codiolum* stage.

Remarks: *Ulothrix* is a widespread genus in marine and brackish waters and is occasionally reported from flowing water habitats. Although a few *Ulothrix* sequences have been generated (e.g., Hayden and Waaland 2002; O'Kelly et al. 2004), the genus awaits a thorough molecular systematic investigation.

Class Ulvophyceae: Order Ulvales

Cloniophora Tiffany (Fig. 3.2o)

Thallus composed of uniseriate filaments and characterized by the cells of the secondary branches being very short in contrast to those of the primary branches, which tend to be much longer than broad. Branching irregular, and the thallus attached by downwardly growing rhizoids. Apical cells of secondary branches conical or bluntly rounded. Cells cylindrical, inflated or capitate, each with a single parietal chloroplast and one or more pyrenoids. Asexual reproduction by biflagellate zoospores; sexual reproduction unknown.

Remarks: *Cloniophora* is generally considered a tropical to subtropical genus, where it is common in fast-flowing streams, although its distribution does include some temperate areas. Until recently, the genus was considered to be a member of the Chaetophorales; however, both molecular and morphological analyses have supported its transfer to the Ulvales (Carlile et al. 2011).

Phylum Streptophyta

Class Charophyceae: Order Charales

Chara Linnaeus (Fig. 3.3a)

Thallus macroscopic, usually lime-encrusted, composed of branched uprights and attached by branched, colorless rhizoids. The primary axis is indeterminate, formed through division of the basal part of the apical cell, and is composed of alternating node and internode cells. Nodes bear a whorl of determinate branchlets, 6–16 in

