

# Systematics of the Green Algae: A Brief Introduction to the Current Status

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**Abstract** Green algae are a monophyletic lineage of Archaeplastida, a supergroup of photosynthetic eukaryotes exclusively originated from primary endosymbiosis. The green algae are divided into two clades, the Chlorophyta and Streptophyta. The Chlorophyta comprises the vast majority of green algae, with three major lineages (Trebouxiophyceae, Ulvophyceae, and Chlorophyceae) forming the “crown group” of Chlorophyta and, as their early offspring, an assemblage of various monophyletic lineages of unicellular prasinophyte algae. Chloroplast phylogenomics and multi-gene phylogenetic analyses not only largely confirmed previous assumptions based on single gene (18S or *rbcL*) analyses, but also revealed novel robust groupings. While a bifurcation of the Chlorophyceae and a clear distinction of four major lineages within the Ulvophyceae have been supported, the internal phylogenetic

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structure and circumscription of Trebouxiophyceae still remain ambiguous. The Streptophyta comprises relatively few algal lineages and embryophytes. The embryophyte land plants are a sister group of streptophyte green algae (Zygnematomyceae or a lineage comprising Zygnematomyceae and Coleochaetophyceae), but transitions of the green algae to the land have taken place several times, even outside the Streptophyta. Progress in green algal systematics at the species level revealed ITS2 rDNA as an appropriate candidate for DNA barcoding and species distinction. Approaches to integrate sequence analyses of several genes with morphology are now state of the art for species delimitations. An improved taxon sampling with consideration of traditional gathered expert knowledge combined with multigene phylogenetic analyses, and improved phylogeny inference methods will be required to clarify areas of ambiguity in the green algal phylogenies. A revisit of morphology is essential to establish synapomorphies for the novel clades in molecular groupings.

## 1 Introduction

Green algae constitute a morphologically and ecologically diverse monophyletic lineage of Archaeplastida (Adl et al. 2005) which also includes embryophytes. Archaeplastida (also referred to as Plantae; Keeling 2004, 2010) is the only supergroup of photosynthetic eukaryotes exclusively originated from primary endosymbiosis. The plastid origin through primary endosymbiosis has been reviewed by a large number of articles, e.g., Bhattacharya et al. (2004), Reyes-Prieto et al. (2007), Baldauf (2008), Gould et al. (2008), Archibald (2009b), and Keeling (2010).

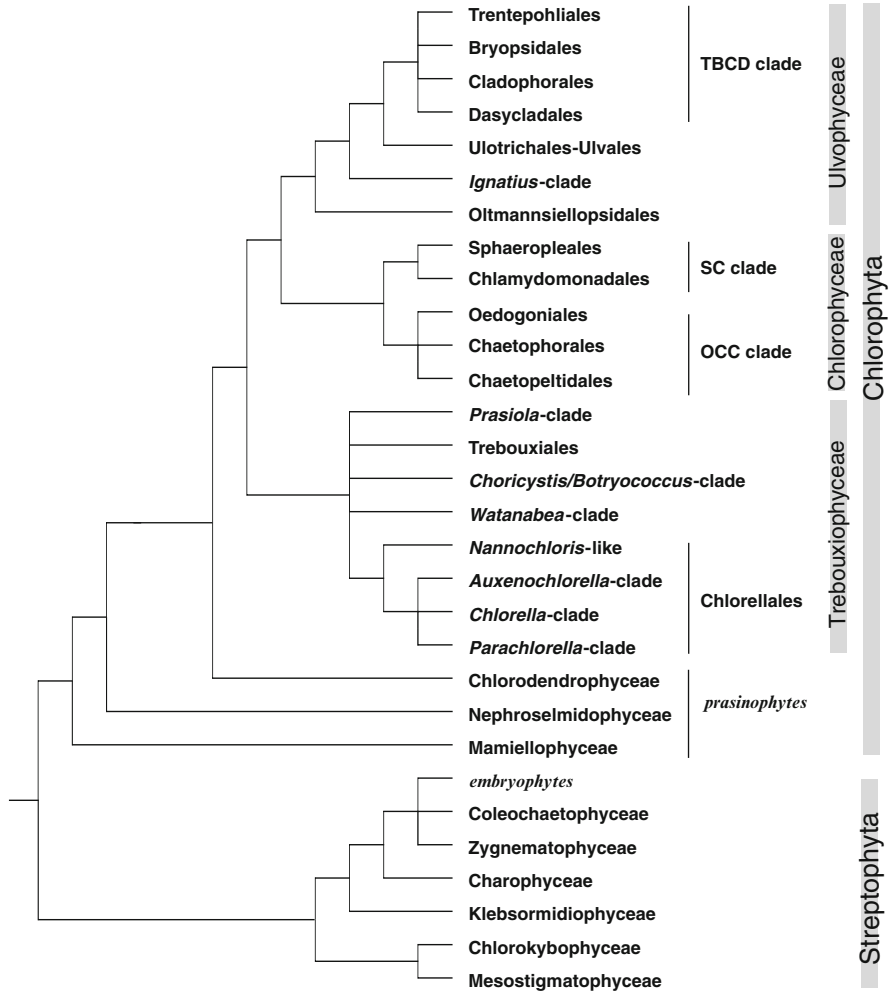
The Viridiplantae, to which all green algae and the embryophytes belong, the Rhodophyta, and the Glaucophyta form the Archaeplastida. The phylum Rhodophyta is often regarded as a sister group to Viridiplantae. The monophyletic origin of Archaeplastida has been supported by nuclear and chloroplast multigene analyses (Rodríguez-Ezpeleta et al. 2005; Archibald 2009b). Green algae share most of their features with embryophytes, including chloroplast structures, pigmentation, cell wall composition, and a characteristic stellate structure in the transition zone between flagellum and basal body (for review, see Lewis and McCourt 2004; Leliaert et al. 2011). Apart from being mostly not of true multicellular organization (see Coleochaetophyceae and Charophyceae; Leliaert et al. 2011) and often confined to aqueous habitats, it is often difficult to delimit the green algae from embryophytes without consideration of their very diverse gross morphologies. Morphological variation of green algae spans from the smallest known eukaryote (the prasinophyte *Ostreococcus*) and tiny flagellates to giant unicells with multiple nuclei or multicellular forms reminiscent of bryophyte gametophytes (*Coleochaete*). The majority of green algae thrive in freshwater or terrestrial habitats, but some microscopic forms (prasinophytes) are abundant in marine phytoplankton. Macroscopic marine forms are only known from the Ulvophyceae. It is typical for green algae to live in various terrestrial habitats (Holzinger 2009). Among green

