Review

Lichen algae: the photosynthetic partners in lichen symbioses

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Abstract

A review of algal (including cyanobacterial) symbionts associated with lichen-forming fungi is presented. General aspects of their biology relevant to lichen symbioses are summarized. The genera of algae currently believed to include lichen symbionts are outlined; approximately 50 can be recognized at present. References reporting algal taxa in lichen symbiosis are tabulated, with emphasis on those published since the 1988 review by Tschermak-Woess, and particularly those providing molecular evidence for their identifications. This review is dedicated in honour of Austrian phycologist Elisabeth Tschermak-Woess (1917–2001), for her numerous and significant contributions to our knowledge of lichen algae (some published under the names Elisabeth Tschermak and Liesl Tschermak).

Key words: chlorobiont, cyanobacteria, cyanobiont, lichenized stramenopiles, phaeobiont, photobiont, phycobiont, xanthobiont

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Introduction

The principal components of the lichen symbiosis are fungus and alga. Their intimate trophic relationship remains central to the lichen concept, despite our growing appreciation that other microorganisms harboured within the thallus might also play significant roles (Lakatos et al. 2004; Grube & Berg 2009; Bates et al. 2011; Grube et al. 2015; Spribille et al. 2016; Muggia & Grube 2018; Mark et al. 2020; Smith et al. 2020; Tzovaras et al. 2020). The lichen-forming fungi typically build distinctive vegetative tissues and characteristic sexual structures, providing numerous biological features for study and significant clues about phylogenetic relationships, which are now relatively well delimited at broader taxonomic levels (Jaklitsch et al. 2016; Lücking et al. 2017a). Lichen algae, by contrast, have proved much more elusive. Most are unicells or simple filaments, with sexual structures unknown or seldom reported. The paucity of phenotypic characters is often aggravated by their plasticity. Lichen algae may look and behave quite differently in symbiosis with different lichen-forming fungi, in the free-living condition in nature and in aposymbiotic laboratory culture (Fig. 1; Ahmadjian 1967; Bubrick 1988). All this has hindered progress in clarifying their identities, phylogenies and life histories. Schwendener (1869) was the first to survey lichen ‘gonidia’ in a phylogenetic context, recognizing them as organisms distinct from the surrounding fungus that correspond to known taxa of free-living algae. In the last half-century, the diversity of lichen-forming algae has been reviewed by various authors (Ahmadjian 1967; Létrouit-Galinou 1968; Henssen & Jahns 1974; Friedl & Büdel 2008), with a particularly thorough literature summary compiled and annotated by Tschermak-Woess (1988a).

In recent decades, our understanding of algal diversity and biosystematics has advanced substantially with the accumulation, analysis and integration of DNA sequence data. Systematic schemes for the eukaryotic algae have changed considerably, as the broad contours of consensus emerge concerning phylogenies and their reconstruction. Recent works have reviewed the current status of some principal algal groups with lichen-forming taxa, such as the genus Trebouxia (Muggia et al. 2017), the class Trebouxioiphyceae (Muggia et al. 2018), the Coccomyxa-Elliptochloris clade (Gustavs et al. 2017), the Trentepohliaceae (Grube et al. 2017a), and the cyanobacteria (Rikkinen 2017). Yet most taxa remain insufficiently understood. Even the most intensively studied genera, such as Trebouxia, are still unresolved with respect to species delimitation, and much new diversity continues to be uncovered (Muggia et al. 2020). A great many algal symbionts, identified phenotypically (often without isolation into culture) or recorded merely as ‘trebouxiod’ or ‘chlorococclean’, have yet to be revisited with DNA sequence analyses. Identities and relationships remain especially problematic among the cyanobacteria (blue-green algae), where sexual reproduction is absent, diversification is ancient (Garcia-Pichel 2009) and horizontal gene transfer events may obscure the vertical components of phylogenies (Zhaxybayeva et al. 2006). The aposymbiotic lives of lichen algae also remain largely unknown, despite their potential importance in active genetic mixing. Here an attempt is made to focus more attention on the algal side of the lichen partnership, still relatively neglected compared to that of the fungus. We include a synopsis of the relevant genera and list citations of algal taxa in lichen symbiosis (Table 1), emphasizing those published since Tschermak-Woess’s (1988a) landmark review, and particularly those accompanied by genetic sequence data.

The Major Algal Groups Involved

Lichen algae are diverse. This may contribute to the distinct distributions and climatic preferences of the symbiotic thalli that
enclose them (Marini et al. 2011). Most are green algae, a paraphyletic grouping of two major clades: the charophytes (Streptophyta), from which embryophytes descend, and the Chlorophyta s. str. (Leliaert et al. 2012). The latter includes nearly all green algae reported as lichen symbionts. Within the Chlorophyta, lichen symbionts are found principally in the classes Trebouxiophyceae and Ulvophyceae. A third class, the Chlorophyceae, is known or suspected to include the partners of several lichens. The prokaryotic blue-green algae (cyanobacteria) encompass most of the remainder, occurring in c. 10% of the nearly 20 000 known lichen associations (Rikkinen 2017). Additionally, two stramenopile algae (a xanthophyte and a phaeophyte) are known to enter into lichen symbioses. The full range of phylogenetic disparity among lichen-forming algae is therefore much wider than that found among the lichen-forming fungi, which all fall within the kingdom’s Dikarya crown group (mostly Ascomycota, with several genera of Basidiomycota). Just what common features might permit those disparate algal lineages to form comparable symbioses with lichen-forming fungi remain enigmatic. As colonizers of exposed, subaerial substrata, potentially suitable algae may be pre-adapted to coping with hydric stresses and high radiation loads (Lange et al. 1990; Gustav et al. 2010; Candotto Carniel et al. 2015). It is striking that most lineages of basidiomycete fungi that independently adopted the lichen lifestyle did not domesticate novel algal genera; instead they chose taxa that associate with ascolichens, such as Coccomyxa, Elliptochloris and Rhizonema (Oberwinkler 2012; Dal Forno et al. 2020; Masumoto 2020; but see Hodkinson et al. (2014) concerning Lepidostromatales). It is also noteworthy that quite a number of lichen algae belong to genera (e.g. Chlorella s. str., Coccomyxa, Elliptochloris and Nostoc) that include species occurring in symbiosis (often endosymbioses) with diverse protists, plants and animals (Adams et al. 2012; Grube et al. 2017b).

Algal partners in lichen symbioses were termed phycobionts by Scott (1957). Subsequently, Ahmadjian (1982) proposed that phycobiont replace phycobiont where cyanobacteria are meant to be included, because they ‘are not algae per se but actually bacteria’. No further argumentation was provided; it was presumed self-evident that algae and bacteria must denote mutually exclusive concepts. Some contemporary treatments distinguish cyanobacteria from algae (e.g. Friedl & Büdel 2008; Grube et al. 2017b), while others consider them as algae (e.g. Graham et al. 2009; Büdel & Kauff 2012; Lee 2018). Clearly, there are significant differences between prokaryotes and eukaryotes. At issue, however, is whether those differences are relevant to the concept of algae. This term has no biosystematic status and cannot attain any by exclusion of the blue-greens. The emblematic algal trait, oxygen-generating photosynthesis, is ultimately derived from cyanobacteria. It was subsequently acquired in multiple events involving primary, secondary and tertiary endosymbioses (Keeling 2004, 2013), and now characterizes diverse lineages included within most of the major eukaryote clades (Archaeplastida, Alveolata, Excavata, Rhizaria, Stramenopila, Cryptista and Haptista). The one and only unifying thread in this polyphylectic algal tapestry (Delwiche 1999) is the common photosynthetic apparatus, originating in cyanobacteria and passed on vertically as well as horizontally. The present work therefore uses the term alga to encompass all non-embryophyte lineages that inherited oxygenic photosynthesis. Phycobiont and photobiont are considered synonymous terms.

Fig. 1. Three filamentous lichen photobiont genera in aposymbiotic and symbiotic states. A–C, Trentepohlia. A, branching filament free-living on bark. B, lichenized by Coenogonium hyphae (arrows) growing over morphologically unchanged algal filament and its new branches (horizontal arrow). C, lichenized by Arthonia rubrocincto; the alga is largely broken up into individual cells or short segments. D–F, Rhizonema. D, cultured isolate from Dictyonema; note false branching (arrowhead). E, trichome ensheathed by cells of mycobiont Dictyonema. F, contorted or broken filaments (arrow) within thallus of Collema furfuraceum. G–J, Nostoc. G, free-living thallus-like macrocolony on soil. H, cultured strain. I, more or less intact filaments (arrows) within thallus of Sticta canariensis. J, contorted or broken up into cell groups (arrows) within cyanomorph of Sticta canariensis. Scales: A–F, H–J = 10 μm; G = 1 cm.
The Algal Role in Lichen Symbiosis

The algal partner is the primary producer, sustaining the lichen association by supplying the fungal partner with carbohydrate products of photosynthesis (Smith 1974). Those with pyrenoids (Fig. 2) possess CO₂-concentrating mechanisms that improve the efficiency of carbon fixation (Smith & Griffiths 1996). Green algal symbionts (chlorobionts) transfer their photosynthate as polyol sugar alcohols such as ribitol (Richardson et al. 1968). Significantly, these compounds also confer desiccation tolerance by providing osmolarity and protecting cell membranes from damage as water is lost (Smith 2019). Polyols are likewise produced by non-symbiotic, aeroterrestrial green algae, particularly under osmotic stress conditions (Darienko et al. 2010; Gustavs et al. 2010, 2011). Blue-green symbionts (cyanobionts) transfer glucose, or glucan, which their fungal partners take up and immediately convert into the sugar alcohol mannitol (Smith & Drew 1965; Hill 1972). When lichenized, the algal symbionts are somehow induced to leak large amounts of carbohydrate to the surrounding fungal cells, a process that quickly ceases when the algae are isolated into culture (Drew & Smith 1967). Fungal penetration of photobionts may occur to varying degrees (Gettler 1934; Tschermak 1941a; Plessl 1963; Galun et al. 1970, 1971; Honegger 1986; Matthews et al. 1989), but these so-called haustoria do not appear to be principal conduits of carbohydrate transfer in ascocarps (Jacobs & Ahmadjian 1971; Collins & Farrar 1978; Hessler & Peveling 1978). The intrusive hyphae of certain basidiolichens that deeply penetrate longitudinally through the centre of their cyanobiont trichomes (Roskin 1970; Oberwinkler 1980, 2012) have not yet been examined with respect to substance transfer. In most foliose and fruticose lichens examined, haustorial penetrations are either absent altogether or do not fully traverse the algal cell wall. To facilitate transfer, the mycobiont secretes a hydrophobic sealant that envelops the cell surfaces of both symbionts at their contact zones, thereby funneling carbohydrate released by the alga to the fungus (Honegger 1991; Trembley et al. 2002a). At least that is the case in the selection of taxa examined so far. Where cyanobacterial symbionts are involved, they provide the lichen fungus with fixed nitrogen as well as carbon (Millbank & Kershaw 1974). In those lichens (chiefly Peltigerales) where a chlorobiont constitutes the main algal layer and cyanobionts are localized within nodules known as cephalodia, the cyanobacteria become highly specialized for nitrogen fixation, with an elevated percentage of cells differentiating as heterocytes (Hitch & Millbank 1975). In lichens with only cyanobacterial photobionts, heterocyte frequency can be much lower at the growing margins of the thallus (Bergman & Hällbom 1981), where photosynthate may be in higher demand.

Whether any substance is transferred from fungus to alga in exchange has yet to be demonstrated. At least some genes relevant to such metabolic transfers appear to be differentially expressed in symbiosis (Kono et al. 2020). Certainly, there has been speculation that the fungal partner might apportion carbohydrate, nitrogen, or other substances back to the algal symbiont to regulate its growth (Ahmadjian 1995) in coordination with that of the mycobiont (Greenhalgh & Anglesea 1979; Hill 1985, 1989; Honegger 1987). The heterotrophic tendencies shown by many lichen algae (Trebouxia, Asterochloris, Elliptochloris, Cocomyxa, Apatococcus) when cultured in the laboratory (Ahmadjian 1993; Gustavs et al. 2016, 2017) suggest the possibility that they could be susceptible to such control. Indeed, Ahmadjian (2001) proposed that Trebouxia is fully dependent upon its mycobiont for nutrition and is therefore unable to survive in the free-living state (Ahmadjian 1988).

Fig. 2. TEM micrographs of some photobiont pyrenoids, with plastoglobuli (round black dots) and penetrating membranes in various positions and orientations. A, Trebouxia, within thallus of Lasallia pustulata. Note pyrenoid structure here more closely resembles that of distantly related Heveochlorella (B) than that of another species (C) of Trebouxia. B, Heveochlorella, within thallus of Calopadia. C, Trebouxia, within thallus of Ramalina usnea. D, bulging exserted pyrenoid of Petroderma maculiforme. E, Diplosphaera, within thallus of Endocarpon pusillum. S = starch grain or plates. Scales: A = 1 µm; B = 200 nm; C–E = 500 nm.
However, he also promoted the seemingly contradictory viewpoint that Trebouxia is a victim of fungal parasitism rather than a mutualist partner (Ahmadjian 1993, 1995, 2002). This would make Trebouxia a host that cannot survive without its parasite.

In any event, proof of fungus-to-alga nutrient transfer is not required to make the case that lichen symbiosis offers advantages to the algal partner. There is considerable evidence that the surrounding fungal tissues and their secondary metabolites may help protect the lichenized alga from desiccation, photoinhibition, temperature extremes and herbivory (e.g. Solhaug & Gauslaa 1996; Kraner et al. 2008; Kosugi et al. 2009; Asplund & Wardle 2013; Gauslaa et al. 2017; Miguez et al. 2017; Sadowsky & Ott 2016; Beckett et al. 2019; Fernández-Marín et al. 2019). Symbiosis may significantly improve the alga’s ability to avoid cellular damage caused by highly reactive forms of oxygen (ROS) generated under stress conditions (Kranner et al. 1998; Wardle 2013; Gauslaa et al. 2017; Miguez et al. 2017; Sadowsky & Ott 2016; Beckett et al. 2019; Fernández-Marín et al. 2019).