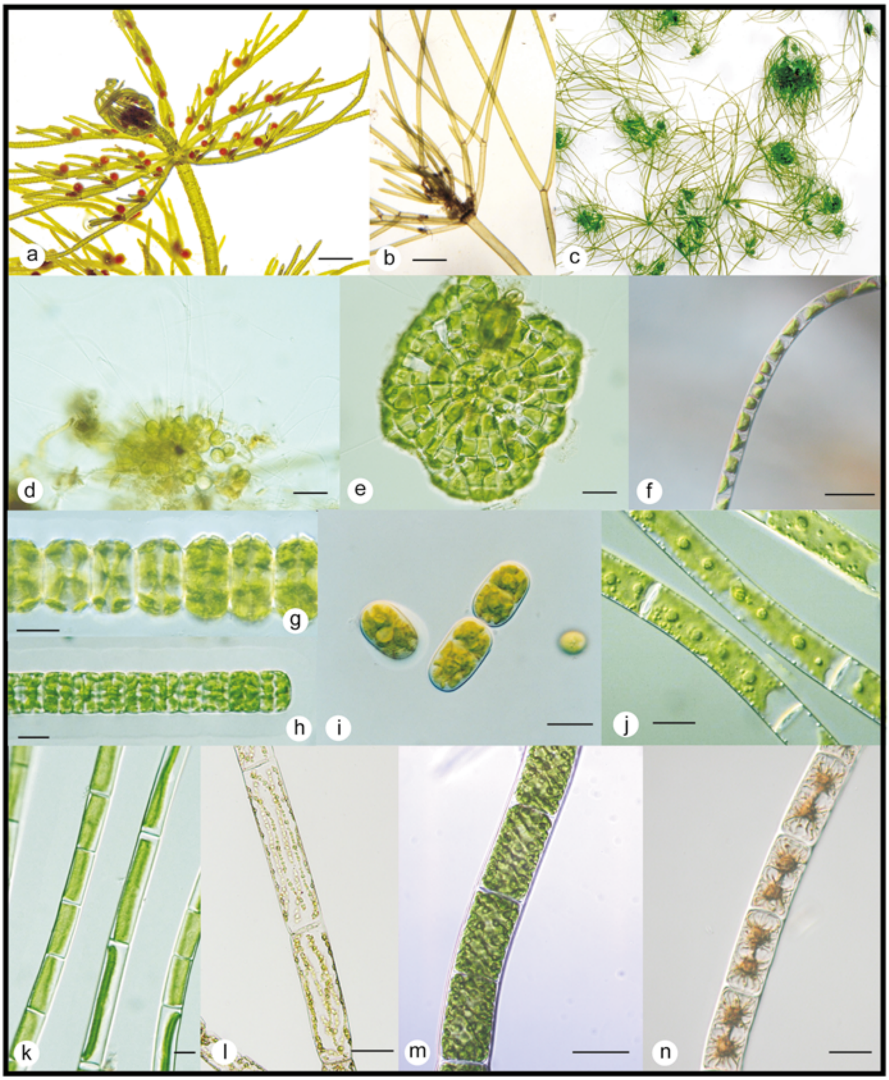

Fig. 3.3 (**a**) *Chara*. (**b**) *Nitella*. (**c**) *Tolypella*. (**d**) *Chaetosphaeridium*. (**e**) *Coleochaete*. (**f**) *Klebsormidium*. (**g**) *Desmidium*. (**h**) *Hyalotheca*. (**i**) *Cylindrocystis*. (**j**) *Mougeotia*. (**k**) *Mougeotiopsis*. (**l**) *Sirogonium*. (**m**) *Spirogyra*. (**n**) *Zygnema*. Scale bars: (**a**–**c**) = 1 cm; (**e**, **l**) = 30 µm; (**d**, **h**, **k**, **m**) = 25 µm; (**f**, **i**, **n**) = 20 µm; (**g**, **j**) = 15 µm. Image authors: (**a**, **c**) C. Carter; (**b**) R. Sheath; (**d**–**g**, **i**, **j**, **n**) Y. Tsukii; (**h**) P. Škaloud; (**k**) J. Brand

number, unbranched, and can be corticate or ecorticate. One or two tiers of stipulodes are present at the base of each node, as are rings of unicellular bract cells at nodes. Internodal cells can elongate to several centimeters in length and are corticate or ecorticate, and can bear single or clustered spinous cells. Asexual reproduction by vegetative propagation of rhizoids, development of buried nodal cells, or by bulbils; sexual reproduction oogamous with gametes produced in multicellular antheridia and oogonia at branchlet nodes.

Remarks: *Chara* can be abundant in hard and alkaline waters, most commonly in lakes and ponds, but is occasionally found in flowing waters. Some sequence data have been generated for members of the genus (e.g., Sanders et al. 2003; Kato et al. 2008), but this species-rich genus awaits thorough molecular systematic revision.

Nitella C. Agardh (Fig. 3.3b)

Thallus macroscopic, usually not lime-encrusted or only lightly so, composed of regularly and symmetrically branched uprights and attached by branched, colorless rhizoids. The primary axis forms through division of the basal part of the apical cell, and is composed of alternating node and internode cells, with the internodes being greatly elongated in comparison to the nodes. Nodes bear a whorl of four or more determinate ecorticate branchlets; branchlets with 3–4 orders of di- or trichotomous branching and acuminate tips. Stipulodes absent. Indeterminate axes up to two or more per node, forming in branchlet axils. Internodal cells can elongate to several centimeters in length and are ecorticate. Asexual reproduction by vegetative propagation; sexual reproduction oogamous with oogonia produced at the forks of branchlets and antheridia produced terminally.

Remarks: *Nitella* can be abundant in softer water areas and lower pH habitats than *Chara*. The phylogeny of *Nitella* based on molecular systematics was investigated by Sakayama et al. (2005, 2006).

Tolypella (A. Braun) A. Braun (Fig. 3.3c)

Thallus macroscopic and not usually heavily lime-encrusted, similar in overall construction to *Nitella*, but with longer branches that are less symmetrical and forming coarse clusters (birds' nests) of branchlets. Branches are ecorticate and lacking spines. Asexual reproduction by fragmentation; sexual reproduction oogamous with oogonia and antheridia in clusters, commonly in the basal parts of branchlets (oogonia with a corona of ten cells in two tiers).

Remarks: *Tolypella* is widespread and relatively common in slow-flowing streams and hard water habitats.