algae, there are many “land plants,” i.e., transitions to the land happened many times in the evolution of Chlorophyta and Streptophyta (Lewis and Lewis 2005; Lewis 2007). Examples for terrestrial green algal life are the biofilms of building facades (Barberousse et al. 2006, 2007), biological soil crusts (Smith et al. 2004; Büdel et al. 2009), or algal crusts on tree bark (Lüttge and Büdel 2010). Excellent reviews on the peculiarities of terrestrial green algae have been presented by López-Bautista et al. (2007) and Rindi (2011). Green algae, especially a variety of members of Trebouxiophyceae, are frequently involved in symbioses with ciliates and metazoa (for review, see Pröschold et al. (2011) and references therein) as well as lichenized fungi, where they are the dominating photobionts (review: Friedl and Büdel 2008).

The Viridiplantae are divided into two major clades, the phyla Chlorophyta and Streptophyta (Lewis and McCourt 2004; Petersen et al. 2006; Pröschold and Leliaert 2007). The vast majority of green algae belongs to the Chlorophyta, whereas the Streptophyta comprise relatively few algal lineages and embryophytes. The embryophytes are a sister group to certain assemblage of streptophyte green algae (recent reviews: Turmel et al. 2007; Becker and Marin 2009; Wodniok et al. 2011). With respect to the phylogeny of the Chlorophyta, recent work confirmed that an array of distinct lineages of prasinophyte green algae (formerly assigned to a single class “Prasinophyceae”) forms the most basal divergences and that four classes, the Chlorodendrophyceae (prasinophyte green algae), Trebouxiophyceae, Chlorophyceae, and Ulvophyceae form the core of Chlorophyta (Turmel et al. 2007; Marin and Melkonian 2010). The current view, which appears to become more and more substantiated particularly from chloroplast phylogenomics (Turmel et al. 2009a, b), supports the assumption that the Trebouxiophyceae emerged before Chlorophyceae and Ulvophyceae (Fig. 1). Therefore, this particular subdivision into three major chlorophytean classes may be called the “TUC crown group” of Chlorophyta (Pombert et al. 2005; Fig. 1). While the single origin of Chlorophyceae is not disputed, the monophyly of Ulvophyceae has only recently been robustly assessed (Cocquyt et al. 2010), but a sufficient evidence for the monophyly of Trebouxiophyceae is still lacking, and its circumscription not fully understood.

It should be noted that our current view of green algal systematics has been shaped by the intriguing results of molecular phylogenetic analyses which became feasible and widely employed in the 1990s following “traditional” algal systematics based on morphology and ultrastructure. Aspects of the taxonomic history of green algal systematics and evolution have recently been reviewed by Lewis and McCourt (2004) and Pröschold and Leliaert (2007), including a discussion of current knowledge. However, green algal systematics is progressing fast, particularly by analyses of novel data sets consisting of concatenated sequences from many loci of both nuclear and chloroplast genomes, as well as organelle-based phylogenomics. A comprehensive state-of-the-art review of green algal phylogenetics has been presented by Leliaert et al. (2011). Therefore, the intention of the present review is to give a brief introduction into current views of green algal systematics.