Symbiosis may significantly improve the alga’s ability to avoid cellular damage caused by highly reactive forms of oxygen (ROS) generated under stress conditions (Kraner et al. 2005). With these protections, and the facilitated display for light capture afforded by a supportive mycobiont structure, lichen algae may greatly expand their ecological range and abundance via symbiosis (Honegger 2012). On the other hand, lichen symbioses are diverse and it is likely that the parameters of the relationship vary among taxa, along environmental gradients, and perhaps also during the course of a single lichen's development. The long history of attempts to maintain or resynchronize lichens in the laboratory has provided a key insight into the nature of this seemingly well-integrated association: it is very much a relationship of contingency. That the partners can often be cultured separately on appropriate media in the laboratory (Ahmadjian 1993; Crittenden et al. 1995; Stocker-Wörgötter & Hager 2008) shows there is no strict physiological impediment to growth without symbiosis. To initiate and support lichen formation, a fluctuating balance of conditions suboptimal for separate fungal or algal growth appears to be necessary. Any combination of culture conditions (light, moisture, nutrient availability) that continuously favours either fungal or algal growth results in the breakdown of symbiotic structures, and the dissociated proliferation of the favours either fungal or algal growth results in the breakdown of symbiotic structures, and the dissociated proliferation of the two partners. There is considerable evidence that the sur- suppressions, and the facilitated display for light capture afforded by a supportive mycobiont structure, lichen algae may greatly expand their ecological range and abundance via symbiosis (Honegger 2012). On the other hand, lichen symbioses are diverse and it is likely that the parameters of the relationship vary among taxa, along environmental gradients, and perhaps also during the course of a single lichen’s development. The long history of attempts to maintain or resynchronize lichens in the laboratory has provided a key insight into the nature of this seemingly well-integrated association: it is very much a relationship of contingency. That the partners can often be cultured separately on appropriate media in the laboratory (Ahmadjian 1993; Crittenden et al. 1995; Stocker-Wörgötter & Hager 2008) shows there is no strict physiological impediment to growth without symbiosis. To initiate and support lichen formation, a fluctuating balance of conditions suboptimal for separate fungal or algal growth appears to be necessary. Any combination of culture conditions (light, moisture, nutrient availability) that continuously favours either fungal or algal growth results in the breakdown of symbiotic structures, and the dissociated proliferation of the two partners. There is considerable evidence that the sur-

Patterns of Symbiotic Pairing

The asymmetrical needs of the lichen symbionts are reflected in the non-reciprocal patterns of pairing that have evolved between mycobionts and photobionts. Photobiont genera frequently associate with multiple, phylogenetically disparate lineages of lichen-forming fungi. The reverse, however, is much less common; mycobiont genera, and often families and even orders, generally tend to lichenize a single algal genus (Rambold et al. 1998; Peršoh et al. 2004). There are a number of notable exceptions. Lichen-forming fungi of the family Verrucariaceae partner with an extremely diverse array of eukaryotic algae, including the only reported cases of stramenopile phycobionts (Thüs et al. 2011). The pinlichean genus Chaenotheca (Coniothyriumycetes) includes species associating with Trebouxia, Trentepohlia, Symbiochloris or Tristostichococcus (Tibell 2001; Škaloud et al. 2016; Pröschold & Darienko 2020). The fruticose lichen genus Stereocaulon may harbour thallus photobionts of either Astrochloris, Vulcanochloris or Chlororidium (Vančurová et al. 2018). Species of Sticta may partner with chlorobionts of Symbiochloris, Coccomyxa, Elliptochloris, Hveovolorea or Chlororidium (Lindgren et al. 2020). Squamulose Psora decipiens is reported to partner with either Astrochloris, Trebouxia, Chlororidium (Ruprecht et al. 2014) or Myrmeccia photobionts (Williams et al. 2017; Moya et al. 2018). In addition, it is well known that many individual mycobionts, particularly in the Peltigerales, may associate with both green and blue-green algae simultaneously, giving rise to cyanobacterial cephalodia within or upon a chlorophyte-
Fig. 3. Liberation and potential co-dispersal of photobionts from the spore-producing structures of certain mycobionts. A, Diplosphaera photobiont (arrows) within perithecium of Endocarpon pusillum; note much smaller size compared to photobiont cells within thalline tissue (t); s = ascospore. B, apothecial surface of foliicolous lichen colonizing plastic cover slip; note epithelial algal cells (arrows) among emerging ascospores (s). C, Heveochlorella photobionts (vertical arrow) within conidiogenous tissue of campylidia and intermixed among filiform macroconidia (oblique arrow). D, hyphophore of Gyalectidium paolae showing diahyphal propagules (bundles of conidial chains dispersed as a unit) with adhering or intermixed Heveochlorella photobionts (arrows). E, campylidal macroconidia, with co-dispersed Heveochlorella photobionts loosely encircled, germinating (arrowheads) on a plastic cover slip. F, diahyphal propagules of Gyalectidium germinating (arrowheads) on a plastic cover slip, with co-dispersed Heveochlorella photobionts. Scales: A, C & D = 20 μm; B = 50 μm; E & F = 10 μm.
containing thallus, or distinct cyanomorph and chloromorph thalli separately or conjoined (Fig. 4) via a common fungal individual (e.g. James & Henssen 1976). Association with both a chlorobiont and a cyanobiont in separate thallus components has also been reported for certain basidiolichen species in Cyphelostereum (Oberwinkler 2012) and Lichenomphalia (Gasulla et al. 2020). In a small number of lichens, green and blue-green photobionts are known to occur intermixed within the same thallus structure (Büdel & Henssen 1987; Henskens et al. 2012). There are distinct physiological advantages to each of these two kinds of photobionts. Cyanobionts can fix nitrogen as well as carbon but require liquid water to rehydrate and resume physiological activity, whereas chlorobionts can rehydrate from vapour, although their CO₂ fixation rates may be more adversely affected by high thallus water contents (Lange et al. 1986, 1993; Green et al. 1993, 2002). Less obvious are the implications of choosing Trentepohlia (Ulvophyceae) versus Trebouxia (Trebouxiophyceae) photobionts; neither fix nitrogen, although they may differ in their tolerance of freezing temperatures (Nash et al. 1987). Interestingly, mycobiont genera Ionaspis and Hymenelia (Lecanoromycetes) include trentepohliophilic and trebouxiophilic taxa, and the single species H. epulotica can apparently associate with photobionts of either of these two very different genera (Lutzoni & Brodo 1995; McCune et al. 2018). Recently, Ertz et al. (2018) demonstrated that the lichen fungus Lecanogapha amylacea can form morphologically distinct sexual and asexual thalli with Trentepohlia and Trebouxia photobionts, respectively. While the above examples show that significant divergences in photobiont selection have arisen in a number of mycobiont lineages, far more conservative tendencies appear to predominate in the majority of lichen-forming fungal groups.

Photobiont choice and the range of compatible pairings for a given mycobiont were first explored experimentally in classic laboratory resynthesis studies using Cladonia cristatella and Lecanora chloroleuca (Ahmadjian et al. 1980; Ahmadjian & Jacobs 1981). Varying degrees of compatibility were observed, with thallus formation reaching different developmental stages depending on the photobiont strain introduced. Nonetheless, overall results generally reflected patterns observable in natural lichens: Cladonia successfully lichenized strains of Asterochloris but not those of Trebouxia (as currently defined), while Lecanora did just the opposite. In the last two decades, genetic markers have been used to characterize the range of photobiont diversity chosen by individual lichen-forming fungal species in nature, and to assess the parameters that might affect their choices. This complex topic has attracted much attention and merits a review of its own, but some general findings can be summarized here. Most mycobionts species appear to be fairly selective; they tend to partner with a limited range of strains or species within a single photobiont genus, but to differing degrees. Some mycobionts accept a substantially broader range of taxa within the photobiont partner genus; this relative liberty is often characteristic of lichen-forming fungi that have attained wider, more cosmopolitan distributions (Blaha et al. 2006; Guzow-Krzemińska 2006; Leavitt et al. 2013; Muggia et al. 2014; Magain et al. 2017; Vančurová et al. 2018), or those capable of colonizing extreme environments with probably fewer photobiont options available (Romeike et al. 2002; Wirtz et al. 2003; Engelen et al. 2010; Pérez-Ortega et al. 2012; Osyczka et al. 2021; Rola et al. 2021). Such mycobionts may be closely related to species that accept a much narrower range of photobiont partners (Fiercey-Normore 2004; Yahr et al. 2004; Otálor et al. 2010; Ontú-Bränström et al. 2017). Some studies have correlated symbiont selection patterns with environmental parameters, such as latitude (Singh et al. 2017), climate (Ridká et al. 2014) and ecological conditions that influence the distribution and availability of photobionts (Yahr et al. 2006; Fernández-Mendoza et al. 2011; Peksa & Škaloud 2011; Vargas Castillo & Beck 2012; Werth & Sork 2014). Photobiont tolerance of heavy metals appears to influence their selection by mycobionts in some lichen communities colonizing metal-rich substrata (Vančurová et al. 2018; Rola et al. 2021) but not others (Beck 2002; Hauck et al. 2007; Bačkor et al. 2010). Many studies stress the intrinsic compatibility requirements of individual fungal taxa as primary determinants of pairing patterns (Yahr et al. 2004; Stenroos et al. 2006; Myllys et al. 2007; Leavitt et al. 2015; Joneson & O’Brien 2017), often in conjunction with ecological factors (Elvebakk et al. 2008; O’Brien et al. 2013; Dal Grande et al. 2018; Juriado et al. 2019; Pino-Bodas & Stenroos 2020). In some communities, mycobionts may have adapted to utilize a common pool or pools of photobionts, whose local availability might thereby be sustained for all users (Beck et al. 2002; Rikkinen et al. 2002; Rikkinen 2003; Sanders et al. 2016; Ontú-Bränström et al. 2018; Cardós et al. 2019). Thallus growth form may also affect photobiont selection patterns. Some authors have suggested that crustose lichens may associate with a broader range of photobionts than do related foliose and fruticose taxa (Yahr et al. 2014; Beck 2002; Hestmark et al. 2017), perhaps because their more extensive and intimate contact with the substratum offers more opportunity to take up additional algae in the course of development. Lichen reproductive mode can also be superimposed upon these factors. Some studies have found that lichens reproducing primarily by vegetative propagules, such as soredia or isidia, associate with a narrower range of photobiont genotypes, presumably due to chiefly vertical transmission of both symbionts together (Dal Grande et al. 2012; Werth & Scheidegger 2012; Otálor et al. 2013; Cao et al. 2015; Hestmark et al. 2016; Steinová et al. 2019). However, other vegetatively reproducing lichens accept a much broader range of photobionts, suggesting that the fungus does not necessarily maintain partnership with its co-dispersed photobiont throughout development (Ohmura et al. 2006, 2019; Nelsen & Gargas 2008, 2009; Wornik & Grube 2010).
Acquisition of New Algal Symbionts

Acquisition of new and different photobionts, ‘photobiont switching’, has clearly been significant in the evolution of lichen relationships. However, this phrase may refer variably to events occurring at different levels of organization. A single mycobiont individual might acquire new photobionts at different times in the course of its development (Friedl 1987; Wedin et al. 2016), or at separate places along its somatic extension (Létrouit-Galinou & Asta 1994). The degree to which the newly lichenized alga may differ genetically from algal strain(s) already in possession will be limited by the innate compatibility range of that mycobiont individual. In contrast, a new fungal individual developing from a meiospore may encounter and select a photobiont strain different from the one its parental genotypes associated with. In this case, a generational change in photobiont partner could be enabled by a generational change in mycobiont genotype. At a phylogenetic level, a cladogram may provide evidence that a fungal lineage has changed its association from one photobiont to another in the course of evolution. But at a finer scale, a great many photobiont switches, perhaps back and forth, might have taken place over many generations; comparing taxa will indicate only the overall result.

New photobionts may be acquired in multiple ways. Contact and capture of free-living photobionts in nature by hyphae emerging from germinated spores (Fig. 5), once thought to be unlikely (Lamb 1959), has been documented in a number of studies (Ward 1884; Werner 1931; Bubrick et al. 1984; Garty & Delarea 1988; Scheidegger 1995; Sanders & Lücking 2002; Sanders 2014). In theory, a single compatible algal individual might be sufficient to generate the entire population within a developing thallus. However, there appear to be many opportunities for additional photobionts to be incorporated from exterior sources. Particularly in early developmental stages, prothallus hyphae extending outward along the substratum from the lichenized portions of the organizing thallus can incorporate additional algal cells (Sanders & Lücking 2002; Sanders 2014). Vegetative propagules, such as soredia or isidia, also begin development with the emergence and proliferation of such hyphae (Jahns et al. 1979; Schuster et al. 1985), anchoring the structure and greatly expanding the available surfaces for potential contact with other compatible photobionts as the thallus is organized. In many crustose lichens, a prothallus remains active at the growing margins of the lichen and may continue to incorporate compatible photobionts falling upon it or encountered on the substratum (Fig. 6; see also Galloe 1927; p. 40, 1932; p. 78; Létrouit-Galinou & Asta 1994). The multitude of discrete, lichenized units that comprise the thallus of squamulose lichens probably also arise from repeated algal capture by a network of prothalline hyphae interconnecting the squamules. Certain soil- and rock-colonizing squamulose lichens produce hyphal aggregates (cords or rhizomorphs) of indeterminate growth that penetrate the substratum extensively (Poelt & Baumgärtner 1964; Sanders et al. 1994), giving rise to new thallus squamules where compatible algal symbionts are encountered and lichenized (Wagner & Létrouit-Galinou 1988; Sanders & Rico 1992; Sanders 1994). The structurally similar rhizinomorphs of certain umbilicate lichens also appear to have this capability (Schuster 1992). In some foliose and fruticose lichens, organized thallus surfaces may themselves be capable of incorporating compatible algal cells that make external contact (Bitter 1904). Lichens that form cephaldodia and/or joined chloromorph and cyanomorph thalli clearly retain this ability (see discussion under Nostoc below). Additionally, certain lichen-forming fungi appear capable of obtaining photobionts from other lichens, upon which their spores may germinate (Hawksworth et al. 1979). The host thallus is eventually destroyed as its photobionts are taken over by the invading hyphae of the aggressor, giving rise to a new lichen (Poelt 1958; Friedl 1987; Feige et al. 1993; Lücking & Grube 2002; Wedin et al. 2016). Thus, capture of free-living algae by spore germings is clearly not the only opportunity for a mycobiont to acquire new photobionts. On the other hand, some interesting transplant experiments with Psora decipiens suggest that lichens may not always be able to switch to more favourable photobionts when needed (Williams et al. 2017).

If acquisition of additional photobionts is indeed a common occurrence in the course of lichen development, lichen thalli may be expected to contain a heterogeneous photobiont population, at least at certain stages. Some authors have observed and illustrated quite different chlorobionts occurring together within single thalli (Voytsekhovich et al. 2011). Data from molecular markers have also addressed this question. Some authors found no evidence of multiple photobiont genotypes in single thalli examined (Paulsrud & Lindblad 1998; Beck & Koop 2001; Singh et al. 2017; Škaloud et al. 2018); others found occasional occurrences (Guzow-Krzemińska 2006; Bačkor et al. 2010; Muggia et al. 2013; Nyati et al. 2013; Řídká et al. 2014; Onúť-Brännström et al. 2018; Vančurová et al. 2018; Molins et al. 2020), or frequent presence (Piercey-Normore 2006; Muggia et al. 2014; Park et al. 2015; Dal Grande et al. 2018; Oszczka et al. 2021). Intrathalline populations of Trebouxia can also vary in simple sequence DNA regions, which may result from clonal replication errors (Mansournia et al. 2012; Dal Grande et al. 2014a). Individual thalli of Parmotrema pseudotinctorum from the Canary Islands were reported to encompass distinct lineages of Trebouxia as well as Asterochloris (Molins et al. 2013). According to Casano et al. (2011), two genetically distinct strains of Trebouxia are always present together in thalli of

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**Fig. 5.** Muriform ascospore (a), probably of Calopadia, germinating on a plastic cover slip placed in a south-west Florida oak hammock, and lichenizing a group of algal cells (arrow), most likely Heveochlorella. Scale = 20 μm.
Ramalina farinacea, and high-throughput sequencing results suggest that a number of other, minority algae might also be present in this lichen (Moya et al. 2017). One constant challenge in assessing photobiont identities is that lichen thallus surfaces are colonized by epibiontic algae (including possible photobionts of other lichens) that are not intimate symbionts of the lichen in question, yet may figure prominently in cultures established or samples obtained from thallus fragments (Warén 1920; Muggia 2013). Confidence that sampled algae are indeed the thallus photobionts can be improved by establishing cultures from single algal cells extracted from within the thallus using a micromanipulator (Beck & Koop 2001), although the procedure is time-consuming. Additional evidence may be sought in TEM micrographs of photobionts within the same thallus (e.g. Català et al. 2016; Molins et al. 2018), particularly where more than one pyrenoid type (Friedl 1989) is present. However, variability should first be assessed among individuals of the same genetic strain because chloroplast structure may vary from cell to cell and often looks substantially different according to the plane of ultrathin section examined. In sequencing, conventional dideoxy chain termination (Sanger) technology will reliably identify a predominant photobiont and ignore any others present in low abundance, while the procedure fails if there are secondary photobionts in sufficient abundance (c. 30%; Paul et al. 2018). High-throughput sequencing will detect minor photobionts but will also be more sensitive to epibiontic algae. A recent comparison of the two sequencing approaches concluded that in most lichens there is a single dominant photobiont genotype, representative of most of the thallus population (Paul et al. 2018).