Class Coleochaetophyceae: Order Chaetosphaeridiales

Chaetosphaeridium Klebahn (Fig. 3.3d)

Thallus microscopic, growing epiphytically, endophytically, or planktonically, composed of individual cells (that can appear to be growing in a gelatinous colony) or clusters of cells connected in a series by long, gelatinous tubes. Cells globose or flask-shaped, bearing a single sheathed hair. Cells with one to two parietal, plate-like chloroplasts with a pyrenoid. Asexual reproduction by biflagellate zoospores; sexual reproduction oogamous with large oogonia and smaller, biflagellate male gametes.

Remarks: *Chaetosphaeridium* is widespread and is distributed from the tropics to polar regions. The genus is recognized as a distinct lineage with high DNA sequence divergence compared with other members of the class (Cimino and Delwiche 2002).

Class Coleochaetophyceae: Order Coleochaetales

Coleochaete Brébisson (Fig. 3.3e)

Thallus can exhibit a number of different morphologies, including forms with well-developed prostrate and erect branched systems, only prostrate branched forms, pseudoparenchymatous forms consisting of adherent branched filaments, and parenchymatous forms. Cells commonly with long, basally sheathed hairs. Each cell with a single parietal and plate-like chloroplast with one to two conspicuous pyrenoids. Asexual reproduction by biflagellate zoospores; sexual reproduction oogamous with flask-shaped oogonia and biflagellate male gametes.

Remarks: *Coleochaete* is widespread and commonly grows as an epiphyte on aquatic vegetation. Species with a flattened, discoidal morphology have been demonstrated to be not monophyletic (Delwiche et al. 2002).

Class Klebsormidiophyceae: Order Klebsormidiales

Klebsormidium P.C. Silva, K. Mattox, and W. Blackwell (Fig. 3.3f)

Thallus composed of uniseriate (occasionally biseriate or with cells as doublets) and unbranched filaments that lack apical/basal differentiation. Cells cylindrical or barrel shaped, usually with smooth walls. Each cell possesses a single parietal and plate-like chloroplast of variable shape that encircles at least half of the cell, and with a single pyrenoid. Some species produce "H" walls; having cell walls of bipartite structure. Asexual reproduction occurs by aplanospore or biflagellate zoospore production; sexual reproduction unconfirmed.

Remarks: *Klebsormidium* is an extremely common genus of green algae in freshwater habitats, especially in temperate regions, although tropical records are known. Molecular phylogenetic investigations of the genus have been used to, in part, describe new species from stream habitats (Novis 2006), provide further support for described morphospecies and demonstrate affinity of some strains with other classes of green algae (Sluiman et al. 2008), demonstrate the lack of congruence between morphology and genetics for many members of the genus (Rindi et al. 2008), and illustrate an unexpected amount of evolutionary divergence within the genus (Rindi et al. 2011).

Class Zygnematophyceae: Order Desmidiales

Desmidium C. Agardh ex Ralfs (Fig. 3.3g)

Thalli composed of long, twisted filaments of cells, often with a thick mucilaginous sheath. Cells rectangular in shape, with a shallow (usually) median constriction; elliptical or with three to five angles in apical view. Each semicell with a single chloroplast (stellate in end view) with one to two pyrenoids. Asexual reproduction by cell division; sexual reproduction via conjugation.

Remarks: *Desmidium* is a widespread genus that is typically found in oligotropic, low pH waters. *Desmidium* is closely related to the next taxon covered, *Hyalotheca* (McCourt et al. 2000; Hall et al. 2008a), and recent molecular analyses suggest that the genus is polyphyletic (Gontcharov 2008; Hall et al. 2008b).

Hyalotheca Ehrenberg ex Ralfs (Fig. 3.3h)

Thallus composed of long filaments of cells that are almost always surrounded by a thick mucilaginous sheath. Cells subcylindrical, only slightly constricted or not at all. One chloroplast per semicell, axial in position, stellate in end view, with a central pyrenoid. Asexual reproduction by cell division or aplanospores; sexual reproduction by conjugation (known more rarely).

Remarks: *Hyalotheca* includes several cosmopolitan species that are known from oligotropic and low pH waters. The genus, thus far, appears to be monophyletic based on molecular analyses (Hall et al. 2008a, b).