There is an important trend to focus on the systematics of green algal genera, i.e., their phylogenetic structures comprising the species. Species descriptions become



**Fig. 1** Simplified schematic consensus phylogeny of the Green Algae. Details of the various clades are discussed in the text. Several lineages of prasinophyte green algae have been omitted for clarity. For the Trebouxiophyceae only those clades that are robustly resolved in 18S rDNA phylogenies and which include several genera are shown

more and more based on several markers and not only on a single gene, 18S, or *rbcL*. Most species-based works in green algae agree on a common molecular marker, i.e., ITS2 rDNA to unequivocally discriminate species (e.g., Müller et al. 2007; Coleman 2009). Certain nucleotide changes in ITS2 (CBCs), when mapped on the secondary structure model, which contains segments largely conserved over phylogenetic distances exceeding genera and families, help to guide decisions of what to include or exclude in a green algal species (Coleman 2003, 2007, 2009; Schultz et al. 2005). ITS2 rDNA is often discussed as the ideal candidate for a DNA

barcode within green algae because there are many examples for its successful application in different major lineages of Chlorophyta (e.g., Pröschold et al. 2005, 2011; Luo et al. 2010) as well as the streptophyte green algae Klebsormidiophyceae (e.g. Rindi et al. 2011). ITS2 rDNA has even been suggested as a “double-edged tool” which is valuable from species to order levels or even higher (Coleman 2003). ITS2 sequence analyses have successfully been employed to assess the monophyly of Sphaeropleales within the Chlorophyceae, even more robustly than 18S rDNA. An automated data analysis approach based on a large (>1,500 sequences) ITS2 data set with a secondary structure-based alignment demonstrated the power to reconstruct evolutionary patterns for highly divergent lineages at the levels of orders and classes (Buchheim et al. 2011).

## 2 Prasinophyte Green Algae

Prasinophytes represent the earliest branches of the Chlorophyta and are also a morphologically heterogeneous assemblage of green algae (for reviews, see Nakayama et al. 1998, 2007; Turmel et al. 2009a; Marin and Melkonian 2010). Most prasinophycean algae are unicellular flagellates possessing a scaly covering and having an asymmetrical cell architecture. Some species lack flagella, others lack scales, and in some cases, both flagella and scales are absent, e.g., in *Ostreococcus tauri*, which is the smallest known eukaryote (Turmel et al. 2009a; Yamaguchi et al. 2011). Coccoid forms may have evolved in several lineages of prasinophytes (Guillou et al. 2004). Most prasinophytes occur in marine habitats where they can be important components of coastal phytoplankton communities (Yamaguchi et al. 2011). Earlier analyses based on 18S rDNA already revealed that there is no monophyletic class “Prasinophyceae” (e.g., Nakayama et al. 1998, 2007). Instead, a paraphyletic assemblage of seven monophyletic groups of prasinophytes have been identified at the base of the Chlorophyta (e.g., Guillou et al. 2004) of which only three have been formally described as independent classes until now, i.e., the Chlorodendrophyceae, Nephroselmidiophyceae, and Mamiellophyceae (Marin and Melkonian 2010; Yamaguchi et al. 2011, and references therein). The position of the Chlorodendrophyceae appears to be basal to, or even within, the radiation of the TUC crown group (Guillou et al. 2004), whereas Nephroselmidiophyceae and Mamiellophyceae occupy rather basal positions within the Chlorophyta (Marin and Melkonian 2010). Prasinophytes are regarded as central to understand evolutionary patterns that accompanied radiation within the Chlorophyta and reduction of cells in some lineages (Turmel et al. 2009a). The whole genomes of two species of *Ostreococcus* (Mamiellophyceae; Palenik et al. 2007; Derelle et al. 2008), the smallest eukaryote, and two strains of *Micromonas* (Mamiellophyceae; Worden et al. 2009) have been sequenced. Evidence for sexual reproduction has been found by genome analyses (Grimsley et al. 2010), despite not being observed in these algae (cryptic sex), which may indicate that the ancestor of Chlorophyta already exhibited sexual reproduction (Archibald

2009a). Full genome analyses also showed that the observed reduction of gene content occurred in conjunction with important changes in cell organization (Turmel et al. 2009a). To date, chloroplast genome data are available for *Nephroselmis*, *Pyramimonas*, *Pycnococcus*, *Monomastix*, and *Ostreococcus* (Turmel et al. 2009a and references therein), and revealed that the ancestor of euglenoid chloroplasts may have been a close relative of the Pyramimonadales lineage (Turmel et al. 2009a), which is probably one of the most basal chlorophytean lineages (Marin and Melkonian 2010). For the green algal origin of plastids of the Chlorarachniophyta, also a prasinophyte, *Tetraselmis* (Chlorodendrophyceae) seems to be a likely candidate (Takahashi et al. 2007). Consequently, prasinophytes may have been involved in two independent secondary endosymbioses (Rogers et al. 2007).

### 3 Trebouxiophyceae

The majority of presently known members of the class are coccoid unicells, in some lineages also colonial coccoids occur. A few lineages may also form filaments, which, however, easily disintegrate (e.g., *Leptosira*, *Stichococcus*). The only known trebouxiophyte genera with firm, often even multiseriate filaments are *Prasiola* and *Rosenvingiella*. Flagellated vegetative forms are not known for the class. Members of Trebouxiophyceae are mostly found in dryer habitats, e.g., in soil, or are aerophytic algae. Many lineages include minute freshwater phytoplankton (e.g., Chlorellales). There are numerous examples for symbioses in ciliates, metazoa (e.g., various species of *Chlorella*, *Micractinium*, *Coccomyxa*, and *Elliptochloris*), and lichens (e.g., *Trebouxia* and *Asterochloris*).

At present, there is consensus that 18S rDNA phylogenies resolve five well-supported clades which comprise multiple genera, i.e., *Prasiola*-clade, Trebouxiales, *Watanabea*-clade, *Choricystis/Botryococcus*-clade, and Chlorellales. There are several other lineages for which only a single species (e.g., *Xylochloris*; Neustupa et al. 2011) or genus (e.g., *Leptosira*, *Lobosphaera*) are known so far. The relationship between these lineages, however, still remains ambiguous.