The Genera of Lichen Algae

Approximately 50 algal genera are currently said to include lichen photobionts. Some may represent identifications that are erroneous or based on outdated circumscriptions of taxa. Others may spin off new genera as their cryptic genetic diversity is further elucidated. It is evident that a small number of very prominent photobiont genera (Asterochloris, Nostoc, Rhizonema, Trebouxia, Trentepohlia) each partner with many hundreds or thousands of lichen-forming fungal species; a number of others (e.g. Coccomysa, Elliptiochloris, Heveochlorella, Symbiochloris) are lichenized by many dozens or hundreds of different mycobiont species, while much of the remainder participate in only a small number of known lichen associations. It seems probable that further surveys will uncover more photobiont genera in the latter category. While it is widely agreed that the diversity of lichen-forming algae remains considerably less well known than that of lichen-forming fungi, this fact alone is unlikely to account for the enormous disparity between the currently recognized number of photobiont genera (c. 50) and that of mycobiont genera (c. 1000; Lücking et al. 2017a). The number of photobiont species described, estimated at c. 100 not long ago (Škaloud & Peksa 2010), shows a similar disparity with the number of lichen-forming fungal species (20 000). Indeed, both the generic and species estimates differ between mycobiont and phycobiont by the same factor of 20. Thus, the imbalance is not likely due to differences in genus/species concepts between algae and fungi. Of course, much of the genetic diversity discovered within photobiont genera in the last few years has been reported as clades that still lack taxonomic recognition; species numbers will surely increase substantially in the near future as such diversity becomes formalized biosystematically. However, this still seems unlikely to close the enormous gap with mycobiont species numbers. Rather, the disparities probably indicate a real ecological asymmetry: the large number of lichen-forming fungal taxa may be partnering with a substantially smaller pool of photobiont taxa, many of which are shared among mycobionts. Such was the conclusion reached recently by Dal Forno et al. (2020) in their detailed comparison of genetic diversity in Dictyonema and its Rhizonema photobionts.

A synopsis of algal genera to which lichen photobionts are currently attributed is given below.

Cyanobacteria

Anabaena Bory ex É. Bornet & C. Flahault — See Nostoc. Strains of Anabaena versus Nostoc are resolved in some analyses (Henson et al. 2002; Rajaniemi et al. 2005; Liu et al. 2013; Elshobary et al. 2015) but formal distinction of the two genera remains controversial (Makra et al. 2019). Tschemak-Woess (1988a) recommended re-examination of earlier reports that Anabaena occurs as cephalodial photobiont of Stereocaulon.

Anacystis Meneghini — According to Bold & Wynne (1985), this generic name has been applied to ellipsoid to cylindrical cyanobacteria that often accumulate in a common gelatinous matrix, with some authors also including spheroidal-celled taxa such as Gloeocapsa and Chroococcus. The much-studied ‘Anacystis nidulans’ is usually treated now under Synechococcus; other taxa are currently placed in Microcystis. Photobionts attributed to Anacystis in the past include the partners of a small number of Peltula species and the cephalodial symbionts of a
Sterocaulon (see Tschermak-Woess 1988a); determining their identities with confidence will require further study.

Brasilonema Fiore et al. — This cyanobacterial genus, forming a distinct clade in molecular analyses (Fiore et al. 2007), has aggregated filamentous genotypes morphologically similar to Syctonema, but only rarely showing false branching. A recent paper reported new species of both Brasilonema and Chroococciidiopsis as co-occurring photobionts of an unidentified lichen growing on gravestones in a northern Florida cemetery (Villanueva et al. 2018). However, as no description or evidence of this association has yet been published, the status of Brasilonema as lichen photobiont awaits corroboration.

Calothrix C. Agardh ex É. Bornet & C. Flahault and Dichothrix G. Zanardini ex É. Bornet & C. Flahault — These filamentous cyanobacteria are members of the Rivulariaceae; their trichomes have a basal heterocyte and gradually narrow towards the apex. The two genera are morphologically similar and both have been reported as lichen photobionts, particularly in association with certain species of Lichina (see Tschermak-Woess 1988a). However, DNA sequences obtained from two such examples instead placed the algae in question in the genus Rivularia (Ortiz-Álvarez et al. 2015). The photobiont of Placynthium nigrum isolated into culture also shows the distinctive Rivulariaceae morphology (apically tapering filaments with basal heterocytes) while the lichenized filaments rather resemble those now placed in Rhizomena (see Geitler 1934). The circumscription of Calothrix and Dichothrix with respect to lichen photobionts currently remains unresolved.

Chroococciidiopsis Geitler (and Myxosarcina H. Printz) — These unicellular cyanobacteria are found in a great diversity of habitats and include extremophiles. Cells divide in sequence by binary fission, often in alternating planes to produce more or less cubical packages of cells. Cells can also undergo multiple fission, often in alternating planes to produce more or less unicellular cyanobacteria are found in a great diversity of habitats and include extremophiles. Cells divide in sequence by binary fission, often in alternating planes to produce more or less cubical packages of cells. Cells can also undergo multiple fission, often in alternating planes to produce more or less

Chroococcus Nägeli — A morphologically distinctive cyanobacterial genus, Chroococcus has relatively large, spherical cells that divide at consecutive right angles to produce small packets of cells, often within concentric, gelatinous sheath layers. A number of reports, compiled by Tschermak-Woess (1988a), attribute thallus and cephalodial photobionts of various lichens to this genus or merely to Chroococcaceae, or Chroococcales. Many are anecdotal and most await reinvestigation with molecular sequence comparisons. The photobionts of certain Dictyonema species, once attributed to Chroococcus, have been shown to belong instead to Rhizomena, a usually filamentous taxon that may be greatly altered morphologically in certain lichen associations (Lücking et al. 2009). The circumscription of Chroococcus and its status as a lichen photobiont genus remain uncertain at present.

Gloeocapsa Kützing — This colonial cyanobacterium has roundish to oblong cells surrounded individually and communally by successive layers of dense mucilage, reflecting the sequence of cell divisions. Morphologically defined at present, Gloeocapsa commonly occurs free-living in moist terrestrial habitats and is also reported as thallus photobiont in several genera of Lichinaceae, and as cephalodial symbiont in certain species of Stereocaulon and Amygdalaria (Tschermak-Woess 1988a). In the lichen Gonohymenia, contacting mycobiont hyphae broadly invaginate the cells of its photobiont, identified as Gloeocapsa (Paran et al. 1971). Geitler (1933) described appressorial hyphae in the lichen Synalissa that branch in synchrony with the binary fission of its Gloeocapsa photobiont. Molecular sequence data are much needed to understand the relationship among taxa currently assigned to Gloeocapsa.

Hyella É. Bornet & C. Flahault — The filamentous cyanobacterium Hyella is a widespread inhabitant of the marine intertidal zone, where it colonizes calcareous substrata such as mollusc shells. The substratum is penetrated by threads arising from a basal system at the surface; endospore-like baecocytes may be formed (Fritsch 1945). Genomic analysis shows Hyella phylogenetically nearest to the genus Chroococcidiopsis (Brito et al. 2020). Hyella is reported to be the photobiont of some species of fungi now assigned to Collemopsisidium (Mohr et al. 2004). However, details of the symbiotic interaction are few; other genera of cyanobacteria, such as Gloeocapsa and Nostoc, are also said to be photobionts for Collemopsisidium [=Pyrenocollema] (Purvis et al. 1992).

Hyphomorpha A. Borzi — These seldom encountered cyanobacteria occur as epiphytes upon tropical liverworts and tree bark, where they form a prostrate filament system. The filaments have an apical cell producing derivatives that may later divide periclinally to become pluriseriate, as do structurally similar species of Sterigmena. Cells of these older portions tend to fall out of alignment and become jumbled into a ‘chroococcoid stage’ (Fritsch 1945). Hyphomorpha was first identified as photobiont in two species of Spilonema lichens by Henssen (1981), who reported confirmation of the alga’s identity by eminent phycologist Lothar Geitler. One of these mycobiont species has been recently reclassified as Erinacellus dendroides (Spribille et al. 2014). At present, the algal genus Hyphomorpha is phenotypically defined; it is currently placed in Fischerellaceae (Büdel & Kauff 2012) or included under Halosiphonaceae (Komárk et al. 2014) within the Nostocales.
Nostoc Vaucher ex É. Bornet & C. Flahault — This genus accommodates cyanobacteria occurring worldwide in fresh water and upon soil, bark and low-growing plants, with some strains highly desiccation-tolerant (Dodds et al. 1995). Phytotypically defined at present, taxa attributed to Nostoc fall within several distinct clades of the Nostocales, making the genus polyphyletic (Rajaniemi et al. 2005; Gaganavishvili & Andrésson 2018). These algae typically form darkly pigmented, mucilaginous macrocolonies of highly variable size and shape, ranging from spheres to irregularly pustulose mats to tangles of cord-like axes. Embedded within the gelatinous matrix are uniseriate trichomes markedly constricted at the cross walls, giving individual cells an almost spherical to barrel-shaped form and the filaments a characteristic string-of-beads appearance. Cell division is diffuse, without apical cells or directional polarity. At intervals along the chain of vegetative cells are slightly larger, thicker-walled, lighter-coloured heterocytes (heterocysts) that specialize as centres of nitrogen fixation. Since the enzyme involved in this process is inhibited by the presence of oxygen, heterocytes lack oxygen-generating Photosystem II (Wolk et al. 1994); electron donors are imported and fixed nitrogen is exported via microplasmodesmal connections with neighbouring vegetative cells (Giddings & Stæhelin 1981; Kumar et al. 2010). Thus, prokaryotic Nostoc and its heterocytic relatives show degrees of cell specialization and intercellular transport characteristic of true multicellular organization (Garcia-Pichel 2009).

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Pannaria and other cyanophilic lichens, both corticolous and saxicolous species sometimes chose closely related strains of Nostoc, and more complex combinations of variable mycobiont selectivity and ecological factors were observed (Elvebakk et al. 2008).

Nostoc participates in a range of symbioses besides those it forms with lichen-forming fungi (Adams et al. 2012). It is taken up by the locally emergent protoplast of the coenocytic, glomeromycete fungus Geosiphon pyriformis, which then produces a swollen bladder within which the endosymbiotic (endocytobiotic) Nostoc is housed. The intracellular location of the algal symbiont and the close affinities of the fungal component to arbucular mycorrhizal fungi make the Geosiphon-Nostoc symbiosis quite distinct from fungal-algal symbioses treated under the lichen concept (Klüge et al. 2002; Schüßler 2012). Nostoc also includes obligatory partners of plants representing several major clades of embryophytes; motile hormogonia are the usual infective agent, and fixed mucilage-secreting chambers within the gametophytes colonies (Rodgers & Stewart 1977). In cycad gymnosperms, increase surface contact between the host and the cyanobacterial from the inner surfaces of these chambers then develop, mucilage-secreting chambers within the gametophytes (Adams & Duggan 2002). Branched filamentous outgrowths from the inner surfaces of these chambers then develop and increase surface contact between the host and the cyanobacterial colonies (Rodgers & Stewart 1977). In cycad gymnosperms, Nostoc colonizes radial cavities in the cortex of specialized, upward-growing coralloid roots (Costa & Lindblad 2002). Symbiosis with the floating aquatic fern Azolla is unique in that the Nostoc (or Anabaena; Svending et al. 2005) is vertically inherited through plant generations, obviating the need for new symbiont capture; the principal cyanobacterium involved cannot be cultivated separately, since its genome shows considerable gene degradation (Ran et al. 2010). In the angiosperm Gunnera, symbiotic Nostoc occurs intracellularly in leaf base tissue (Bergman et al. 1992). Some of these symbiotic strains, as well as free-living isolates, appear to be similar or closely related to those occurring within lichen thalli or cephalodia, whereas certain other Nostoc strains might be more specialized as lichen photobionts (O’Brien et al. 2005; Stenroos et al. 2006). Recent genomic comparisons identified certain genes of potential relevance to symbiosis in Nostoc, suggesting also that symbiotic strains may have larger genomes than non-symbiotic ones (Gagunashvili & Andrésson 2018).

Rhizonema Lücking & Barrie — This cyanobacterial genus was resurrected recently to accommodate filamentous, heterocyte-producing photobionts previously assumed to belong to Scytonema, but distinct from that lineage in their 16S rRNA sequences (Lücking et al. 2009). Rhizonema species may be boreal as well as tropical; they are at present known mainly from lichen symbioses but free-living or liverwort-associated populations have also been reported (Cornejo et al. 2016). The filaments may be broken up into cell clusters or remain as discrete trichomes (Fig. 1E & F), with sporadic lateral proliferation that has been interpreted as true branching based on the appearance of a mature branch junction (Lücking et al. 2014). This would presumably distinguish Rhizonema from Scytonema, which shows false branching. Thus, when Vô (2016) observed paired false branching in photobionts of Vietnamese Cyphellostereum and Dictyotena, she concluded that the algae were Scytonema rather than Rhizonema, apparently without corroborating molecular data. However, recent observations of Rhizonema, isolated into culture from Dictyotena and identified with genetic sequence comparisons, show branching that appears distinctly false (Fig. 1D). Interestingly, a 19th century illustration of a Dictyotena seri- ceum thallus (Bornet 1873: plate 12) depicted the photobiont with both double-false branching and seemingly true branching with a junction similar to that shown in Lücking et al. (2014). The range of branch development modes possible in Rhizonema strains clearly requires further study in both lichenized and aposymbiotic material.

Major genera of lichen-forming fungal partners known so far include Coccocarpia, Erioderma (Peligerales), and the basidiomycetes Acantholichen, Dictyotena, Cora, Corella and Cyphellostereum (all Hygrophoraceae). In those basidiolichens, the Rhizonema trichome is usually penetrated longitudinally by a single, central mycobiont haustorium quite unlike anything reported in other lichen groups (Roskin 1970; Oberwinkler 1980, 1984, 2012; Slocum 1980; Tschermark-Woess 1983). Such elaborate intrusive structures differ dramatically from the very limited penetrations known in other lichenized algae and might represent specialized absorptive structures. Carbon transfer has not yet been studied in basidiolichens.

Rivularia C. Agardh ex É. Bornet & C. Flahault — The trichomes of this cyanobacterial genus occur in clusters, often on submerged rocks; each filament has a heterocyte at the base and tends to taper gradually towards the apex. The genus includes the photobionts of a couple of maritime species of Lichina, whose algal symbionts were previously attributed to the morphologically similar genus Calothrix (Ortiz-Álvarez et al. 2015).

Scytonema C. Agardh ex É. Bornet & C. Flahault — This aquatic or aerophilic genus of cyanobacteria has trichome walls unconstricted at the septa, with vegetative cells usually wider than long, prominent heterocytes, and thick sheaths that are often darkly pigmented. Scytonema is traditionally recognized by the frequently paired (‘double’) false branches, where segments created by a break in the trichome continue linear growth by simply reorienting laterally and emerging from their formerly common sheath. Trichome breaks may arise where intercellular material is deposited as a separation disc, or one or more cells degenerate, or at intercalary heterocyte positions (Bhāradwāja 1933). Once considered a significant photobiont genus, including both principal and secondary (cephalodial) lichen symbionts, Scytonema in its current sense encompasses an uncertain but much reduced number of lichen algae. Photobionts previously ascribed to Scytonema have been shown by DNA sequence analyses to belong to a quite distinct clade, now designated Rhizonema (Lücking et al. 2009). Nevertheless, at least one recent photobiont sequence (16s rRNA), from a Heppia thallus, appears to fall within Scytonema in the strict sense (Vô 2016). This may provide some corroboration for previous attributions of Heppia photobionts to Scytonema based on morphology of cultured isolates (Wetmore 1970). The cell shape and division planes of the Heppia photobionts are radially transformed to produce cell clusters in the lichenized state, reverting quickly to typical filamentous growth when cultured aposymbiotically (Marton & Galun 1976). In
Pyrenothrix nigra, the lichenized filamentous cyanobiont shows the double-false branching typical of Scytonema (Tschermak-Woess et al. 1983), although Lücking et al. (2009) suggested that its photobiont might be Rhizomonas. This is quite plausible, since there is some doubt as to whether the two cyanobacterial genera can be reliably distinguished by their mode of branching (see comments under Rhizomonas). More sequence data are clearly needed to clarify the extent to which lichen symbioses may involve the genus Scytonema in its current, more restricted sense.

Stigonema C. Agardh ex É. Bornet & C. Flahault — This cyanobacterial genus is recognized by its complex, branching axes with cells dividing in perpendicular planes as in true parenchyma. Filaments are uniseriate at the apex but become locally multiserial proximally by periclinal divisions, often but not necessarily associated with the formation of true branches laterally. After division, cells retain continuity at the central portion of the septum, where micropores traverse the septal wall (Butler & Allsopp 1972). Stigonema has been reported as thallus photobiont in Ephebe and Spilonema, and also as cephalodial partner in numerous species of Stereocaulon (Tschermak-Woess 1988a). The genus awaits molecular treatment, remaining morphologically defined for the time being.