Class Zygnematophyceae: Order Zygnematales

Cylindrocystis Meneghini ex De Bary (Fig. 3.3i)

Cells usually solitary, occasionally filamentous, or as groups of cells in a gelatinous matrix. Cells short and cylindrical with broadly rounded apices, with smooth walls. Cells with two axial, stellate chloroplasts, each with a central pyrenoid. Chloroplasts can have radiating extensions that are extended to the outer edges of the cell. Asexual reproduction by cell division; sexual reproduction by homothallic or heterothallic conjugation.

Remarks: *Cylindrocystis* is a widespread genus that is most commonly found in low pH waters. The genus was demonstrated to be not monophyletic based on molecular analyses (Gontcharov and Melkonian 2010).

Mougeotia C. Agardh (Fig. 3.3j)

Thallus composed of uniseriate, unbranched filaments of cylindrical cells that are much longer than broad, sometimes with anchoring rhizoids. Cells with one (or rarely two) axial plate-like chloroplasts almost as long as the cell, with pyrenoids usually in a linear series. Asexual reproduction by aplanospores and parthenospores; sexual reproduction by scaliform conjugation (involving cells of two different filaments), or, more rarely, lateral conjugation (involving adjacent cells of a single filament). Remarks: *Mougeotia* is widespread in freshwater habitats, and approximately 138 species are recognized worldwide. Molecular analyses thus far indicate that the genus is monophyletic (Hall et al. 2008a).

Mougeotiopsis Palla (Fig. 3.3k)

Thallus composed of uniseriate, unbranched filaments of cylindrical cells that are somewhat longer than broad. Cells with one axial plate-like (or slightly curved) chloroplast with a thickened and granulated margin, chloroplasts almost as long as the cell, and lacking pyrenoids. Vegetatively very similar to *Mougeotia* except for the features of the chloroplast. Sexual reproduction by isogamous scaliform conjugation. Remarks: *Mougeotiopsis* is much more rarely reported than *Mougeotia*; known from freshwater habitats of low pH.

Sirogonium Kützing (Fig. 3.3l)

Thallus composed of uniseriate filaments of cells that are two to five times as long as broad, and with plane end walls (adjacent cell walls of neighboring cells are flat). Mucilaginous sheath much reduced compared with *Spirogyra* and hence filaments do not feel slippery to the touch. Cells contain two to ten parietal, ribbon-like chloroplasts that are either straight and lying parallel to the long axis of the cell, or spiraled no more than half of a turn from one end of the cell to the other. Asexual reproduction by akinetes; sexual reproduction by scaliform conjugation, but lacking conjugation tubes. Remarks: *Sirogonium* is widespread in freshwater habitats, although not commonly reported. *Sirogonium* is likely not a distinct genus from *Spirogyra* based on molecular phylogenetic investigations (Drummond et al. 2005; Hall et al. 2008a; Chen et al. 2012; Stancheva et al. 2013).

Spirogyra Link (Fig. 3.3m)

Spirogyra is characterized by unbranched, uniseriate filaments containing 1–16 chloroplasts, and with a mucilaginous sheath that results in the filaments feeling slippery to the touch, filaments sometimes attached by rhizoids. Cells may be one to six times as long as broad. Chloroplasts distinctive, ribbon-like in shape and parietal in position, and spiraled through the cell. Degree of spiraling depends on the species, and ranges from less than one to several complete spirals in a cell. Each chloroplast contains several pyrenoids. Nucleus large and positioned centrally, suspended by cytoplasmic strands from the edges of the cell. Adjacent walls of neighboring cells can be either flat (i.e., plane) or folded (i.e., replicate). Species-level identification is highly dependent on characters associated with the process of sexual reproduction, which occurs by either lateral (involving adjacent cells of a single filament) or scaliform (involving cells of two different filaments) conjugation; mature zygospores are also necessary for species-level identification.