The *Prasiola*-clade comprises numerous examples of morphological plasticity, which seems to be a characteristic feature of the whole class. Morphologically defined species (morphotypes, morphospecies) may be distributed over several phylogenetic lineages and morphologically rather distinct algae may appear closely related in phylogenetic analyses. For example, *Stichococcus bacillaris*, which forms short filaments that easily disintegrate into cylindrical cells, are distributed over multiple lineages within the clade (Neustupa et al. 2007 and references therein). In 18S rDNA as well as *rbcL*-based phylogenies, species and strains of the microscopic genus *Stichococcus* are the closest relatives of *Prasiola* and *Rosenvingiella*, which are macroscopic filamentous or blade-shaped marine algae, often with tissue-like cell layers (Rindi et al. 2004, 2007). Also for the uniseriate filamentous forms of *Prasiola* and *Rosenvingiella*, a higher genetic diversity has been found than their simple morphology may indicate (Rindi et al. 2004). *Prasiola* species are involved

in a symbiotic relationship with the fungal genus *Mastodia*, which is regarded as a model to study interactions and processes in fungal–algal symbioses (Pérez-Ortega et al. 2010). Phylogenies based on rbcL gene sequences show that the algal partner is most closely related to *Prasiola borealis*. While most relationships within the *Prasiola*-clade remain ambiguous due to a relative poor resolution of the 18S rDNA sequences (Rindi et al. 2007), one lineage-including species of *Koliella*, *Raphidonema*, *Pabia*, and *Pseudochlorella*, is well supported as distinct from other members of the *Prasiola*-clade (Dariencko et al. 2010; Neustupa et al. 2011).

The Trebouxiales (with three currently known genera, *Trebouxia*, *Asterochloris*, and *Myrmecia*) are common photobionts in lichen symbiosis (Friedl and Büdel 2008). *Trebouxia* is the most common lichen photobiont, and there is still a growing number of works which focus to reveal the algal species diversity within certain groups of lichens. Most often, algal-specific primers to directly amplify the *Trebouxia* ITS rDNA from lichen specimens without culturing are employed. Species diversity of *Trebouxia* appears larger than reflected by morphology (cryptic speciation) and has still not been fully explored. Intriguing examples have been presented by Blaha et al. (2006) and Skaloud and Peksa (2010). The 18S rDNA phylogenies showed that *Trebouxia* as previously defined was paraphyletic with *Myrmecia* and therefore, in a polyphasic approach using ITS and actin intron sequences as well as morphology, the genus *Asterochloris* has recently been segregated from *Trebouxia* (Skaloud and Peksa 2010).

Within the *Choricystis/Botryococcus*-clade, several genera thrive in symbioses as well as free living. *Elliptochloris* has been identified as symbiotic in lichens (Friedl and Büdel 2008) and marine invertebrates (Letsch et al. 2009), but species of *Elliptochloris* were also found free living on tree bark (Eliáš et al. 2008). *Coccomyxa*, the sister-group to *Elliptochloris* in the 18S rDNA phylogenies, includes symbionts of lichens and ciliates (previously summarized under “*Zoochlorella*”) (Pröschold et al. 2011) as well as free-living species (Zoller and Lutzoni 2003; Friedl and Büdel 2008). Species of *Choricystis* species are known as phytoplankton members (Fawley et al. 2005) and as symbionts in sponges (Handa et al. 2006; Pröschold et al. 2011). The oil-producing *Botryococcus* is a prominent member of this clade (Senousy et al. 2004; Weiss et al. 2010).

Most of the currently known members of the *Watanabea*-clade were traditionally assigned to *Chlorella*, but appeared distinct from the type of *Chlorella*, *C. vulgaris*, in molecular phylogenies as well as morphological features (Dariencko et al. 2010). A new genus, *Chloroidium*, has been established to encompass the previous species *C. ellipsoidea*, *C. trebouxioidea*, and *C. saccharophila*. The *Watanabea*-clade also includes *Heterochlorella*, a newly established genus to encompass previous “*Chlorella*” *luteoviridis* (Neustupa et al. 2009). Two more lineages of *Chlorella*-like algae which, however, are distinct from the two aforementioned lineages, are *Kalinella* (Neustupa et al. 2009) and *Heveochlorella* (Zhang et al. 2008). So far, only a single symbiotic member of the *Watanabea*-clade has been reported, i.e., as a still unidentified strain from the lichen *Psoroglaena epiphylla* (Nyati et al. 2007).