Tolypothrix Kützing ex É. Bornet & C. Flahault — These are filamentous cyanobacteria resembling Scytonema but with usually single- rather than double-false branches emerging from filament breaks; one side of the break grows out as the false branch, the other usually differentiates as a heterocyte. Tolypothrix has been reported as photobiont of the ‘primitive lichenized’ Thermotopsis jamaicensis based on morphology in collected material (Henssen 1990). Molecular sequences obtained from cahelodila of Placopsis placed the cyanobionts in or near Tolypothrix (Raggio et al. 2012).

Green algae (Viridiplantae – Archaeoplastida)

Apatococcus F. Brand — Abundant and widely distributed as a free-living organism, Apatococcus has long been known as an omnipresent subaerial unicellular alga, inevitably encountered but not chosen by discriminating germling hyphae of lichen-forming fungi. Now it appears that Apatococcus includes lichen symbionts as well. Light microscopic observations of algal symbionts cultured from several maritime lichen species first implicated Apatococcus as a photobiont (Watanabe et al. 1997); molecular sequence comparisons later identified Apatococcus strains as partners of Scilicosporum (Beck 2002) and Fusicida species (Zahradníková et al. 2017). Cells are spherical with alternating perpendicular planes of division, producing cuboidal packets of transiently adherent daughter cells. Autospores and billagelate zoospores are also formed (Ettl & Gärtner 2014). Autospores may be of unequal size within a sporangium (Gärtner & Ingolić 1989), as also occurs in Watanababean genera such as Chloroidium and Jaagichlorella. As with Elliptochloris and Trebouxia, Apatococcus is facultatively heterotrophic; it is very slow growing in culture unless carbohydrate is supplied (Gustavs et al. 2016). This observation is particularly interesting because the similarly heterotrophic behaviour of Trebouxia in culture was central to Ahmadjan’s (1988, 2002) argument that Trebouxia cannot exist free-living. The seemingly ubiquitous Apatococcus shows quite clearly that a photobiont exhibiting strongly heterotrophic tendencies in culture may nonetheless abound free-living in nature.

Asterochloris Tschermak-Woess — First described to accommodate the trebouxioid photobiont of a single lichen in the Pertusariaceae (Tschermak-Woess 1980a), this major photobiont clade now encompasses the former Trebouxia subgenus Eleutherococcus (Tschermak-Woess 1989; Škaloud & Peksa 2010). It corresponds roughly to Archibald’s (1975) restricted concept of genus Trebouxia, a source of continual confusion. Asterochloris species produce aplanospores, or zoospores in culture, but most strains do not form the appressed, low-number autospores characteristic of Trebouxia in the current sense. Its deeply-lobed chloroplast becomes flattened and parietal during cell division, while that of Trebouxia remains more or less central (Tschermak-Woess 1989). Pyrenoids are present; in TEM they may be distinguished as the irregularis-, erici-, or magna-types of Friedl (1989). Chloroplast morphology is highly variable and its utility as a marker in species delimitation was emphasized by Škaloud et al. (2015). As with Trebouxia, a considerable amount of genetic diversity is revealed at the molecular level in Asterochloris (Škaloud & Peksa 2010; Peksa & Škaloud 2011).

Sexual fusion of biflagellate isogametes to form a quadriflagellate zygote has been documented in cultures of A. woessiae (Škaloud et al. 2015). The detection of genes specific to meiosis in A. glomerata (Armaleo et al. 2019) provides further support for a functioning sexual cycle in Asterochloris.

Asterochloris is associated principally with mycobionts of the Cladoniaceae, Stereoculaecae, and the genus Lepraria. These fungal partners appear to range from moderately to rather highly selective of their Asterochloris symbionts; there is also some indication that mycobionts of different clades are choosing particular Asterochloris lineages, showing distinct climatic preferences related to rainfall regime (Peksa & Škaloud 2011).

Auxenochlorella (I. Shihira & R. W. Krauss) T. Kalina & M. Puncchárová — Within the Chlorellaceae, Auxenochlorella is related to the fully heterotrophic genus Prototheca, and its type species, A. protothecoides, is also known for its heterotrophic tendencies in culture (Darienko & Pröschold 2015). Auxenochlorella has been implicated in regard to the identity of the photobiont associated with Psoroglaena stigonemoides in the Verruciaceae (Nyati et al. 2007; Thüss et al. 2011). Unlike Chlorella, Auxenochlorella lacks a pyrenoid. The genus also includes ‘zoochlorellae’ symbionts of the cnidian Hydra that are now considered a new species, A. symbiontica (Darienko & Pröschold 2015).

Bracteacoccus Tereg — Bracteacoccus are small, spherical unicells that have a multinucleate stage as they mature, and reproduce by zoospores or aplanospores; chloroplasts lack pyrenoids (Kouwets 1996). Currently included in the Sphaeropleales (Fučíková et al. 2014), Bracteacoccus appears at present to be the only genus of the class Chlorophyceae into which lichen photobionts have been placed with supporting DNA sequence data. The corresponding mycobionts are two species of the basidiomycete Salzbacteromyces in the Lepidostomatales (Hodkinson et al. 2014; Masumoto 2020).

Cephaleuros Kunze ex E. M. Fries — These foliicolous relatives of Trentepohlia form macroscopic, multicellular thalli visible as
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small, fuzzy yellow-orange patches on leaves and fruit in tropical and subtropical climates. *Cephaleuros* species typically grow beneath the cuticle of the leaf substratum, forming rounded to lobed thalli of more or less integrated horizontal filaments. These give rise to the erect setae and sporangiophores that emerge through the overlying cuticle. Usually, *Cephaleuros* develops within the space it excavates between the host cuticle and epidermis; in some cases, filaments penetrate deeper among the epidermal or mesophyll cells of the leaf, provoking a localized phellogen wound response. The alga can therefore be mildly pathogenic, but it is more often described as 'parasitic', despite an absence of information concerning any nutritional exchange with the plant host. Occasionally, the alga may develop upon the leaf cuticle, like other epiphylls. The behaviour may vary according to the species of *Cephaleuros* or that of the host plant (Ward 1884; Suto & Ohtani 2009; Brooks et al. 2015). Lichenization by foliicolous *Strigula* fungi is said to curb the alga’s invasion of host tissue and its localized pathogenic effects (Joubert & Rijkenberg 1971).

 Morphologically, *Cephaleuros* can somewhat resemble the related foliicolous genus *Phycopeltis*, which is not subcuticular and generally lacks vertical hairs and complex, long-stalked sporangiophores. According to molecular sequence analyses, however, the nearest relatives of *Cephaleuros* lie not within *Phycopeltis* but rather *Stomatochroon* (Zhu et al. 2017), a microscopic colonizer of the leaf’s substomatal cavities. While trentepohliaceous taxa currently ascribed to *Phycopeltis* and *Trentepohlia* are phylogenetically intertwined, *Cephaleuros* appears to be essentially monophyletic (López-Bautista et al. 2016; Rindi et al. 2009; Nelsen et al. 2011; Zhu et al. 2017).

*Cephaleuros* is one of the few lichen photobiont genera for which life cycle events have been observed in some detail. Thompson & Wujek (1997) describe a haplodiplontic life cycle with heteromorphic multicellular phases. The familiar thallus corresponds to the gametophyte; fusion of gametes produces a zygote that germinates directly as zoosporangia. Flagellate sporophytes bearing a putative meiosporangium. Flagellate cells and sexual reproduction are unknown. True *Chlorella* also includes a number of mucilaginous, colonial forms in its current circumscription (Luo et al. 2010; Bock et al. 2011). Many of the lichen photobionts previously attributed to *Chlorella* s. lat. (e.g. Tschermak-Woess 1988a) are among those taxa moved to other genera, especially *Chlororidium*; others await re-examination. At present, only a couple of lichen-forming fungal species have been observed to fruit within the *Chlorella* genus. *Chlororidium* others remain to be identified with certainty. Molecular sequences confirm that true *Chlorella* occurs as endosymbionts of the ciliate *Paramecium bursaria* (Hoshina et al. 2004; Summerer et al. 2008) and the cnidarian *Hydra* (Kovačević et al. 2010), which may also utilize *Auxenochlorella* as its algal symbiont (Pröschold et al. 2011). Chloroplast ultrastructure likewise suggests that the green endosymbiont of the colonial ciliate *Ophrydium versatill* is a true *Chlorella* (Forsberg & Lindblad 1996). However, the phylogenetic affinities of other ‘zoochlorellal’ symbionts appear to fall elsewhere in the advanced stages of development may produce abundant sporangia from portions of its thalli remaining relatively free of mycobiont domination. Interestingly, both symbionts grow and sporulate independently upon the leaf substratum, although the fungus *Strigula* will produce pycnidia and perithecia only after successful lichenization. These observations highlight the flexibility of the symbionts in this particular association.

Chlamydomonas Ehrenberg — This well-known unicellular green algal genus chiefly encompasses aquatic taxa that are flagellate in the vegetative state and unlikely candidates for lichen symbiosis. However, a number of aeroterrestrial species are also known (Ettl & Gärnter 2014). One species of *Chlamydomonas* (*C. augustae*) was described in association with the ascomycete *Pyronema laetissimum*, growing on leaf litter in Latvia (Skuja 1943). It was included in Tschermak-Woess’s (1988a) review of phycobionts as ‘facultatively lichenized’. However, Skuja’s (1943) distinguished this association from lichen and lichenoid symbioses, making comparisons instead with green algae known to grow abundantly on the surfaces of perennial basidiocarps. The *Chlamydomonas* was abundantly present among the dense hyphal base below the *Pyronema* apothecium, but no tissue layer was differentiated, nor were any distinctive contact interfaces noted between symbionts. Skuja also mentioned that other apothecia of the same fungus were fruiting nearby without the alga present. The operculate discomycetes (*Pezizales*), to which *Pyronema* belongs, are not otherwise known to include lichen-forming members. The *Pyronema-Chlamydomonas* association is worthy of further investigation but seems unlikely to fit the criteria usually ascribed to lichen symbioses.

Chlorella Beijerinck — A once-notorious miscellany of indistinguishable ‘little round green things’, this trebouxiophycean genus has been radically deconstructed, particularly with the help of DNA sequence comparisons (Huss et al. 1999). Many formerly included species have been moved to different genera, orders, even classes, while taxa surrounding the type species *C. vulgaris*, and *C. sorokiniana*, are retained as true *Chlorella*. In TEM, they show a distinctive pyrenoid surrounded by a thick sheath of starch and bisected centrally by a single thylakoid (Ikeda & Takeda 1995; Němcová & Kalina 2000; Hoshina et al. 2010). Flagellate cells and sexual reproduction are unknown. True *Chlorella* also includes a number of mucilaginous, colonial forms in its current circumscription (Luo et al. 2010; Bock et al. 2011). Many of the lichen photobionts previously attributed to *Chlorella* s. lat. (e.g. Tschermak-Woess 1988a) are among those taxa moved to other genera, especially *Chlororidium*; others await re-examination. At present, only a couple of lichen-forming fungal species have been observed to co-occur with *Chlorella*.*
Chlorosarcinopsis Nadson — Resurrected to accommodate segregates from Chlorella s. lat. (Darienko et al. 2010). Chloriodium falls within the trebouxiophycean assemblage now formalized as Watanabeales (Li et al. 2021). Cells have a parietal chloroplast with or without a pyrenoid; in C. saccharophilum, a prominent pyrenoid with surrounding plastoglobuli and traversing membranes has been observed (González et al. 2013). Reproduction is by autospores, often of variable number and different sizes within a single sporangium. The genus encompasses diverse taxa found in a wide variety of habitats (Darienko et al. 2018), including extremophiles capable of using a variety of carbon sources (Nelson et al. 2017). Since its recent emendation, Chloriodium includes photobiont partners of a growing number of lichen-forming fungi, including some species of Gomphillaeae, Verrucariaceae, Psora, Stereocaulon and Sticta.

Chlorosarcinopsis Herndon — In the course of her studies on lichen haustoria, Plessl (1963) identified as Chlorosarcina [=Chlorosarcinopsis] minor the photobionts she isolated from two species of Lecidea, L. plana and L. lapicida. Chlorosarcinopsis has traditionally accommodated spherical unicellular green algae dividing to form cuboidal packets. According to Neustupa (2015), the genus is polyphyletic, with members scattered among the Chlamydomonadales (Chlorophyceae). As this clade is not otherwise known for lichen symbionts (but see Skuja 1943), the photobionts of the Lecidea species in question need further study.

Cocccobotrys Chodat (now Uvulifera Molinari-Novoa) — This green alga forms irregular cuboidal cell packages or branched multisierate filaments in culture (Neustupa 2015). The genus Cocccobotrys was described by Chodat (1913) and emended by Vischer (1960) to accommodate the putative photobiont C. verrucariae isolated from a thallus of Verrucaria nigrescens. Thüs et al. (2011), on the other hand, reported Diplosphaera as photobiont of the V. nigrescens thallus they sampled. Cocccobotrys verrucariae was also cited with microscopy as ‘probably Cocccobotrys’ (Canals et al. 1997) was isolated from Botrylepraria lesdainii, another member of the Verrucariales (Kukwa & Pérez-Ortega 2010). A second species of Cocccobotrys was described by Warén (1920) as the photobiont of Lecidea fulgina, but Tschermak-Woess (1988a) expressed doubt that the alga he described belongs in Cocccobotrys. The photobiont status of species in this genus should be corroborated. Genetic sequence analyses place Cocccobotrys in the Trebouxiophyceae (e.g. Thüs et al. 2011; Mikhail'yuk et al. 2020), but its affinities among the defined clades within this class remain uncertain. Molinari-Novoa (2016) recently found Cocccobotrys Chodat to be a later homonym of a name applied to an anamorphic basidiomycete and renamed the algal genus Uvulifera.

Coccomyxa Schmidle — This trebouxiophycean algal genus is notable for the diversity of habitats and ecological circumstances in which its species are known to occur. Environmental surveys have found Coccomyxa sequences to be among the most widely distributed OTUs, and notably well represented in cold high-latitude climates (Metz et al. 2019). It is commonly reported free-living on terrestrial substrata and in aquatic environments, including those highly polluted with heavy metals and radioactive materials (see Gustavs et al. 2017). Coccomyxa species are subspherical to ovoid-ellipsoidal unicells, often embedded colonially in thick gelatinous sheath material with concentric layering that reflects the cell division pattern. The chloroplast is parietal, not markedly lobed, and lacks a pyrenoid. In TEM, thylakoid bands often show a distinctly longitudinal orientation over the length of the chloroplast, with interspersed starch grains (Peveling & Galun 1976; Palmqvist et al. 1997). Flagellate cells and sexual reproduction are unknown; cells subdivide into packages of 2–8 autospores (Tschermak-Woess 1988a). Recent assessments of species number within the genus range from seven (Darienko et al. 2010) to as many as 27 (Malavasi et al. 2016). The genus is thought to include the photobionts of diverse lichen-forming fungi, such as species of Icmadophila, Micarea, Nephroma, Peligeria, Solorina, the stalked-apheliate genera Baecomyces, Dibaecis and Phyllobaeis, and the basidiomycete Lichenomalphalia (Table 1). Some of these reports await confirmation with genetic sequence data. The photobionts do not form a single clade but instead represent several distinct lineages within Coccomyxa, intermixed among free-living isolates (Darienko et al. 2015). In lichen symbiosis, the cells are often more spheroidal, and extensive gelatinous sheath material is not usually produced (Tschermak-Woess 1988a). Interestingly, while the cells of Coccomyxa and Elliptochloris photobionts are tightly enveloped by mycobiont hyphae, their walls are usually not penetrated (Tschermak 1941a; Geitler 1955; Plessl 1963; but see Coppins 1983: figs 2 & 55). This has been attributed to degradation-resistant polymers resembling sporopollenin in the multi-layered cell wall (Honegger & Brunner 1981; Brunner & Honegger 1985). However, Coccomyxa cells are fully penetrated by Aphelidium collabens, a parasitic basal within, or sister to, the kingdom Fungi (Seto et al. 2020).

Species of the genus Coccomyxa also live in poorly understood symbioses within molluscs (Stevenson & South 1974; Syasina et al. 2012) and echinoderms, and endocytotically within ovules and other tissues of the gymnosperm Ginkgo biloba (Trémouillaux-Guiller et al. 2002; Trémouillaux-Guiller & Huss 2007). Molecular sequence comparisons have shown that some zoochlorellae isolated from certain strains of Paramecium bursaria correspond to Coccomyxa, while most others are true Chlorella (Hoshina & Imamura 2008).