Remarks: polyploidy events may have contributed to the taxonomic diversity within the genus (McCourt and Hoshaw 1990), which is substantial (almost 400 species are currently recognized). *Spirogyra* is an extremely common and recognizable genus of green algae that can, under slow-flowing and nutrient-rich conditions, become abundant and mat-forming. Molecular analyses have highlighted substantial variation within the genus that does not always correlate with vegetative morphology, suggesting that the genus *Sirogonium* is not distinct from *Spirogyra* (Drummond et al. 2005; Hall et al. 2008a), and indicating large amounts of cryptic diversity within the genus (Chen et al. 2012; Stancheva et al. 2013).

Zygnema C. Agardh (Fig. 3.3n)

Filaments of *Zygnema* are recognizable by their uniseriate and unbranched nature, and by the presence of two axial stellate chloroplasts in each cell, each with a central pyrenoid. A central nucleus is present between the two chloroplasts. Filaments can be attached in flowing water habitats by rhizoidal extensions. As for *Spirogyra*, species-level identification is highly dependent on characters associated with the process of sexual reproduction, which can occur by lateral (involving adjacent cells of a single filament; rare for *Zygnema*) or scaliform conjugation (involving cells of two different filaments; more common for *Zygnema*); mature zygospores are also necessary for species-level identification. Aplanospores and akinetes are occasionally formed.

Remarks: like *Spirogyra*, the genus is widely distributed and can form large growths. Approximately 120 species are known. Mesospore color was recently found to correlate with molecular clades recovered in analyses of the *cox*3 and *rbc*L gene regions (Stancheva et al. 2012); these same analyses also suggested that *Zygogonium* is likely not distinct from *Zygnema*. Sequence data for the *psb*A gene have also been recently published for a few species (Kim et al. 2012).

Acknowledgments Collection and characterization of some of the green algae illustrated in this chapter was supported by a grant from the U.S. National Science Foundation (DEB-0841734). The following people are thanked for allowing the use of their green algal images: Ignacio Bárbara, William Bourland, Jerry Brand, Chris Carter, David John, Fabio Rindi, Robert Sheath, Pavel Škaloud, Yuuji Tsukii, and Peter York. Many images were originally located on the Protist, UTEX, Natural History Museum and AlgaeBase websites.

References

Allan JD (1995) Stream ecology: structure and function of running waters. Chapman and Hall, London

An SS, Friedl T, Hegewald E (1999) Phylogenetic relationships of *Scenedesmus* and *Scenedesmus*-like coccoid green algae as inferred from ITS-2 rDNA sequence comparisons. Plant Biol 1:418–428

Bock C, Pröschold T, Krienitz L (2010) Two new *Dictyosphaerium*-morphotype lineages of the Chlorellaceae (Trebouxiophyceae): *Heynigia* gen. nov. and *Hindakia* gen. nov. Eur J Phycol 46:267–277

Bock C, Pröschold T, Krienitz L (2011) Updating the genus *Dictyosphaerium* and description of *Mucidosphaerium* gen. nov. (Trebouxiophyceae) based on morphological and molecular data. J Phycol 47:638–652

Boedeker C, Eggert A, Immer A et al (2010) Biogeography of *Aegagropila linnaei* (Cladophorophyceae, Chlorophyta): a widespread freshwater alga with low effective dispersal potential shows a glacial imprint in its distribution. J Biogeogr 37:1491–1503

Boedeker C, O'Kelly CJ, Star W et al (2012) Molecular phylogeny and taxonomy of the Aegagropila clade (Cladophorales, Ulvophyceae), including the description of Aegagropilopsis gen. nov. and Pseudocladophora gen. nov. J Phycol 48:808–825

Brouard J-S, Otis C, Lemieux C et al (2011) The chloroplast genome of the green alga *Schizomeris leibleinii* (Chlorophyceae) provides evidence for bidirectional DNA replication from a single origin in the Chaetophorales. Genome Biol Evol 3:505–515

Buchheim MA, Michalopulos EA, Buchheim JA (2001) Phylogeny of the Chlorophyceae with special reference to the Sphaeropleales: a study of 18S and 26S rDNA data. J Phycol 37:819–835

Buchheim M, Buchheim J, Carlson T et al (2005) Phylogeny of the Hydrodictaceae (Chlorophyceae): inferences from rDNA data. J Phycol 41:1039–1054