The Chlorellales have been the focus of intensive taxonomic research during recent years. This group unites the Chlorellaceae, which is subdivided into the

*Chlorella*- and *Parachlorella* clades (Krienitz et al. 2004), with the “*Auxenochlorella*-clade” (Pröschold et al. 2011). While the latter comprises peculiar coccoid green algae without chlorophylls (Aslam et al. 2007), the order Chlorellales comprises mostly unicellular coccoids of minute size which thrive in an extremely broad range of habitats. For example, species of *Chlorella* (close relatives of the type species, *C. vulgaris*) have been described from terrestrial habitats (e.g., rock surfaces in Antarctica; Hu et al. 2008), symbioses with ciliates and sponges (*C. vulgaris*, *C. variabilis*, *C. heliozoae*; Hoshina et al. 2010; Pröschold et al. 2011), as well as freshwater phytoplankton (Henley et al. 2004; Krienitz et al. 2004). An overview of the “true” *Chlorella* species and genera most closely related with *Chlorella*, i.e., members of the *Chlorella*-clade of Chlorellales, has been presented by Luo et al. 2010. Several new genera which belong to the *Chlorella*-clade have been described from freshwater phytoplankton, e.g., *Meyerella* (Fawley et al. 2005), *Hegewaldia* (Pröschold et al. 2010), *Heynigia*, and *Hindakia* (Bock et al. 2010). Members of the same genus, *Micractinium*, are known as common components of freshwater phytoplankton (with cell wall appendices, bristles, inducible by grazers, Luo et al. 2006) as well as symbionts in the ciliate *Paramecium bursaria* (Pröschold et al. 2011). Many genera of the Chlorellales are common picoplanktonic green algae in freshwater, e.g., *Picochlorum*, *Nannochloris*, and *Marvania* (Henley et al. 2004). A new genus of marine phytoplankton, *Marinchlorella*, which is a member of the *Parachlorella*-clade, has recently been described on the basis of ultrastructural characters and 18S rDNA phylogenies (Aslam et al. 2007). A new genus of *Chlorella*-like phytoplankton, *Chloroparva*, a close relative of “*Chlorella*” *minutissima* within the “*Nannochloris*-like” clade of Chlorellales (Fig. 1), has also recently been described on the basis of 18S rDNA phylogenetic analyses, ultrastructure, and oleic fatty acids (Somogyi et al. 2011). Extensive ultrastructural studies in Trebouxiophyceae have become rare. However, an excellent ultrastructural study that focuses on the life cycle and reproduction by autospores in *Chlorella* and *Parachlorella* revealed ultrastructural features which support the separation of *Parachlorella* from *Chlorella*, independent of molecular phylogenetic analyses (Yamamoto et al. 2005). For the *Auxenochlorella*-clade, three genera of heterotrophic algae are currently known. *Auxenochlorella* has been described as a free-living aerophytic alga (Kalina and Punčochárová 1987), reported from symbioses with *Hydra* (Pröschold et al. 2011) as well as from a lichen symbiosis (*Psoroglaena stigonemoides*, Nyati et al. 2007). *Prototheca* species are well known as pathogens in vertebrates, e.g., cattle and humans, and the genus *Helicosporidium* in insects (Tartar et al. 2002; Tartar and Boucias 2004; de Koning and Keeling 2006). The close phylogenetic relationships of both parasitic genera have been resolved by 18S rDNA (Tartar et al. 2002) and phylogenomic analyses of mitochondrial (Pombert and Keeling 2010) and chloroplast DNA (de Cambiaire et al. 2007). As expected for parasitic algae not performing photosynthesis, the chloroplast genomes were rather reduced compared to other green algae (de Cambiaire et al. 2007). In 18S rDNA phylogenies, the three genera form a rather long branch, which almost certainly is due to systematic errors in phylogenetic inferences (long branch attraction, Verbruggen and Theriot 2008). Therefore,



deciphering whether or not they form a single monophyletic lineage, and their position within the Chlorellales is still a challenging task.

The circumscription of Trebouxiophyceae is not fully understood yet. The Oocystaceae, a monophyletic group of coccoid green algae, may form another multigenera group within the Trebouxiophyceae. First, Hepperle et al. (2000) showed affinities of the Oocystaceae to the Trebouxiophyceae, despite it exhibiting rather long branches, but its relationship within the class could not be resolved. Later, an affiliation of the Oocystaceae with Chlorellales had been found (Krienitz et al. 2003; Pažoutová et al. 2010; Neustupa et al. 2011). Oocystaceae was even used as outgroup taxa in 18S rDNA phylogenies to address relationships within the Trebouxiophyceae (Pröschold et al. 2011). Species of *Geminella* were also resolved, forming a clade of the Trebouxiophyceae (Mikhailyuk et al. 2008), but appeared rather distant from other members of the class. The phylogenetic positions of Oocystaceae and the *Geminella*-clade are in urgent need of reevaluation; both clades may even represent two additional independent clades diverging within the TUC crown group.

Sexual reproduction in Trebouxiophyceae has so far been observed only in two genera, *Micractinium* (references in Pröschold et al. 2010) and *Prasiola* (references in Rindi et al. 2004). Analysis of the whole genome of *Chlorella variabilis*, symbiont of the ciliate *P. bursaria*, however, revealed evidence for the presence of sexual reproduction in which flagellated stages may have been involved or at least genes involved in these processes may have been retained (Blanc et al. 2010). Therefore, it is tempting to conclude that sexual reproduction is more widespread in Trebouxiophyceae than assumed from observations (cryptic sexuality). Absence of flagellated stages is very widespread in lineages of the Trebouxiophyceae (e.g. *Watanabea*- and *Choricystis/Botryococcus*-clades), but genomic evidence for flagellar motion in *C. variabilis*, a species for which only reproduction by nonmotile autospores is known, has been found (Blanc et al. 2010). This may indicate that the many autosporic lineages in Trebouxiophyceae may have ancestors with flagellated reproductive stages as well. Chloroplast phylogenomics could not resolve the monophyletic origin of the Trebouxiophyceae, but revealed an affiliation of the green flagellate *Pedinomonas* (whose phylogenetic position has been unclear so far) with the Trebouxiophyceae, particularly with the Chlorellales (Turmel et al. 2009b). Phylogenomic analyses based on mitochondrial DNA, however, did not support a relationship of *Pedinomonas* with Trebouxiophyceae, but both phylogenomic analyses certainly suffer from poor taxon sampling, which is a problem inherent to all phylogenomic analyses so far (Rodríguez-Ezpeleta et al. 2007).