Deuterostichochoccus Pröschold & Darienko — A recent segregate of Stichococcus s. lat. (Pröschold & Darienko 2020), this trebouxio-
phycean genus currently includes, in addition to free-living iso-
lates, the photobiont of two Placopsis species (Beck et al. 2019) and Staurothele clopima (Hodač et al. 2016); the latter is also known to partner with Diplosphaera algae (Thüs et al. 2011).

Dictychloropsis Geitler — See Symbiochloris.

Dilabifilum Tschermak-Woess — Polymorphic, unicellular to sar-
cinoid to filamentous algae with pyrenoids and quadriflagellate zoospores have been included in this ulvalean genus. They occur free-living, as photobionts, or both. Recently, Darienko & Pröschold (2017) deconstructed Dilabifilum, recognizing at generic level several distinct clades resolved in their gene-based
Elliptochloris Bialosuknia — This prasialoane genera appears to contain the majority of the unicellular photobiont strains attributed until recently to the related Stichococcus. Apparently, the two morphologically plastic genera are often not distinguishable microscopically, although Diplosphaera may produce distinctive, adherent two-celled clusters in division. Pyrenoids may be absent (Pröschold & Darienko 2020) or weakly visible (Ettl & Gärnter 2014) but some taxa falling within the Diplosphaera clade, including lichen photobionts, show prominent pyrenoids in TEM (Fig. 2E). The main fungal partners of Diplosphaera are members of the Verrucariaceae. Photobiont strains compared so far appear to represent the same species and are similar to free-living collections (Pröschold & Darienko 2020).

In association with certain lichen genera, such as Endocarpon and Staurothelium, Diplosphaera photobionts ‘escape’ vegetative hyphal contacts and penetrate into the hymenial layer of developing perithecia, where they freely intermix among the asci (Fig. 3A). These algal cells are typically much smaller than those within the algal layer of the vegetative thallus; they scatter everywhere when a hand-cut section is water-mounted, indicating that unlike the photobionts in the vegetative thallus, those entering the perithecia are not bound in place by lichenizing contacts with the mycobiont. The unassociated photobionts may adhere to the large ascospores as they are ejected, and can be dispersed with them. Many readily detach and divide apysymbiotically; they are available to the mycobiont if the spore germinates successfully (Stahl 1877; Bertsch & Butin 1967; Ahmadjian & Heikkilä 1970) or might otherwise divide to form free-living populations. Potentially co-dispersable photobionts also occur in the conidiomata and ascomal epithecia of many foliicolous lichens of the Verrucariaceae. Dispersal of liberated photobionts may thereby provide a direct connection between lichenized and free-living populations of the alga.

Elliptochloris Tschermak-Woess — Like its sister genera Coccomyxa, Elliptochloris has subspherical to ellipsoidal unicells with a parietal chloroplast, bearing two opposed indentations in the type species E. bilobata (Tschermak-Woess 1980b). Sexual or flagellate stages are unknown; reproduction occurs by autospores, of which there are usually two morphologically distinct types. Autosporangia may contain a low number (usually four in cultured E. bilobata) of spherical spores appressed together at flattened junctions, or more numerous (16–32) cylindrical-ellipsoidal spores (Tschermak-Woess 1980b; Darienko et al. 2016). The multilayered cell wall, as in Coccomyxa, is impregnated with degradation-resistant polymers, which are thought to explain the lack of haustorial penetration by their lichen-forming partners (Brunner & Honegger 1985). However, haustoria have been noted in certain species of Micarea (Coppen 1983: figs 2 & 55), a lichen-forming genus known to partner with Elliptochloris and Coccomyxa photobionts. Unlike Coccomyxa, at least some species of Elliptochloris possess pyrenoids, and layered mucilaginous sheaths are typically lacking. However, gelatinous extracellular material may be copious in free-living populations, and was observed in association with Protothelena thalli where the photobiont population grew beyond the reach of mycobiont hyphae (Tschermak-Woess 1985).

Elliptochloris is somewhat less often reported than Coccomyxa but is known from a similarly diverse array of habitats. It is said to be quite strongly heterotrophic in culture, where it depends heavily on organic materials to thrive; this might in part account for its less frequent recovery in isolation procedures (Gustav et al. 2017). Species of Elliptochloris are known to partner with mycobionts of diverse genera including Catillaria, Catolechia, Fuscidea, Micarea, Sticta, Stictis, Verrucaria, and the basidiolichen-forming Bryoalvala and Multicavula (see Table 1). They also occur as endosymbionts of the marine anemone Anthopleura (Letch et al. 2009).

Gloecystis Nägeli — Taxa treated under this genus are unicellular green algae that form occasionally macroscopic colonies of ellipsoidal cells with a parietal chloroplast possessing a pyrenoid. Thick, colourless, often layered gelatinous sheaths surround the cells. Reports of Gloecystis as photobiont of Cryptidiscus [Bryophagus] gloecapsa and Epigloea batractosa were cited by Ahmadjian (1967) and Tschermak-Woess (1988a). There is doubt as to whether Epigloea is lichenized (Kirk et al. 2001; not included in Lücking et al. 2017a), although distinctly symbiotic contacts with living, unicellular green algae were illustrated by Jaag & Thomas (1934) and Döblinger (1984).

According to Neustupa (2015), the algal genus Gloecystis is highly polyphyletic, encompassing members of both Chlorophyceae and Trebouxiophyceae. The identities of the photobionts associated with the mycobionts mentioned above will therefore require further study.

Halofilum Darienko & Pröschold — This is another genus that now accommodates taxa previously treated under Dilabilium (Darienko & Pröschold 2017). These algae consist of branched filaments with parietal chloroplasts containing pyrenoids; flagellated stages are unknown. The species H. ramosum occurs as photobiont of Hydropunctaria maura and Wahlenbergiella strictula (Verrucariaceae), as well as free-living (Darienko & Pröschold 2017).

Heveochlorella J. Zhang et al. — Unicellular algae attributed to Heveochlorella have a prominent, somewhat lobed chloroplast with a central pyrenoid that is readily visible with light microscopy. TEM shows the pyrenoid surrounded by several irregular starch plates and penetrated centripetally by thylakoid-derived tubules that are lined with pyrenoglobuli (Fig. 2B). Cells reproduce by autospores, usually in low number (2–8) and not infrequently of unequal size within sporangia, at least in culture (Zhang et al. 2008; Ma et al. 2013; Sanders et al. 2016). Darienko & Pröschold (2019) recently subsumed both Heveochlorella (Zhang et al. 2008) and the related Heterochlorella (Neustupa et al. 2009), which has not been reported from lichen symbioses, into the resurrected genus Jaugiclorella. These algae belong to the trebouxiophyccean clade recently formalized as Watanabeales (Li et al. 2021).

The first indication that lichen symbionts belonged in this group was the report of Heveochlorella isolated as photobiont from one specimen of Sticta and two of Pseudocyphellaria from Taiwan (Dal Grande et al. 2014b). Soon thereafter, the ‘trebouxioid’ photobionts associated with folicious
**Leptosira** and **Pilocarpaceae** were also attributed to this genus (Sanders *et al*. 2016). More recently, a study of **Sticta** lichens worldwide reported **Heveochlorella** to be the photobiont of numerous specimens from New Zealand and Indian Ocean islands, including six identified species and many undetermined collections (Lindgren *et al*. 2020). In the opinion of Darienko & Pröschold (2019), the algae encompassed by **Jaagichlorella**, though distributed worldwide, are rare taxa. While more surveys will be necessary to evaluate this view, a number of observations suggest that these algae might be in fact quite common and merely overlooked. We know, for example, that folicolous lichens of the **Gomphillaceae** and **Pilocarpaceae** occur in abundance throughout much of the humid tropics (Santesson 1952; Lücking 2008), although it is not yet clear how consistently they harbour **Heveochlorella** (**Jaagichlorella**) photobionts. Recent sampling of the phyllosphere community in Asian tropical forests has revealed a major representation of **Heveochlorella** genotypes (Zhu *et al*. 2018), as well as several new species in related genera (Li *et al*. 2020, 2021). Some of the most frequently detected OTUs in environmental surveys of marine habitats (Metc *et al*. 2019) were also attributed to **Heveochlorella**.

In many folicolous lichens, dividing **Heveochlorella** photobionts may escape the lichenizing vegetative hyphae and proliferate among the spore-generating fungal structures, upon apothecia and within specialized conidiomata such as campylium and hyphophores (Fig. 3B & C). They can be dispersed from these structures, as are the fungal spores or diahyphae to which the algal cells may adhere (Fig. 3D–F). Once dispersed, they may become lichenized by the germinating fungal propagules, or divide to produce independent populations on the substratum (Sanders 2014; Sanders & de los Ríos 2015). Co-dispersal and relichenization thereby provide **Heveochlorella** with abundant opportunities for exchange between lichenized and free-living populations.

**Interfilum** Chodat — This genus of aeroterrestrial charophytes (Streptophyta) includes taxa that form single, paired or sacronoid packets of cells or grow filamentously, often closely resembling unrelated **Chlorophyta**, such as Desmococcus (Mikhailyuk *et al*. 2008). It is sister to clades of the widely distributed Klebsormidium (Rindi *et al*. 2011). **Interfilum** was reported by Voytskevich *et al*. (2011) as a secondary photobiont within the algal layer of Micarea and Placynthiella thalli collected in Ukraine, based on light microscopic examination of thalli and cultured isolates. The principal photobionts in those lichens were reported to be Elliptochloris and Radiococcus, respectively. As the charophytes are not otherwise known as lichen symbionts, and other algal genera were cited as the main photobionts within the thalli in question, further study of the reported associations is warranted.

**Jaagichlorella** Reisigl — See **Heveochlorella**.

**Leptosira** A. Borzí — This photobiont grows asunicells tightly wrapped by mycobiont hyphae or separated by copious sheath material free of the mycobiont; in agar culture, it produces short filaments (Tschermak-Woess 1953). **Leptosira** is a trebouxiothecan of uncertain placement, appearing in the vicinity of the Microthamniales clade in recent gene-based phylogenies (Lemieux *et al*. 2014; Neustupa 2015; Hallmann *et al*. 2016). According to Mattox & Stewart (1984), ’Pleurastrum terrestré’ (a synonym of Leptosira obovata, now L. terrestris; Friedl 1996) is so similar ultrastructurally to the genus Trebouxia that they could be combined in the same genus. Ahmadjian (1988) went one step further, opining that Trebouxia was merely the lichenized form of this taxon. However, the aforementioned gene-based cladograms do not show a close relationship between Leptosira and the Trebouxiales.

**Leptosira terrestres**, in lichen symbiosis with Vezdaea aestivalis, grows subcuticularly (Tschermak-Woess & Poelt 1976), a distinction shared with the photobiont Cephaleuros. Leptosira is also among the very few photobiont genera (Phycopeltis and Cephaleuros are others) reported to produce zoospores in the lichenized state (Tschermak-Woess & Poelt 1976).

**Lithotrichon** Darienko & Pröschold — Another genus separated from the Dilabifilum (Ulvales) complex, Lithotrichon forms clustered cell packets as well as branching filaments and is distinguished from similar genera by SSU and ITS sequence data. The species L. pulchrum occurs as photobiont of the freshwater lichen Hydropunctaria rhetrophila (Darienko & Pröschold 2017).

**Myrmecia** Printz — These spherical to pyriform unicells have a parietal chloroplast, without a pyrenoid, extending around most of the cell, with 2–4 broad lobes defined by deep notches. Cells proliferate via zoospores, aplanospores, or autosporates (Ettl & Gärtner 2014). Gene-based phylogenies consistently place Myrmecia in the Trebouxiales, sister to Trebouxia (Muggia *et al*. 2020) or to the Asterochloris + Vulcanochlorella clade (Vancúrová *et al*. 2015). Myrmecia occurs free-living as well as in lichen symbiosis. An aerobic alga, originally described as Friedmaniella from Negev Desert rocks, is now recognized as Myrmecia israelensis (Friedl 1995) and was recently reported as lichen photobiont (Thüs *et al*. 2011; Moya *et al*. 2018). Psora decipiens and a number of species in the Verrucariaceae are among the lichen-forming fungi known to partner with Myrmecia.

**Nannochloris** Naumann — The genus Nannochloris has encompassed simple, extremely tiny (1.5–2 μm) chlorophyte algae that reproduce by binary division or autosporates. Circumscription of the genus has been controversial, but molecular data indicate that most of the species belong in Chlorellales (Henley *et al*. 2004). Tschermak-Woess (1981) recognized Nannochloris normandiae as the photobiont partner of lichen-forming Normaldinapulchella; in other works, Nannochloris has been mentioned more indirectly in the context of photobionts (e.g. Lohtander *et al*. 2003). However, Thüs *et al*. (2011) found only Diplosphaera as photobiont in the 10 Normaldinapulchella thalli they examined and, more recently, Pröschold & Darienko (2020) reduced Nannochloris normandiae to synonymy with Diplosphaera chodatii (Prasiolales). Thus, clear evidence of lichen photobionts belonging in Nannochloris appears to be lacking at present.