Buchheim MA, Sutherland DM, Schleicher T et al (2011) Phylogeny of the Oedogoniales, Chaetophorales and Chaetopeltidales (Chlorophyceae): inferences from sequence-structure analysis of ITS2. Ann Bot 107:109–116

Caisová L, Marin B, Sausen N et al (2011) Polyphyly of *Chaetophora* and *Stigeoclonium* within the Chaetophorales (Chlorophyceae), revealed by sequence comparisons of nuclear-encoded SSU rRNA genes. J Phycol 47:164–177

Caisová L, Marin B, Melkonian M (2013) A consensus secondary structure of ITS2 in the Chlorophyta identified by phylogenetic reconstruction. Protist 164:482–496

Carlile AL, O'Kelly CJ, Sherwood AR (2011) The green algal genus Cloniophora represents a novel lineage in the Ulvales: a proposal for Cloniophoraceae fam. nov. J Phycol 47: 1379–1387

Chen C, Barfuss MHJ, Pröschold T et al (2012) Hidden genetic diversity in the green alga *Spirogya* (Zygnematophyceae, Streptophyta). BMC Evol Biol 12:77

Cimino MT, Delwiche CF (2002) Molecular and morphological data identify a cryptic species complex in endophytic members of the genus *Coleochaete* Bréb. (Charophyta: Coleochaetaceae). J Phycol 38:213–1221

Delwiche CF, Karol KG, Cimino MT et al (2002) Phylogeny of the genus Coleochaete (Coleochaetales, Charophyta) and related taxa inferred by analysis of the chloroplast gene rbcL. J Phycol 38:394–403

Dodds WK (2002) Freshwater ecology: concepts and environmental applications. Academic Press, San Diego

Drummond CS, Hall J, Karol KG et al (2005) Phylogeny of *Spirogyra* and *Sirogonium* (Zygnematophyceae) based on *rbc*L sequence data. J Phycol 41:1055–1064

Durako MR (2007) A reassessment of *Geminella* (Chlorophyta) based upon photosynthetic pigments, DNA sequence analysis and electron microscopy. MS thesis, University of North Carolina, Wilmington

Friedl T, Rybalka N (2012) Systematics of the green algae: a brief introduction to the current status. Prog Bot 73:259–280

Gontcharov AA (2008) Phylogeny and classification of Zygnematophyceae (Streptophyta): current state of affairs. Fottea 8:87–104

Gontcharov AA, Melkonian M (2010) Molecular phylogeny and revision of the genus *Netrium* (Zygnematophyceae, Streptophyta): *Nucleotaenium* gen. nov. J Phycol 46:346–362

Graham LE, Graham JM, Wilcox LW (2009) Algae, 2nd edn. Benjamin Cummings, San Francisco

Guiry MD (2012) How many species of algae are there? J Phycol 48:1057–1063

Guiry MD, Guiry GM (2015) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway, http://www.algaebase.org. Accessed 15 Dec 2015

Hall JD, McCourt RM (2015) Conjugating green algae including desmids. In: Wehr JD, Sheath RG, Kociolek JP (eds) Freshwater algae of North America. Ecology and classification. Academic, San Diego, pp 429–457

Hall JD, Karol KG, McCourt RM et al (2008a) Phylogeny of the conjugating green algae based on chloroplast and mitochondrial nucleotide sequence data. J Phycol 44:467–477

Hall JD, McCourt RM, Delwiche CF (2008b) Patterns of cell division in the filamentous Desmidiaceae, close green algal relatives of land plants. Am J Bot 95:643–654

Hanyuda T, Wakana I, Arai S et al (2002) Phylogenetic relationships within Cladophorales (Ulvophyceae, Chlorophyta) inferred from 18S rRNA gene sequences, with special reference to *Aegagropila linnaei*. J Phycol 38:564–571

Hayakawa Y, Ogawa T, Yoshikawa S et al (2012) Genetic and ecophysiological diversity of *Cladophora* (Cladophorales, Ulvophyceae) in various salinity regimes. Phycol Res 60:86–97

Hayden HS, Waaland JR (2002) Phylogenetic systematics of the Ulvaceae (Ulvales, Ulvophyceae) using chloroplast and nuclear DNA sequences. J Phycol 38:1200–1212