## 4 Chlorophyceae

In contrast to the Trebouxiophyceae, the Chlorophyceae includes a variety of unicellular or colonial flagellates (e.g., *Chlamydomonas*, *Volvox*; Nakada et al. 2008) and many members with firm unbranched (e.g., *Oedogonium*; Alberghina

et al. 2006) or branched filaments (e.g., *Stigeoclonium*, Michetti et al. 2010). Members of Chlorophyceae thrive mostly in freshwater or terrestrial habitats, and there are only very few symbiotic genera, e.g., *Scenedesmus* in ciliates (Pröschold et al. 2011). Chlorophyceae are not known yet from lichen symbioses (Friedl and Büdel 2008). Recent reviews of the Chlorophyceae are based on 18S rDNA (e.g., Müller et al. 2004) or chloroplast phylogenomics (e.g., Turmel et al. 2008). Consensus has been reached that the Chlorophyceae may be divided into five clades, Volvocales, Sphaeropleales, Oedogoniales, Chaetopeltidales, and Chaetophorales, which are robustly resolved in most phylogenetic analyses (Fig. 1). Monophyletic origin and distinction of Sphaeropleales has been substantiated by ITS2 secondary structure-based analyses (Keller et al. 2008). The actual conception of the group and its subdivision into clades has recently been reviewed by Krienitz et al. (2011). A recent overview of Volvocales [sometimes also called Chlamydomonadales, e.g., Müller et al. (2004)] can be found in Gerloff-Elias et al. (2005). Using a comprehensive large-scale data set of more than 400 18S rDNA sequences, the overall phylogenetic structure of the group has been revealed and phylogenetically-defined names have been applied to the monophyletic clades that constitute the Volvocales using PhyloCode (Nakada et al. 2008). Recent studies with expanded taxon samplings that would allow testing generic concepts or species delineations are still lacking for the Chaetopeltidales and Oedogoniales. A preliminary 18S rDNA analysis already indicated a polyphyletic origin for *Oedogonium* within the Oedogoniales (Alberghina et al. 2006). A most recent 18S rDNA-based overview of the Chaetophorales with its subdivisions can be found in Caisová et al. (2011).

Chloroplast phylogenomic analyses support a dichotomy of Chlorophyceae, i.e., a CS clade uniting the orders Chlamydomonadales (= Volvocales) and Sphaeropleales versus the OCC clade which comprises the orders Oedogoniales, Chaetopeltidales, and Chaetophorales (Turmel et al. 2008; Fig. 1). Until now, a total of eight chloroplast genomes has been sequenced for the six orders of both clades together (Brouard et al. 2011 and references therein). Recent analyses of 18S rDNAs alone have favored the dichotomy as seen in cpDNA phylogenetic analyses (Caisová et al. 2011), whereas analyses of concatenated 18S and LSU (28S) rDNA sequences (Buchheim et al. 2001) have supported only the CS clade (Shoup and Lewis 2003; Müller et al. 2004). As outlined by Lewis and McCourt (2004) and Leliaert et al. (2011), each of the two clades is defined by a unique absolute basal body configuration. Members of the CS clade produce biflagellated motile cells, while members of the OCC clade exhibit quadriflagellated stages or, in Oedogoniales, have multiple flagella (stephanokont zooids) (Alberghina et al. 2006). From chloroplast genomic data, it has been assumed that the ancestral state in Chlorophyceae may have been quadriflagellate motile cells with the DO + DO orientation, and the CW condition of flagellar basal bodies developed later convergently in the CS and OCC clades (Brouard et al. 2008; Turmel et al. 2008). Important conclusions for the evolution of green algae and the Chlorophyceae became possible by comparisons of genomes, i.e., that of the model organism *Chlamydomonas reinhardtii* with those of the multicellular *Volvox*

(Prochnik et al. 2010) and the more ancestral prasinophytes *Ostreococcus* spp. (Peers and Niyogi 2008).