**Neocystis** F. Hindák — Members of this trebouxiothecan genus produce mucilaginous colonies of spherical to ellipsoidal or crescent-shaped cells that reproduce by autosporates (Neustupa 2015). Cultures assigned to Neocystis as well as other genera were recently reviewed with molecular sequence analyses, revealing considerable taxonomic redundancy assigned to only two closely related,
individuals are incorporated by the mycobiont’s Strigulaceae in foliicolous lichen communities, where they partner with molecular markers. It would be useful to test how well such traits correlate with such cases by features of the septal wall near plasmodesmata. (2013). An alga identified as principal photobiont (Voytsekhovich 2011). Members of this trentepohliaceous genus are most often seen as coppery orange discs a few mm in diameter on leaf surfaces in humid subtropical and tropical regions, with one or two species extending to cooler regions such as oceanic Europe (Rindi et al. 2004). Thallus discs consist of a monostromatic layer of closely appressed, bifurcating filaments (Fig. 6A). Unlike those of Cephalotus, Phycopeltis thalli are supracuticular, non-pathogenic, and at least some species readily colonize other functionally displayed plant substrata besides leaves. Sporangia are usually borne erect on a very short stalk, and release quadrilagellate zoospores through a pore at the end opposite to the point of attachment. Gametangia are sessile and develop from intercalary compartments of the horizontal filament system in most species; gametes are biflagellate and isomorphic, and their fusion has been observed (Thompson & Wujek 1997). The life cycle of Phycopeltis is believed to be haplodiplontic, with alternation of gametophytes and sporophytes that are isomorphic, rather than heteromorphic as in Cephalotus and Stomatochroon (Thompson & Wujek 1997). If this is the case, recognizing meiosporangia by the presence of tetrads might be the only means of distinguishing the phases phenotypically, but there do not appear to be such reports. Whether the gametophytes and sporophytes are equally susceptible to lichenization would be an interesting question to examine. Although distinguishing Phycopeltis from Trentepohlia under current morphological concepts appears fairly straightforward, DNA sequence data show species of the two genera to be intertwinable phylogenetically (Zhu et al. 2015, 2017; Grube et al. 2017a). Phycopeltis is particularly under-sampled at present. The morphological distinction between the two genera may also break down in the lichenized condition. Although Phycopeltis species can retain their placoid thallus characteristics when partnering with certain folicolous mycobionts (Grube & Lücking 2002), in other lichens the algal filaments may be broken up into individual cells indistinguishable from those of Trentepohlia (see fig. 9; Lücking 2008). Using TEM, Matthews et al. (1989) believed they could differentiate the two genera in such cases by features of the septal wall near plasmodesmata. It would be useful to test how well such traits correlate with molecular markers. As widespread colonizers of the warm-temperate and tropical phyllophere, species of Phycopeltis are important photobionts in folicolous lichen communities, where they partner with diverse leaf-dwelling mycobionts including species of Arthonia, Chroodiscus, Mazzonia, Opegrapha, Porina, Pristodiscus, and supracuticular taxa of Strigulaceae, among others (Santesson 1952; Lücking 2008). Multiple Phycopeltis thalli may occur edge-to-edge within a single folicolous lichen, as additional individuals are incorporated by the mycobiont’s expanding prothallus (Sanders 2002). There are some reports of algal gametangia or sporangia being produced in the lichenized state, particularly in those taxa where the Phycopeltis thalli are sparsely covered by the mycobiont (Santesson 1952; Lücking 1994; Sanders 2002). In at least one species of Phycopeltis (P. epiphyton), the highly degradation-resistant biopolymer sporopollenin was detected in the cell wall (Good & Chapman 1978). Its presence in the walls of other photobionts (Coccomyxa and Elliptochloris) has been correlated with the absence of haustorial penetration by mycobionts (Honegger & Brunner 1981; Brunner & Honegger 1985). However, at least some strains of lichenized Phycopeltis may be deeply penetrated by mycobiont haustoria, such as those of Porina (Matthews et al. 1989). Prasiola Meneghini — This trebouxiophycean seaweed of high-latitude supratidal zones is exceptional for its class in having a multicellular, macroscopic blade-like thallus. It is often abundant and readily visible both free-living and in symbiosis with mycobiont Mastodia tessellata (Verrucariaceae). Two or three distinct species of Prasiola appear to serve as photobiont to the bipolarly distributed Mastodia (Garrido-Benavent et al. 2017, 2018). There has been some discussion, on structural grounds, as to whether this fungal-algal partnership ought to be considered a true lichen (Lud et al. 2001; Kohlmeyer et al. 2004; Pérez-Ortega et al. 2010). There is no fungal cortex, nor does symbiosis substantially change algal thallus morphology; its anatomy, however, is significantly altered, as algal cells become well separated by a proliferation of encircling mycobiont hyphae (Kowalčik & Batista Pereira 2001; Lud et al. 2001). The symbiosis therefore entails considerably more structural transformation than that produced by the marine fungus Mycophycias upon its seaweed host Ascopodium (Xu et al. 2008), or Turgidocladum upon Bldingia (Pérez-Ortega et al. 2018). From a phylogenetic perspective, it is worth noting that close relatives of both the mycobiont (Verrucariaceae) and the alga (Prasiolales) participate in symbioses that are unambiguously lichenic. Pseudodochlorodum Wille — These ulvalvean algae have variably packet-forming to filamentous morphologies and may be differentiated into prostrate and erect filament systems. Darienko & Pröschold (2017) moved into this genus a couple of photobionts previously treated under Dilabifillum, recognizing the photobiont of Arthopyrenia kelpii as Pseudodochlorodum arthropynaeae, and the photobiont of Hydropunctaria mauro作为P. commune, which is also widespread as a free-living alga on intertidal rocks. Pseudodochlorodum arthropynaeae has a pyrenoid surrounded by thick plates of starch and traversed by several narrow, thylakoid-derived membranes lacking pyrenoglobuli (Namba & Nakayama 2021). Pseudocholerella J. W. G. Lund — This unicellular genus of Chlorella-like algae is now placed in the Prasiolales. Molecular data support inclusion of the photobiont of at least one lichen-forming fungus, Trapelia coarctata (Darienko et al. 2016). Other reports attribute to Pseudocholerella the photobionts of certain Micarea, Placyntiella and Stereocaulon species (see Tschermák-Voess 1988a; Voytsekhovich et al. 2011). However, molecular sequence studies have so far identified photobionts from Micarea as Coccomyxa and Elliptochloris, and those from the green algal layer of Stereocaulon as Asterochloris, Chloroidium and Vulcanochloris.
**Pseudococcomyxa** Korshikov — Isolates identified as *Pseudococcomyxa simplex* have been reported as photobionts of a maritime *Leproloma* sp. (Watanabe et al. 1997) and also *Micarea prasina* (Voytsekhovich et al. 2011), based on light microscopy and culture studies. The genus *Pseudococcomyxa* has been distinguished morphologically from *Coccomyxa* by the polarized secretion of mucilage to form a cap at one end of the cell. However, Darienko et al. (2015) found this character to be culture-dependent, and the *Pseudococcomyxa* strains they analyzed phylogenetically appeared intermixed with those of *Coccomyxa* (see also Yahr et al. 2015). Isolates attributed to *P. simplex* in particular occurred in several distinct clades. Darienko et al. (2015) reassigned all these strains to *Coccomyxa*. While lichen photobiont isolates attributed to *Pseudococcomyxa* remain to be examined, support for distinction of the genus from *Coccomyxa* now appears to be lacking.

**Pseudostichococcus** L. Moewus — Morphologically similar to *Stichococcus*, this genus was recently revised with molecular data (Pröschold & Darienko 2020). It currently includes the photobiont partner of *Neocatapyrenium rhizinosum* (Hodać et al. 2016) in the *Verrucariaeae*.

**Pseudotrebouxia** P. A. Archibald — See *Trebouxia*.

**Radiococcus** Schmidle — Species of this genus have been reported to occur as principal photobiont in thalli of two species of *Placynthiella* (*P. icmalea* and *P. uliginosa*) from the Ukraine (Voytsekhovich et al. 2011). Corroboration with DNA sequence data is needed, particularly since diverse, unrelated taxa have been repeatedly ascribed to this genus in the past (Wolf et al. 2003). According to a recent taxonomic treatment, *Radiococcaceae* and *Radiococcus* belong in the order *Sphaeropleales* of the *Chlorophyceae* (Neustupa 2015), although these names are still being applied to taxa falling in other groups, such as the *Trebouxiophyceae* (e.g. Metz et al. 2019).

**Stichococcus** Nägeli s. lat. — In its broad sense, *Stichococcus* (*Prasiolales*) has encompassed smallish unicellular to filamentous algae of notably labile morphology, the most commonly recognized form represented by short-cylindrical cells. The chloroplast is parietal, often extending to no more than half of the cell circumference, not markedly lobed, with or without a pyrenoid. Culture conditions appear to have a significant effect on cell form. The straight or slightly curved, rod-shaped cells may separate or remain together after division to form very short filaments or swell to more spherical shapes, and may or may not produce a surrounding gelatinous sheath (Ettl & Gärtner 2014). Quite a number of lichen photobionts have been ascribed to *Stichococcus*, but as their diversity is studied at the molecular level, these taxa are being placed in segregate genera or other prasioleane clades. Some seven to nine clades have now been recognized within *Stichococcus* s. lat. (Hodać et al. 2016; Pröschold & Darienko 2020). All *Stichococcus*-like photobionts examined in a study of the *Verrucariaeae* by Thüs et al. (2011), were shown to belong in *Diplosphaera*. Others now appear to fall within *Pseudostichococcus*, *Deuterostichococcus* or *Tristichococcus* (Pröschold & Darienko 2020). It is not yet clear whether *Stichococcus* in the restricted sense (near to type species *S. bacillaris*) includes lichen photobionts.

**Symbiochloris** Škaloud et al. — Formally described by Škaloud et al. (2016), the genus corresponds to a distinct clade of *Dictyochloropsis* s. lat. previously recognized by Dal Grande et al. (2014b). *Symbiochloris* is currently thought to include all lichen photobionts previously included in *Dictyochloropsis*, as well as some free-living taxa. Principal mycobiont partner genera are *Lobaria*, *Pseudocyphellaria*, *Sticta* and their recent segregates *Crocodia*, *Dendriscosticta* and *Ricasolia*, all members of the *Lobariaceae*. Other lichens reported harbouring *Symbiochloris* photobionts include species of *Biatora*, *Brigantiaea*, *Chaeathoea*, *Megalospora* and *Phlyctis*.

The net-like chloroplast of *Symbiochloris*, similar to that of *Dictyochloropsis*, has reticulations that vary in form, thickness and orientation according to species and developmental stage (Škaloud et al. 2005, 2016). Lichenized populations reproduce by aplanospores, but zoospore production may be observed in isolated culture. Cells of free-living populations often attain much larger sizes and their surfaces may be covered with scales (Tschermak-Woess 1995).

**Trebouxia** Puymaly — The principal crop of the alga-farming fungi, unicellular *Trebouxia* is thought to include the photobionts chosen by the largest proportion (nearly half) of known mycobiont species. Together with the closely related *Asterochloris*, *Trebouxia* is chlorobiont of most *Lecanorales* and *Teloschistales*, as well as many other taxa of the other species-rich lcanoromycetid orders (Miadlikowska et al. 2014). Species of *Trebouxia* are spherical or occasionally ellipsoidal unicells with a variously lobed, axial chloroplast that fills much of the cell and bears a prominent pyrenoid (Fig. 2A & C). There is considerable diversity of pyrenoid ultrastructure within the genus, involving differences in the morphology of penetrating membranes and the distribution of starch deposits and pyrenoglobuli, when present (Pveling 1966, 1969; Fisher & Lang 1971; Friedl 1989). CO₂-fixing Rubisco is concentrated in the pyrenoids, which in some instances also comprise additional, smaller, satellite substructures within the chloroplast (Ascaso et al. 1995). Although pyrenoid types do not correspond precisely to the *Trebouxia* clades supported in molecular sequence analyses, and several are strikingly convergent with pyrenoids of distantly related algae, they can nonetheless be useful in distinguishing certain groupings of taxa at close range (Friedl 1989; but see also Muggia et al. (2010)). Some 30 species of *Trebouxia*, distributed among four major clades, are currently recognized. However, this figure is believed to grossly underestimate the true genetic diversity present in the genus (Leavitt et al. 2015; Muggia et al. 2020). The boundaries among the formally described species remain largely unresolved, since much of the genetic diversity uncovered in recent studies is not fully congruent with the phenotypically defined taxa. Muggia et al. (2017) postulated that the application of a phylogenetic species concept would at least triple the number of species currently recognized in *Trebouxia*.

Two different groups were long distinguished within *Trebouxia* s. lat. (Ahmadjian 1960), which was previously known as *Cystococcus*. Archibald (1975) recognized two genera, *Trebouxia* and *Pseudotrebouxia*, based on differences in cell division which were judged sufficient to separate them into two distinct orders. However, Gärtner (1985) and Tschermak-Woess (1989) found Archibald’s subdivision untenable and reunited the genus, while acknowledging that differences in cell division were present. Tschermak-
Woess (1989) distinguished two subgenera: *Trebouxia* (corresponding roughly to *Pseudotrebouxia*), which forms aplanospores (or zoospores in culture) and also autospores, and *Eleutherococcus* (later *Asterochloris*), which produces aplanospores/zoospores but not autospores. Autospores are distinguishable from aplanospores in that they are produced in lower numbers and are tightly appressed together within the sporangium such that their walls form angular junctions between them (Tschermak-Woess 1989). Another difference is the position of the chloroplast during cell division, which remains more or less central in *Trebouxia* but becomes parietal and flattened in *Asterochloris* (Ahmadjian 1960; Tschermak-Woess 1989). Molecular data firmly distinguish the two clades, which have been formally recognized as distinct genera for the past decade (Skaloud & Peksa 2010).

As a lichen symbiont, *Trebouxia* is abundant in a great diversity of habitats worldwide. It is said to be infrequently reported in the free-living state, although researchers who sample substrata with microscopy have often found it (Tschermak-Woess 1978; Bubrick et al. 1984; Mukhtar et al. 1994; Sanders 2005; Handa et al. 2007; Uber 2008; Neustupa & Štíferová 2013), with the notable exception of Degelius (1964). Clearly, the germinating spores of trebouxiophilic mycobiants manage to obtain it, often without needing to produce an extensive mycelium (Werner 1931; Clayden 1998). Recent environmental sequencing studies have found *Trebouxia* on a variety of surfaces (Darienko et al. 2013; Hallmann et al. 2013, 2016; Yung et al. 2014) and well represented in soil, fresh water and even marine environments (Metz et al. 2019), although one cannot be certain that the detected sequences represent free-living individuals. By contrast, two other principal lichen photobiont genera, *Trentepohlia* and *Nostoc*, are uncontroversially well known in the free-living state. The comparison may not be fair, however, because *Trentepohlia* and *Nostoc* both form easily recognized macrocolonies (bright orange tufts and distinctive gelatinous globs, respectively) whereas *Trebouxia* cannot be distinguished without a microscope and some degree of effort. In any case, a shadow of doubt still seems to haunt the status of free-living *Trebouxia* populations, to judge from the cautious wording in even quite recent literature (e.g. Friedl & Büdel 2008). Although he never claimed to have searched for it in nature, Ahmadjian (1988, 1993, 2001, 2002) repeatedly affirmed that *Trebouxia* existed only in highly coevolved symbiosis with lichen fungi and did not occur free-living. Yet he acknowledged that aposymbiotic populations of *Trebouxia* could appear in nature. He even proposed, as have others, that they arose from the breakdown of lichenized propagules, such as soredia and isidia, that reach microhabitats unsuitable for the partners to develop symbiotically (Ahmadjian 1988). Ahmadjian asserted, however, that such populations were not truly free-living, except in a ‘secondary sense’. Apparently, he meant that they were ephemeral rather than stably established, but stable or not, aposymbiotic populations of *Trebouxia* are likely to be significant. Like other micro-organisms, many algae take advantage of ephemeral resources and transiently favourable microenvironments, then complete their life cycles with sexual reproduction when conditions deteriorate. Some then survive as resistant spores; others may escape adversity by entering into lichen symbioses. Within a lichen thallus, an algal population may be perpetuated for many years, yet continually disperse via soredia, isidia, lichenized fragments and other propagules that can seed new free-living populations. This has been characterized as photobiont ‘escape’ from the lichen fungus (Werth 2010). It may be equally valid to view relichenization as photobiont escape from conditions that aposymbiotic populations might not long endure.

Although stages of flagellar development within a lichen thallus were reported (Slocum et al. 1980), authors have expressed skepticism that *Trebouxia* could produce motile or sexual cells in the symbiotic state (Tschermak-Woess 1989), where all algal cells are held by one or more appresorial hyphae (Honegger 1990). In aposymbiotic culture, by contrast, the production and release of *Trebouxia* zooids are well documented (Ahmadjian 1960, 1967; Tschermak-Woess 1989; Takeshita 2001). The huge genetic diversity present (Muggia et al. 2020) and its structure within populations (Kroken & Taylor 2000) suggest that *Trebouxia* is reproducing sexually, but virtually nothing is known about how or when the sexual cycle proceeds in nature. Although it is often said that sexual reproduction has not been observed in this genus, both Warén (1920) and Ahmadjian (1960) reported and illustrated the fusion of flagellate isogametes in *Trebouxia* cultures. However, Ahmadjian (1988, 2001) believed that these features were vestiges of the alga’s free-living ancestry that no longer play any role in their present life histories. Further investigation of aposymbiotic populations is needed, since considerable indirect evidence suggests that they may reveal key events in the *Trebouxia* life cycle.

*Trentepohlia* C. Martius — The filamentous taxa currently treated under this cosmopolitan genus are among the most familiar of subaerial algae, often forming readily visible yellowish orange tufts on bark, rocks and other substrata in a wide variety of environments. They are also among the phycobionts chosen by the most diverse lichen-forming ascomycetes, including members of the *Arthoniomyces*, *Coniocybomyces*, *Dothidiomyces*, *Eurotiomyces* (Pyrénulales) and ostropalean *Lecanoromycetes* such as the species-rich *Graphidaceae*. Members of the order *Trentepohliales* and its sole family *Trentepohliaceae* present a distinctive combination of features: phragmoplast cell division with plasmodesmata (otherwise characteristic of charophycean algae), a uniquely structured flagellar apparatus, peculiar sporangiophores, and distinctive orange pigmentation. Consequently, widely divergent interpretations of their phylogenetic affinities have been proposed, with some authors even placing the group in a separate class of its own (van den Hoek et al. 1995). However, rDNA sequence data firmly place the subaerial *Trentepohliales* among orders of mainly marine taxa within the *Ulvophyceae* (López-Bautista & Chapman 2003; Leliaert et al. 2012).

Among the taxa currently treated under *Trentepohlia*, a number of genera were described to accommodate the morphological diversity represented, most recently *Printzina* (Thompson & Wujek 1992). However, DNA sequence analyses have so far shown that the phenotypic similarities recognized are unreliable indicators of phylogenetic affinity (López-Bautista et al. 2006; Rindi et al. 2009). This also applies to some of the morphological traits currently used to distinguish *Trentepohlia* species from those of *Phycopeltis*. Free-living and lichenized isolates of *Trentepohlia* occur intermixed in gene-based phylogenies (Nelsen et al. 2011; Hametner et al. 2013).
Tritostichococcus Pröschold & Darienko — This recent segregate of Stichococcus s. lat. (Pröschold & Darienko 2020) includes the Stichococcus-like photobionts that associate with Chaenotheca, a genus of lichen-forming fungi that partner with a remarkably broad spectrum of photobionts (Tibell 2001).