Hegewald E, Wolf M (2003) Phylogenetic relationships of *Scenedesmus* and *Acutodesmus* (Chlorophyta, Chlorophyceae) as inferred from 18S rDNA and ITS-2 sequence comparisons. Plant Syst Evol 241:185–191

Ichihara K, Shimada S, Miyaji K (2013) Systematics of *Rhizoclonium*-like algae (Cladophorales, Chlorophyta) from Japanese brackish waters, based on molecular phylogenetic and morphological analyses. Phycologia 52:398–410

John DM, Rindi F (2015) Filamentous (non-conjugating) and plant-like green algae. In: Wehr JD, Sheath RG, Kociolek JP (eds) Freshwater algae of North America. Ecology and classification. Academic Press, San Diego, pp 375–427

John DM, Whitton BA, Brook AJ (2011) The freshwater algal flora of the British Isles: an identification guide to freshwater and terrestrial algae, 2nd edn. Cambridge University Press, Cambridge

Kato S, Sakayama H, Sano S et al (2008) Morphological variation and intraspecific phylogeny of the ubiquitous species *Chara braunii* (Charales, Charophyceae) in Japan. Phycologia 47:191–202

Kim J-H, Boo SM, Kim YH (2012) Morphology and plastid *psb*A phylogeny of *Zygnema* (Zygnemataceae, Chlorophyta) from Korea: *Z. insigne* and *Z. leiospermum*. Algae 27:225–234

Krienitz L, Bock C, Luo W et al (2010) Polyphyletic origin of the *Dictyosphaerium* morphotype within Chlorellaceae (Trebouxiophyceae). J Phycol 46:559–563

Leliaert F, Smith DR, Moreau H et al (2012) Phylogeny and molecular evolution of the green algae. Crit Rev Plant Sci 31:1–46

Lowe RL, LaLiberte GD (2007) Benthic stream algae: distribution and structure. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology, 2nd edn. Academic, Amsterdam, pp 327–356

McCourt RM, Hoshaw RW (1990) Non-correspondence of breeding groups, morphology, and monophyletic groups in *Spirogyra* (Zygnemataceae: Chlorophyta) and the application of species concepts. Syst Bot 15:69–78

McCourt RM, Karol KG, Bell J et al (2000) Phylogeny of the conjugating green algae (Zygnemophyceae) based on *rbc*L sequences. J Phycol 36:747–758

McManus HA, Lewis LA (2011) Molecular phylogenetic relationships in the freshwater family Hydrodictyaceae (Sphaeropleales, Chlorophyceae), with an emphasis on *Pediastrum duplex*. J Phycol 47:152–163

McManus HA, Lewis LA, Schultz ET (2011) Distinguishing multiple lineages of *Pediastrum duplex* with morphometrics and a proposal for *Lacunastrum* gen. nov. J Phycol 47:123–130

Mei H, Luo W, Liu GX et al (2007) Phylogeny of Oedogoniales (Chlorophyceae, Chlorophyta) inferred from 18S rDNA sequences with emphasis on the relationships in the genus *Oedogonium* based on ITS-2 sequences. Plant Syst Evol 265:179–191

Mikhailyuk TI, Sluiman HJ, Massalski A et al (2008) New streptophyte green algae from terrestrial habitats and an assessment of the genus *Interfilum* (Klebsormidiophyceae, Streptophyta). J Phycol 44:1586–1603

Nakada T, Nozaki H (2015) Flagellate green algae. In: Wehr JD, Sheath RG, Kociolek JP (eds) Freshwater algae of North America. Ecology and classification. Academic Press, San Diego, pp 265–313

Novis P (2006) Taxonomy of *Klebsormidium* (Klebsormidiales, Charophyceae) in New Zealand streams and the significance of low-pH habitats. Phycologia 45:293–301

OKelly CJ, Wysor B, Bellows WK (2004) *Collinsiella* (Ulvophyceae, Chlorophyta) and other ulotrichalean taxa with shell-boring sporophytes form a monophyletic clade. Phycologia 43:41–49