Many studies over the last 5 years focused more on taxa of the CS clade, less on members of the OCC clade. For both clades, phylogenetic analyses concluded that traditional species delineation based on morphology is not congruent with the molecular distinction. This general finding holds true from minute phytoplankton species (Krienitz et al. 2011), prominent examples of colonial coccoids [e.g., *Pediastrum* and *Hydrodictyon*; McManus and Lewis (2005, 2011)], to more complex branched filamentous forms [e.g., *Chaetophora* and *Stigeoclonium*; Caisová et al. (2011)]. In minute common phytoplankton species of the Sphaeropleales, the morphological difference in solitary versus colonial forms was found in disagreement with phylogenetic groupings and therefore the species were assigned to a single genus *Mychonastes* with the species distinguished primarily by differences in their ITS2 rDNAs (Krienitz et al. 2011). Sequence analyses of ITS2 rDNA became almost a standard marker to delineate species within *Scenedesmus*, *Acutodesmus*, and *Desmodesmus* and differences in ITS2 were found congruent with morphological features as seen by scanning-electron-microscopy (Hegewald et al. 2010). ITS2 sequence comparisons have also been successful in the unambiguous identification of *Scenedesmus* and *Desmodesmus* isolates from lake phytoplankton (Johnson et al. 2007). Chloroplast genes have frequently been used as molecular markers to test species and genus assignments in the Volvocales, but not in the Sphaeropleales. For example, a data set of three concatenated chloroplast genes revealed a new genus, *Parallela*, within the Volvocales of the CS clade in combination with light and electron microscopy (Novis et al. 2010). New species of the coccoid *Asterococcus* and the colonial flagellate *Gonium* have been recovered using plastid-encoded *rbcl* and nuclear-encoded ITS rDNA, combined with ultrastructure (Nakazawa et al. 2004; Hayama et al. 2010).

## 5 Ulvophyceae

The Ulvophyceae is probably morphologically the most diverse group of the Chlorophyta (Cocquyt et al. 2010; Leliaert et al. 2011). Morphologies range from microscopic unicells to multicellular thalli and giant cells with unique types of cytomorphology. The class may be regarded as predominantly marine; it includes all macroscopic marine representatives of the Chlorophyta. Only in recent years, monophyly of the class as well as its internal phylogenetic structure have been assessed using multigene analyses, i.e., concatenated 18S rDNA and a number of other nuclear and plastid genes. The Oltmannsiellopsidales, consisting of quadriflagellate unicells or coccoids arranged in disks or packets, may be the most basal lineage of Ulvophyceae (Friedl and O'Kelly 2002; Watanabe and Nakayama 2007; Fig. 1). Its basal position has been confirmed by mitochondrial genome sequence comparisons (Pombert et al. 2006). The *Ignatius* clade, comprising unicellular

cocoids, is another more basal lineage of Ulvophyceae, which is independent of any other groups of the class (Watanabe and Nakayama 2007; Fig. 1). The Ulvales–Ulotrichales is a morphologically rather diverse clade, comprising most microscopic forms of Ulvophyceae. It includes two cytomorphological types: unicellular algae with a single nucleus and chloroplast, e.g., the unicellular or sarcinoid *Pseudendoclonium*, *Planophila*, and *Desmochloris* (Friedl and O’Kelly 2002; Darienko et al. 2009), and those with multicellular bodies composed of uninucleate cells, forming branched or unbranched filaments (e.g., *Acrosiphonia*, *Ulothrix*, *Uronema*; O’Kelly et al. 2004), blades or tubular forms (e.g., *Ulva* which is known to form “green tides,” e.g., the Qindao nuisance alga, Leliaert et al. 2009; O’Kelly et al. 2010). So far, there has been no support from phylogenetic analyses to separate the Ulvales–Ulotrichales clade into orders (Leliaert et al. 2011). The single origin for a rather large assemblage of lineages within the Ulvophyceae, termed the “Trentepohliales–Bryopsidales–Cladophorales–Dasycladales (TBCD)” clade (Fig. 1), has been revealed by multigene analyses (Cocquyt et al. 2010). The TBCD clade unites lineages of various cytomorphological organization (see Cocquyt et al. (2010) and references therein). The Trentepohliales is a unique lineage of exclusively terrestrial members forming filaments of uninucleate cells. The Trentepohliales includes a variety of important photobionts in lichen symbiosis (for review see Nelsen et al. 2011). For a comprehensive treatment of genus boundaries and a phylogenetic assessment of the Trentepohliales based on 18S rDNA and rbcL genes, see López-Bautista et al. (2006) and Rindi et al. (2009). The Bryopsidales (also referred to as Caulerpales) comprise mainly marine macroscopic lineages with siphonous forms consisting of a single giant cell with millions of nuclei or a single macronucleus. The order Cladophorales consists of mostly branched filaments of the siphonocladous type (Cocquyt et al. (2010) and references therein) and the marine tropical Dasycladales of siphonous forms. A large number of works have contributed to this present-day view of the phylogenetic structure of Ulvophyceae; they have been reviewed and summarized by Cocquyt et al. (2010) and Leliaert et al. (2011).

## 6 Streptophyte Green Algae

The streptophyte green algae comprise not more than four or five morphologically rather simple lineages and two advanced lineages with true multicellular organization (McCourt et al. 2004; Becker and Marin 2009): the scaly flagellate Mesostigmatophyceae (Marin and Melkonian 1999), the sarcinoid Chlorokybophyceae (McCourt et al. 2004), the unbranched filamentous Klebsormidiophyceae (for overview see Mikhailuyuk et al. 2008; Sluiman et al. 2008), and the Zygnematomphyceae which are characterized by conjugation as the method of sexual reproduction and the absence of flagellated cells (Fig. 1). The unicellular genus *Spirotaenia*, traditionally classified as a member of the Zygnematomphyceae, likely