Trochiscia Kützing — This genus of unicellular algae is characterized by an often-thick cell wall with spine- or wart-like projections, an irregularly stellate chloroplast, and two forms of endogenous spore production, resulting in hundreds of small cylindrical autospores or just two rounded endospores (Tschermak 1941b). Trochiscia currently appears to be placed among the Chlorophyceae, in or near Sphaeropleales (Fucíková et al. 2019). It was identified as photobiont of Polyblasia amota and P. hyperborea (Tschermak 1941b; Ahmadjian 1967) in the Verrucariaceae, but those reports appear to be in doubt (Ettl & Gärtner 2014) and further studies are needed. Trochiscia was not among the photobionts detected in the survey by Thüs et al. (2011) of the algal partners of Verrucariaceae.

Vulcanochloris Vancurová et al. — This newest addition to the Trebouxia family encompasses three recently described species with a distinctive, highly dissected chloroplast structure, and molecular sequences that place them as sister to Asterochloris (Vancurová et al. 2015). They are known mainly as principal photobionts from some thalli of Stereocaulon vesuvianum in the Canary Islands, although there is also a very recent report of Vulcanochloris from a Stereocaulon thallus collected in highland Bolivia (Kosecka et al. 2021). Most other Stereocaulon lineages investigated to date appear to associate with Asterochloris or Chloroidium (Vancurová et al. 2018). Vulcanochloris has also been recently reported as a minority photobiont in thalli of Ramalina farinacea (Moya et al. 2017).

Stramenoplia (Heterokontae)

Heterococcus Chodat — The yellow-green (xanthophyte) algae lack fucoxanthin, the golden brownish plastidal carotenoid otherwise characteristic of the photosynthetic stramenopiles. The absence of fucoxanthin makes them rather easy to confuse with green algae. Their zoospores, however, will have the characteristic stramenopilous flagellum bearing stiff, hollow, tripartite appendages (mastigonemes). Heterococcus forms irregular filaments and/or cell clusters when isolated into culture (Zeitler 1954). Molecular sequences support the light microscope identification of Heterococcus as photobiont in thalli of three species of Verrucariaceae (Hydropunctaria rhitophila, Verrucaria funckii and V. hydrela) that are each in separate clades and not closely related to one another (Thüs et al. 2011). Another xanthophyte, Heterothrix (now Xanthoneophila; Silva 1979) was identified via light microscopy as photobiont of Staurothele clavimoides (Pereira Riquelme 1992) but that interesting report requires corroboration.

Petroderma Kuckuck — Petroderma maculiforme is a small crustose brown alga (Phaeophyceae) found on rocks in the lower intertidal zone of western North America and Europe. In San Francisco Bay, it is particularly common on discarded plastic (Sanders et al. 2004). The alga is a disc of tightly branched, radiating horizontal filaments, rather similar in morphology to the chlorophyte Phycopeltis but with a dense carpet of short, erect filaments arising proximally from the horizontal system. In the free-living state, these erect filaments may bear unicellular or plurilocular sporangia (soidangia) terminally (Fritsch 1945). Chloroplasts typically possess one or several large pyrenoids that are prominent in electron micrographs (Fig. 2D) but not readily visible with light microscopy. The pyrenoids are traversed by branching tubules arising from invagination of the plastidial boundary membranes (rather than
filaments are separated by fungal tissue, into which they grow and branch downwards rather than upwards as in the free-living condition (Sanders et al. 2004). Petroderma is the only member of the Phaeophyceae known to enter into lichen symbiosis. However, certain larger brown seaweeds, such as Ascophyllum, have intimate, mutualistic associations with verrucariaceous fungi (Garbary & London 1995; Garbary & MacDonald 1995) that are generally not considered to be lichens on structural grounds, since the fungus grows within algal tissues as a conventional mycelium (Hawksworth 1988).

Table 1. Taxonomically grouped list of photobiont genera and mycobionts reported in association with them. The family names of the mycobionts are included in the Lichenologist 367.

| Alga | Fungal symbionts | References & comments |
|------|------------------|-----------------------|
| **[Brasilonema] sp.** | ? | Villanueva et al. (2018). Lichen not identified; need evidence that algal isolate is lichen photobiont. |
| **Calothrix and Dichothrix** | Lichina spp., Placynthium nigrum | see Tschermak-Woess (1988a) |
| **Chroococcidiopsis sp.** | Anema nummularium, Peccania cerebriformis, Psorotrichia columnaris, Gonohymenia sp. | Büdel & Henssen (1983); Büdel (1985). id: LM, culture. |
| **Chroococcidiopsis sp.** | Peltula spp. and ‘other cyanolichen genera’ | Büdel (1999). Unpublished 16S rDNA data of B. Büdel & T. Friedl. cited. |
| **Chroococcidiopsis sp.** | Anema nummularium, Peltula euploca, Thyrea pulvinata | Fewer et al. (2002) |
| **[Chroococcidiopsis] sp.** | ? | Villanueva et al. (2018). Lichen not identified; need evidence that algal isolate is a lichen photobiont. |
| **Chroococcidiopsis/ Chroococcidiopsidales** | Peltula bolanderi, P. clavata, P. euploca, P. impressa, P. obscurans, P. placodians | Vö (2016) |
| **Gloeocapsa sp.** | Species of Anema, Edwaideria, Gonohymenia, Heppia, Jenmania, Peccania, Phyliscum, Psorotrichia, Pyrenopsis, Synalissa and Thyrea; cephalodia of Amygdaloria and Stereocaulon spp. | Numerous LM reports summarized by Tschermak-Woess (1988a); Friedl & Büdel (2008); Brodo et al. (2001). id: LM. |
| **Hyelia sp.** | Collemopsidium sp. | see Ahmadjian (1967). id: LM. |
| **Hyphomorpha sp.** | Spilonema dendroides, S. schmidtii | Henssen (1981). id: LM. |
| **Myxosarcina sp.** | Peltula euploca | Friedl & Büdel (2008) |
| **Nostoc sp.** | Nephroma resupinatum, Peltigera britannica, P. canina, P. membranacea; cephalodia of Peltigera aphthosa, P. venosa | Paulsrud et al. (2000, 2001). High genetic specificity, also for cephalodia formation, overrules geography. |
| **Nostoc sp.** | Collema multiporititum | Oksanen et al. (2002) |
| **Nostoc sp.** | Nephroma, numerous spp. | Lohtander et al. (2003) |
| **Nostoc sp.** | Leptogium puberulum, Massalongia carnosa, Placopsis contortuplicata, P. paretillina, Psoroma cinnamomeum | Wirtz et al. (2003). Maritime Antarctica; two main clades that also include free-living Nostoc. |
| **Nostoc sp.** | Collema crispum, Leptogium gelatinosum, Lobaria amplissima, L. hallii, Massalongia carnosa, Nephroma bellum, N. helveticum, Pannaria conoplea, Peltigera canina, P. degeneri, P. didactyla, P. horizontalis, P. lepidophora, P. membranacea, P. neopolydactyla, P. rufescens, Sistia beauvoisii, S. fuliginosa; cephalodia of Peltigera aphthosa | O’Brien et al. (2005) |
| **Nostoc sp.** | Pseudocyphellaria crocata, (=) P. neglecta, (=) P. perpetua | Summerfield & Eaton-Rye (2006) |
| **Nostoc sp.** | Pannaria andina, P. araneosa, P. atroaphila, P. conoplea, P. durietszii, P. elixii, P. euphylla, P. farinosa, P. fulvenscens, P. isabellina, P. lobulifera, P. mosenii, P. obscura, P. pallida, P. patagonica, P. rubiginella, P. rubiginosa, P. sphinctrina, P. tavaresi | Elvebak et al. (2008) |
| **Nostoc sp.** | Degelia atlantica, D. plumbea | Otálora et al. (2013) |
| Table 1. (Continued) |
|-----------------------|
| **Alga** | **Fungal symbionts** | **References & comments** |
| Nostoc sp. | Polychidium muscicola | Jayalal et al. (2012) |
| Nostoc sp. | Species of Fuscopannaria, Krasiova, Pannaria, Parmellella and Physma | Magain & Séerusiaux (2014). Homoiomerous (gelatinous) vs stratified anatomy correlated with Nostoc strain, not fungal family, across Pannariaceae and Collemataceae. |
| Nostoc sp. | Leptogium lichenoides, Peltigera islandica, P. ponojensis | Joneson & O’Brien (2017) |
| Nostoc sp. | Peltigera sections Peltigera and Retifoviatae | Magain et al. (2018) |
| Nostoc sp. | Pectenia plumbea | Cardós et al. (2019) |
| **Rhizonema ordinarum** | Cora arachnodaevia, C. barbulata, C. bovei, C. dewisanti, C. dewisanti-mexicana, C. elephas, C. hawksworthiana, C. hochesuordensis, C. pseudobovei, Cora sp.; cephalodia of Stereocaulon fronduliferum | Dal Forno et al. (2020) |
| R. interruptum lineage | Coccocarpia filiformis, C. palmicola, C. stellata, Cora applanata, C. aspera, C. auriculeslia, C. canari, C. crisposesia, C. galapagoensis, C. hymenocarpa, C. melvinii, C. paracifernii, C. reticulifera, C. smaragdina, C. soredavida, C. squamiformis, C. strigosas, C. suturifera, C. terrestris, C. viilewao, Cora sp. Cyphellostereum sp., Dictyonema aeruginosum, D. barbatum, D. darwinianum, D. hernandezii, D. interruptum [= D. coppinsi], D. phyllogenum, D. sericeum, D. schenkianum, Dictyonema sp.; cephalodia of Stereocaulon fronduliferum and S. ramulosum | Dal Forno et al. (2020) |
| R. neotropicum | Acantholichen pannarioides, Coccocarpia palmicola, Cora gigantea, C. lesloactua, C. rubrosanguinea, Corella sp., Dictyonema sp. | Dal Forno et al. (2020) |
| Rhizonema sp. | Acantholichen pannarioides, Coccocarpia filiformis, C. palmicola, C. stellata, Dictyonema aeruginosum, D. coppinsii, D. glabratum, D. hernandezii, D. phyllogenum, D. schenkianum, D. sericeum, Coccocarpia; cephalodia of Stereocaulon fronduliferum and S. ramulosum | Lücking et al. (2009). Shows photobiont more closely related to Nostoc clade than to Scytonema s. str. Lücking et al. (2014): formal description of genus Rhizonema. |
| Rhizonema sp. | Athelia andina, Cyphellostereum pusiolum | Oberwinkler (2012). Mycobiont also associates with green photobiont. |
| Rhizonema sp. | Athelia phytophila | Jülich (1972). Reported as Scytonema. Athelia poeltii also said to associate with filamentous cyanobacteria; Jülich (1978). |
| Rhizonema sp. | Coccocarpia palmicola, Erideroderma pedicellatum, E. sorediatus, Leptogium sp., Lichinodium sp., Moelleropsis nebulosa, Parmellella parvula | Cornejo & Scheidegger (2016); Cornejo et al. (2016). Boreal env. (Newfoundland). Also symbiotic among liverwort Frullania asagrayana. |
| Rhizonema sp. | Lichinodium ahleri, L. sirosiphoideum (Leotiomycetes) | Prieto et al. (2019) |
| Rhizonema sp. | Dictyonema moorei | Masumoto (2020) |
| Rivularia sp. | Lichina confinis, L. pygmaea | Ortiz-Álvarez et al. (2015) |
| Scytonema sp. | Pyrenothrix nigra | Tschermak-Woess et al. (1983). id: LM & TEM. |
| Scytonema sp. | Species of Heppia, Lichinodium, Thermutis and Zahlbrucknerella | Henssen (1994). DNA sequence data needed. Might be Rhizonema, but see Vö (2016) concerning Heppia. |
| Scytonema sp. | Heppia lutosa | Vö (2016). A 16s rRNA sequence suggests true Scytonema, not Rhizonema. |
| Stigonema sp. | Species of Ephebe and Spilonema | Henssen & Jahns (1974). id: LM. |
| Stigonema sp. | Cephalodia of Stereocaulon | Lavoie et al. (2020) |
| Tolypothrix sp. | Thetmutopsis sp. | Henssen (1999) |
| cf. Tolypothrix | Cephalodia of Placopsis perrugosa and P. sterophylla | Raggio et al. (2012) |
| **Domain Eukarya, Eukaryote supergroup Archaeplastida, Kingdom Plantae, Division Chlorophyta Class Trebouxiophyceae, Order Chlorophyta** | **Auxenochlorella** | **Psoroglaena stigonemoides** | Thus et al. (2011) |
| Near A. protothecoides | Psoroglaena stigonemoides | Nyati et al. (2007). Strain P-1015. |
Table 1. (Continued)

| Alga                  | Fungal symbionts                      | References & comments                                                                 |
|-----------------------|---------------------------------------|----------------------------------------------------------------------------------------|
| **Near Chlorella sorokiniana** | Porphidia crustulata                  | Li et al. (2013)                                                                        |
| **Nannochloris normandinae** | Normandina pulchella                  | Tschermak-Woess (1988a), Pröschold & Darienko (2020) synonymize N. normandinae with Diplosphaera chodatii. |
| **Class Trebouxiophyceae, Order Prasiolales** |                                    |                                                                                        |
| Deuterostichococcus allas and D. antarcticus | Placopsis antarctica, P. contortuplicata | Beck et al. (2019). Reclassified by Pröschold & Darienko (2020).                      |
| D. deasonii           | Staurothele clopima                   | Hodač et al. (2016); Pröschold & Darienko (2020).                                      |
| **Diplosphaera chodatii** | Dermatocarpon luridum var. luridum    | Fontaine et al. (2012); Doering et al. (2020).                                          |
| Diplosphaera sp.      | Agonimia koreana, A. opuntiella, A. repleta, A. tristicula, Bagliettoa parmigera, Catapyrenium cinereum, C. daedaleum, Dermatocarpon luridum, D. miniatum, Endocarpon adscendens, E. diffracellum, E. pallidulum, E. pusillus, Flakes papillata, Neocatapyrenium rhizosomus, Normandina acrglypta, N. pulchella, Placidiopsis cortiligeina, Placopyrenium buceki, Polyblastia cupularis, P. viridescens, Staurothele areolata, S. clopima, S. clopimoides, S. drummondi, S. fissa, S. frustulenta, Verrucaria elaeina, V. hochstetteri, V. nigrescens, V. pratermissa, V. rupestris (Verrucariaceae) | Thüs et al. (2011). Morphologically similar to Stichococcus, but not close to type sp. S. bacillaris. |
| Diplosphaera sp.      | Ramalinia farinacea                   | Maya et al. (2017). Minority photobiont.                                                |
| **Prasiola borealis** | Mastodia tessellata                   | Moniz et al. (2012). Authors refer to symbiotic form as lichenized. Stipe section shows photobiont well-embedded in fungal tissue. |
| P. borealis and one undescribed sp. | Mastodia tessellata                   | Pérez-Ortega et al. (2012); Garrido-Benavent et al. (2017).                           |
| P. delicata           | Mastodia tessellata                   | Moniz et al. (2014); Garrido-Benavent et al. (2018).                                   |
| Prasiola sp.          | Mastodia tessellata                   | Thüs et al. (2011).                                                                    |
| **Pseudochlorella pyrenoidosa** | Micarea assimilata                   | Zeitler (1954); Tschermak-Woess (1988a).                                              |
| P. signiensis         | Trapelia coarctata                    | Darienko et al. (2016).                                                                |
| Pseudochlorella sp.   | Stereocaulon stricturn                | Brunner & Honegger (1985). Pyrenoid ultrastructure suggests this strain might be Chloroidium, as indicated by DNA sequences from other Stereocaulon photobionts.   |
| Pseudochlorella sp.   | Placynthiella dasaea                  | Voitsekhovich et al. (2011). id: LM, culture.                                             |
| Pseudochlorella sp.   | Umbilicaria antarctica                | Park et al. (2015). In some thallus samples, along with Trebouxia, Status as photobiont needs corroboration. |
| **Pseudostichococcus clade** | Neocatapyrenium rhizosomus            | Hodač et al. (2016); Pröschold & Darienko (2020).                                      |
| **Tritostichococcus coniocyes** | Chaenotheca sp.                        | Pröschold & Darienko (2020)                                                            |
| **Class Trebouxiphycceae, Order Trebouxiales** |                                    |                                                                                        |
| Asterochloris antarctica | Cladonia sp.                          | Kim et al. (2020)                                                                       |
| Asterochloris clade 1 | Cladonia corymbescens, C. furcata, C. pyxidata, C. rangiferina | Řídká et al. (2014)                                                                    |
| Asterochloris clade 2 | Cladonia furcata                      | Řídká et al. (2014)                                                                     |
| Asterochloris clade 2 | Cladonia subtenuis                    | Yahr et al. (2006)                                                                     |
| Asterochloris clade 9 | Cladonia cariosa, C. coniocraea, C. delavayi, C. fruticulosa, C. praetmissa, C. scabriuscula, C. verticillata | Řídká et al. (2014)                                                                    |
| Asterochloris clade 12 | Cladonia pyxidata                     | Řídká et al. (2014)                                                                     |
| Asterochloris clade 16 | Cladonia fruticulosa                  | Řídká et al. (2014)                                                                     |
| A. echinata           | Lepraria caesioalba, L. rigidula       | Škaloud et al. (2015)                                                                   |
| A. erici              | Cladonia calycanta, C. chlorophaea, C. crispata, C. floerkeana, C. gracilis ssp. turbinata, C. ramulosa, C. squamosissima | Nakano & Iguchi (1994). id: LM, culture.                                               |