Prescott GW (1951) Algae of the western Great Lakes area, with an illustrated key to the genera of desmids and freshwater diatoms. Wm. C Brown, Dubuque

Pröschold T, Leliaert F (2007) Systematics of the green algae: conflict of classic and modern approaches. In: Brodie J, Lewis J (eds) Unravelling the algae: the past, present, and future of algal systematics. CRC Press (Taylor and Francis Group), Boca Raton, pp 123–153

Rindi F, McIvor L, Sherwood AR et al (2007) Molecular phylogeny of the green algal order Prasiolales (Trebouxiophyceae, Chlorophyta). J Phycol 43:811–822

Rindi F, Guiry MD, López-Bautista J (2008) Distribution, morphology, and phylogeny of *Klebsormidium* (Klebsormidiales, Charophyceae) in urban environments in Europe. J Phycol 44:1529–1540

Rindi F, Mikhailyuk TI, Sluiman HJ et al (2011) Phylogenetic relationships in *Interfilum* and *Klebsormidium* (Klebsormidiophyceae, Streptophyta). Mol Phylogenet Evol 58:218–231

Sakayama H, Miyaji K, Nagumo T et al (2005) Taxonomic re-examination of 17 species of *Nitella* subgenus *Tieffallenia* (Charales, Charophyceae) based on internal morphology of the oospore wall and multiple DNA marker sequences. J Phycol 41:195–211

Sakayama H, Arai S, Nozaki H et al (2006) Morphology, molecular phylogeny and taxonomy of *Nitella comptonii* (Charales, Characeae). Phycologia 45:417–421

Sanders ER, Karol KG, McCourt RM (2003) Occurrence of *matK* in a *trnK* Group II intron in charophyte green algae and phylogeny of the Characeae. Am J Bot 90:628–633

Sheath RG, Vis ML (2015) Red algae. In: Wehr JD, Sheath RG, Kociolek JP (eds) Freshwater algae of North America. Ecology and classification. Academic Press, San Diego, pp 237–264

Shubert LE, Gärtner G (2015) Nonmotile coccoid and colonial green algae. In: Wehr JD, Sheath RG, Kociolek JP (eds) Freshwater algae of North America. Ecology and classification. Academic Press, San Diego, pp 315–373

Sluiman HJ, Guihal C, Mudimu O (2008) Assessing phylogenetic affinities and species delimitations in Klebsormidiales (Streptophyta): nuclear-encoded rDNA phylogenies and ITS secondary structure models in *Klebsormidium*, *Hormidiella*, and *Entransia*. J Phycol 44:183–195

Stancheva R, Hall JD, McCourt RM, Sheath RG (2012) Systematics of the genus *Zygnema* (Zygnematophyceae, Charophyta) from Californian watersheds. J Phycol 48:409–422

Stancheva R, Hall JD, McCourt RM et al (2013) Identity and phylogenetic placement of *Spirogyra* species (Zygnematophyceae, Charophyta) from California streams and elsewhere. J Phycol 49:588–607

Stevenson RJ, Bothwell ML, Lowe RL (1996) Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego

Tippery NP, Fučiková K, Lewis PO et al (2012) Probing the monophyly of the Sphaeropleales (Chlorophyceae) using data from five genes. J Phycol 48:1482–1493

Ustinova I, Krienitz L, Huss VAR (2001) *Closteriopsis acicularis* (G.M. Smith) Belcher et Swale is a fusiform alga closely related to *Chlorella kessleri* Fott et Nováková (Chlorophyta, Trebouxiophyceae). Eur J Phycol 36:341–351

Vanormelingen P, Hegewald E, Braband A et al (2007) The systematics of a small spineless *Desmodesmus* species, *D. costato-granulatus* (Sphaeropleales, Chlorophyceae), based on ITS2 rDNA sequence analyses and cell wall morphology. J Phycol 43:378–396

Wehr JD, Sheath RG, Kociolek JP (2015) Freshwater algae of North America, ecology and classification. Academic Press, San Diego

Zulkifly SB, Graham JM, Young EB et al (2013) The genus *Cladophora* Kützing (Ulvophyceae) as a globally distributed ecological engineer. J Phycol 49:1–17