represents another independent lineage of streptophyte green algae (Gontcharov and Melkonian 2004), confirming the earlier notion of Mollenhauer (1986). Multicellular organization and oogamous sexual reproduction exhibit the Coleochaetophyceae which form parenchymatous tissue (*Coleochaete* and *Chaetosphaeridium*; for review see Delwiche et al. 2002), and the Charophyceae (stoneworts) which form branched filaments with apical growth (McCourt et al. 2004; Becker and Marin 2009). A lineage uniting the flagellate *Mesostigma* and the sarcinoid *Chlorokybus* may represent the earliest diverging lineage of the Streptophyta as it was indicated by plastid phylogenomic analyses (Lemieux et al. 2007). Earlier studies suggested *Mesostigma* emerged even before the divergence of the Streptophyta and Chlorophyta (Lewis and McCourt 2004). Its basal position within the Streptophyta, however, is not debated anymore since a multi-gene family (BIP) and a GapA/GapB gene duplication shared with *Mesostigma* and other Streptophyta to the exclusion of Chlorophyta have been found (Nedelcu et al. 2006; Petersen et al. 2006). The Klebsormidiophyceae diverged after the *Mesostigma/Chlorokybus* lineage and is sister to a clade uniting the Zygnematophyceae, Charophyceae, and Coleochaetophyceae (Becker and Marin 2009; Wodniok et al. 2011). Which streptophyte algal group may be the closest living relatives of embryophytes has been the subject of a hot debate (see Chapman and Waters 2002 for comments), which began soon after an early multigene analysis suggested the Charophyceae as sister group to embryophytes (Karol et al. 2001). Most recent analyses of nuclear genes as well as chloroplast phylogenomic analyses, however, revealed either the Zygnematophyceae or a group uniting the Zygnematophyceae with Coleochaetophyceae is the sister group to embryophytes (Turmel et al. 2007; Wodniok et al. 2011). The Charophyceae is now seen as an earlier divergence and not as the closest relatives of land plants.

The Zygnematophyceae, in particular, the family Desmidiaceae, are the most species rich and taxonomically complex streptophyte green algae (Gontcharov and Melkonian 2011). However, due to a problematic species concept, the real taxonomic diversity of the Desmidiaceae family is not known with certainty (Kouwets 2008; Gontcharov and Melkonian 2011). The polyphyletic nature of almost all genera in Desmidiaceae has been recovered using nuclear and chloroplast-encoded molecular markers (e.g., Gontcharov and Melkonian 2008, 2011; Hall et al. 2008, and references therein), and there is still more work required to identify structural synapomorphies for the newly identified clades (Hall et al. 2008).

Recently, an increased interest in the common terrestrial Klebsormidiophyceae led to the discovery of a new member of the class, *Interfilum* (Mikhailyuk et al. 2008). Phylogenetic structures as well as species delineations within *Klebsormidium* have been analyzed using 18S, ITS, and rbcL sequences (Rindi et al. 2011), and new species have been described (Novis 2006). Concurrently, with the progress in *Klebsormidium* systematics, there have been further ecophysiological studies on the genus (Karsten et al. 2010; Karsten and Rindi 2010; Holzinger et al. 2011).

## 7 Conclusions

Phylogenies based on a single marker gene (mostly 18S rDNA) have already revealed most phylogenetic structures within Chlorophyta and Streptophyta; not much has changed since an already decent taxon sampling was achieved for most green algal groups in the early 2000s. The 18S rDNA is still the “universal marker” to uncover green algal diversity, e.g., in phytoplankton (Piganeau et al. 2011). Multigene sequencing and/or chloroplast phylogenomics not only confirmed previously resolved major lineages in the Chlorophyta, but revealed several novel robust groupings, e.g., in the Ulvophyceae or the assessment of the closest living relative of the embryophytes. There are still many “weak” areas in the phylogeny of Chlorophyta which continue to be ambiguous or unresolved. In particular, the circumscription and internal phylogenetic structure of the Trebouxiophyceae are still challenging. More analyses based on sequences from many single gene loci of at least the nuclear and chloroplast genomes are required, but systematic errors need to be overcome by increased taxon sampling and improved phylogeny inferences methods (Rodríguez-Ezpeleta et al. 2007; Verbruggen and Theriot 2008; Cocquyt et al. 2010). Transcriptome analyses using next generation sequencing (e.g., Timme and Delwiche 2010) is another promising and powerful tool for testing phylogenetic hypotheses in the green algae. Systematics, in general, attempts to recover the actual phylogenetic relationships as close as possible by using as many characters as possible, and, therefore, more than just phylogenies are needed. In many groups we now are left with a molecular grouping that cannot be explained satisfactorily by morphology or other phenotypical characters. The situation may be best exemplified in the Desmidiaceae (Zygnematophyceae) where the traditional generic concepts almost constantly fail. Morphology needs to be revisited and much work is needed to find structural or other phenotypical synapomorphies to define the molecular groupings. There are several good examples (e.g., in the Chlorellales, Trebouxiophyceae) where a reevaluation of morphology resulted in congruence with the molecular groupings and features whose phylogenetic significance has not been understood so far. Taxon sampling will become even more important for future studies in green algal systematics, not only in terms of numbers of taxa to be included, but also which taxa to select. Previous sequence analyses may guide us well to find the right critical taxa, but to consider traditional gathered expert knowledge from morphology, ultrastructure and ecology of a certain group of green algae will be pivotal.

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