(Continued)
| Alga               | Fungal symbionts                        | References & comments          |
|--------------------|----------------------------------------|--------------------------------|
| **Asterochloris excentrica** | Lepraria caesioalba, L. neglecta, L. rigidula | Škaloud & Peksa (2010) |
| A. friedii        | Lepraria caesioalba, L. lobificans      | Škaloud et al. (2015)          |
| A. friedii        | Lepraria achariana, L. finkii          | Kosecka et al. (2021)          |
| A. friedii        | Cladonia fimbriata                     | Pino-Bodas & Stenroos (2020)  |
| A. gaertneri      | Lepraria incana, L. rigidula           | Škaloud et al. (2015)          |
| A. glomerata      | Cladonia humilis                       | Nakano & Iguchi (1994), id: LM, culture. |
| A. glomerata      | Diplochistes muscorum                  | Škaloud & Peksa (2010)         |
| A. glomerata      | Stereocaulon pileatum, S. saxatile, Stereocaulon sp. | Peksa & Škaloud (2011) |
| A. glomerata      | Cladonia coniorea, C. squamosa, Stereocaulon evolutoides, S. pileatum | Řídka et al. (2014) |
| A. glomerata      | Cladonia deformis, C. pleurota         | Steinová et al. (2019)         |
| A. glomerata      | Cladonia grayi                         | Armaleo et al. (2019)          |
| A. glomerata      | C. caroliniana, C. cornuta, C. deformis, C. hondoensis, C. krogiana, C. mitis, C. monomorpha, C. oricola, C. phyllophora, C. piedmontensis, C. pleurota, C. submissis, C. subulata, C. uncials | Pino-Bodas & Stenroos (2020) |
| A. glomerata/irregularis clade | Cladonia cariosa, C. cervicornis ssp. verticillata, C. phyllophora | Rola et al. (2021) |
| A. irregularis    | Squamaria lentigera                    | Beck et al. (2002)             |
| A. irregularis    | Cladonia furcata, Lecidea fuscoatra, L. plana, Lepraria caesioalba, Poriopia crustulata, P. flavocerulescens, P. macrocarpa, Poriopia spp., Stereocaulon vesuvianum | Beck (2002) |
| A. irregularis    | Cladonia arbuscula, C. mitis, Stereocaulon botryosum, S. pileatum, S. subcoralloides | Škaloud & Peksa (2010); Škaloud et al. (2015). |
| A. irregularis    | Stereocaulon alpinum, S. apolysticum, S. intermedium, S. paschale, S. symphycheilum, S. tomentosum, S. vesuvianum | Vančurová (2012) |
| A. irregularis    | Stereocaulon botryosum, S. pileatum, S. subcoralloides, S. vesuvianum, Stereocaulon sp. | Peksa & Škaloud (2011) |
| A. irregularis    | Cladonia deformis, C. pleurota         | Steinová et al. (2019)         |
| A. irregularis    | Cladonia albonigra, C. alinii, C. amaurocraea, C. botrytes, C. crispata, C. ecnocyna, C. graciilis, C. granulans, C. kanewski, C. labradorica, C. macrophylla, C. ulginosa, C. uncials | Pino-Bodas & Stenroos (2020) |
| A. italicana      | Cladonia capitellata, C. scabriuscula   | Škaloud et al. (2015)          |
| A. italicana      | Cladonia coccifera, C. diversa         | Steinová et al. (2019)         |
| A. italicana      | Stereocaulon condensatum               | Vančurová (2012)               |
| A. italicana      | Cladonia bellidiflora, C. borbonica, C. brevis, C. callosa, C. capullata, C. ciliata, C. foliacea, C. groenlandica, C. islandica, C. lepidophora, C. mawsonii, C. merochlorophae, C. neozeelandica, C. pleurota, C. portentosa, C. prolifica, C. pulvinata, C. rapi, C. rigida, C. subcervicornis, C. subsubulata, C. ustulata, C. weymouthii | Pino-Bodas & Stenroos (2020) |
| A. italicana clade | Diplochistes muscorum                  | Rola et al. (2021)             |
| A. leprarii       | Lepraria caesioalba, L. neglecta       | Škaloud et al. (2015)          |
| A. lobophora      | Cladonia cf. bacillaris, Diplochistes muscorum, Lepraria alpina, L. borealis, L. caesioalba | Škaloud et al. (2015) |
| A. lobophora      | Cladonia coccifera                     | Steinová et al. (2019)         |
| A. lobophora      | Cladonia rei                           | Pino-Bodas & Stenroos (2020)  |

(Continued)
| Alga            | Fungal symbionts                                                                 | References & comments                  |
|-----------------|----------------------------------------------------------------------------------|----------------------------------------|
| Asterochloris labophora/ phycobiontica clade | Cladonia cariosa, C. rei, Diploschistes muscorum | Rola et al. (2021)                     |
| A. magna        | Porpidia contraponenda                                                           | Beck (2002)                            |
| A. magna        | Cladonia chlorophaea, C. decorticata                                            | Pino-Bodas & Stenroos (2020)           |
| A. mediterranea | Cladonia cervicornis, C. concoluta, C. foliacea, C. rangiformis                  | Moya et al. (2015)                     |
| A. mediterranea | Cladonia calycantha, Stereocaulon pachycephalum                                 | Kosecka et al. (2021)                   |
| A. mediterranea | Cladonia corsicana, C. crispata, C. cryptochlorophaea, C. diversa, C. glauca, C. rei | Pino-Bodas & Stenroos (2020)           |
| A. phycobiontica | Anzina [Varicellaria] carneonivea                                               | Tschermak-Woess (1980); Škaloud et al. (2015). |
| A. phycobiontica | Stereocaulon alpinum                                                             | Vančurová (2012)                       |
| A. phycobiontica | Lepraria neglecta                                                                | Škaloud & Peksa (2010)                 |
| A. phycobiontica | Lepraria alpina, L. caesioalba, L. neglecta, Lepraria sp.                        | Peksa & Škaloud (2011)                 |
| A. pseudoirregularis | Cladonia gracilis, Cladonia sp.                                                    | Kim et al. (2020)                      |
| A. pseudoirregularis | Cladonia amaurocraea, C. gracilis, C. granulans, C. vulcani, Pycnothelia papillaria | Pino-Bodas & Stenroos (2020)           |
| A. sejongensis  | Cladonia pyxidata, Sphaerophorus globosus                                        | Kim et al. (2017)                      |
| A. stereocaulonicola | Stereocaulon alpinum                                           | Kim et al. (2020)                      |
| A. woessiae     | Cladonia foliacea, Lepraria borealis, L. caesioalba, L. crassissima, L. nigrincta, L. nylanderiana, Lepraria sp., Stereocaulon saxatile | Škaloud et al. (2015)                 |
| A. woessiae     | Cladonia coccifera                                                               | Steinová et al. (2019)                 |
| A. woessiae     | Cladonia conista, C. foliacea                                                    | Pino-Bodas & Stenroos (2020)           |
| A. woessiae clade | Diploschistes muscorum                                         | Rola et al. (2021)                     |
| Asterochloris sp. | Bagliettoa cazzae                                                              | Thüs et al. (2011)                     |
| Asterochloris sp. | Psora decipiens                                                               | Ruprecht et al. (2014). Also Trebouxia and a Chloroidium in this lichen sp., but see Williams et al. (2017). |
| Asterochloris sp. | Lepraria borealis, Ochrolechia frigida                                         | Engelen et al. (2010, 2016), Maritime Antarctica. |
| Asterochloris sp. | Lecidea lurida, Psora decipiens, Squamarina cartilaginea                        | Schaper & Ott (2003), Gotland, Sweden.  |
| Asterochloris sp. | Ramalina farinacea                                                              | Škaloud et al. (2017). Minority photobiont. |
| Asterochloris sp. | Porpidia from southern South America                                           | Ruprecht et al. (2020). All mycobiont species also partnered with Trebouxia. |
| Asterochloris sp. | Cladonia acuta, C. aggregata, C. andesita, C. arbuscule ssp. boliviana, C. calycantha, C. chlorophaea, C. confusa, C. dactylota, C. didyma, C. furcata, C. granulosa, C. isabellina, C. melanopoda, C. pocillum, C. ramulosa, C. cf. subradiosa, C. vouaxii, Lepraria cryptovouuxii, L. hadkinsoniana, Stereocaulon myrioarpum, S. tomentosum | Kosecka et al. (2021) |
| Asterochloris sp. | Cladonia arbuscula, C. fimbriata, C. foliacea, C. rei, Diploschistes muscorum, Lepraria alpina, L. borealis, L. caesioalba, L. lobificans, L. neglecta, L. nigrincta, L. nylanderiana, L. rigidula, Pilophorus sp., Stereocaulon botryosum, S. paschale, S. pileatum, S. saxatile, S. subcoralloides, S. tomentosum, S. vesuvianum | Nelsen & Gargas (2008). Formal emendation of genus by Škaloud & Peksa (2010) to include Trebouxia subgen. Eleutherococcus Tschermak-Woess. |
| Asterochloris sp. | Cladia aggregata, Cladonia cf. bacillaris, C. evansi, C. fimbriata, C. perforata, C. rangiferina, Lepraria atramentosa, L. caesiella, L. caesioalba, L. incana, L. lobificans, L. nigrincta, L. nivalis, L. nylanderiana, Lepraria spp., Pilophorus acicularis, P. cf. cereolus, Stereocaulon dactylophyllum, S. paschale, S. saxatile, S. tomentosum, S. vesuvianum, Stereocaulon spp. | Nelsen & Gargas (2008) |
| Alga | Fungal symbionts | References & comments |
|------|-----------------|-----------------------|
| **Asterochloris spp.** | Species of *Lepraria* and *Stereocaulon* | Peksa & Škaloud (2011) |
| **Asterochloris spp.** | Cladonia furcata | Řídká et al. (2014) |
| **Myrmecia biatorellae** | *Catapyrenium rufescens, Dermatocarpon hepaticum, D. tuckermanni, Lecidea berengeriana, Lobaria limo, Polysporina simplex, Psora decipiens, P. globifera, Psoroma hypnorum, Sarcogyne privigna, Verrucaria submersella* | Thüs et al. (2011) |
| **M. biatorellae** | *Cladonia furcata* | Řidká et al. (2014) |
| **M. biatorellae** | *Fuscidea cyathoides var. japonica, Leproloma sp.* | Watanabe et al. (1997). Maritime lichens. id: LM. |
| **M. biatorellae** | *Placidium squamulosum* | Voytsekhovich & Beck (2016) |
| **M. biatorellae** | *Heteroplacidium contumescens, H. imbricatum, Placidium acarosporoides, P. arboreum, P. chilense, P. lachneum, P. lacinulatum, P. squamulosum, P. umbrinum (Verrucariaceae)* | Thüs et al. (2011) |
| **M. biatorellae** | *Psora decipiens* | Williams et al. (2017). Austrian samples. |
| **M. israelensis** | *Psora decipiens, P. saviczii, Placidium pilosellum, Placidium spp., Clavascidium spp.* | Moya et al. (2018) |
| **Myrmecia sp.** | *Psora decipiens* | Williams et al. (2017). Transplant study; algal layer degenerates, no photobiont switching. |
| **Trebouxia aggregata** | *Xanthoria parietina* | Beck & Mayr (2012) |
| **T. angustibotaba** | *Acarospora sinopica, Porpidia tuberculosa, Tremolecia atrata* | Beck (2002) |
| **T. angustibotaba** | *Protoparmelia badia* | Singh et al. (2017) |
| **T. angustibotaba** | *Pseudoephbe sp.* | Garrido-Benavent et al. (2020) |
| **T. arboricola** | *Lecania cyrtella, Lecanora sp., Lecidella elaeochroma, Xanthoria parietina* | Beck et al. (1998) |
| **T. arboricola** | *Anaptychia ciliaris* | Helms et al. (2001); Dahlkild et al. (2001). |
| **T. arboricola** | *Pleurosticta acetabulum* | Beck & Koop (2001) |
| **T. arboricola** | *Chaenotheca phaeocephala* | Tibell & Beck (2002) |
| **T. arboricola** | *Ramalina farinacea, R. pollinaria, R. silicuosa* | Tschaikner et al. (2007). id: LM, cultures. |
| **T. arboricola** | *Caloplaca fernandeziana, C. orthoclada* | Vargas Castillo & Beck (2012) |
| **T. arboricola** | *Xanthoria aureola, X. calicola, X. capensis, X. cincta, X. flavovirescens, X. ilicis, X. hypophysoides, X. ligulata, X. parietina, X. polycarpa, X. turbinata* | Nyati et al. (2013, 2014) |
| **T. arboricola** | *Ochrolechia sp., Xanthoria calicola, X. parietina* | Voytsekhovich & Beck (2016) |
| **T. arboricola clade** | *Acarospora conifii, Ramalina thrusta* | Jung et al. (2019) |
| **T. arboricola/T. gigantea clade** | *Xanthoparmelia spp.* | Leavitt et al. (2013) |
| **T. arboricola/T. gigantea clade** | *Cladonia cariosa, C. rei, Diploschistes muscorum* | Osyczka et al. (2021) |
| **Clade A (arboricola/gigantea group)** | *Species of Melanelixia, Melanohalea, Montanelia, Oropogon, Parmotrema, Protoparmeliopsis, Rhizoparmelia and Xanthoparmelia* | Leavitt et al. (2015) |
| **T. ‘arnoldoi’** | *Buellia zoharyi* | Molins et al. (2020) |
| **T. asymmetrica** | *Buellia zoharyi* | Helms et al. (2001); Molins et al. (2020). |
| **T. asymmetrica** | *Fulgensia fulgida, Toninia sedifolia* | Beck et al. (2002) |
| **T. asymmetrica** | *Protoparmeliopsis muralis* | Guzow-Krzemińska (2006) |
| **T. asymmetrica** | *Caloplaca teicholyta, Cinnarina contorta* | Voytsekhovich & Beck (2016) |
| **T. asymmetrica** | *Cinnarina spp.* | Molins et al. (2018) |
| **T. asymmetrica clade** | *Placidium sp.* | Jung et al. (2019) |
| **T. australis** | *Lecanora farinacea, L. polytropa, Rhizocarpon geographicum* | Beck (2002) |

(Continued)
| Alga            | Fungal symbionts                                                                 | References & comments                  |
|-----------------|----------------------------------------------------------------------------------|----------------------------------------|
| *Trebouxia*     |                                                                                  |                                        |
| *brindabellae*  | *Protoparmelia badia*                                                            | Singh et al. (2017)                     |
| *T. corticola*  | *Parmotrema tinctorum*                                                           | Ohmura et al. (2006, 2019)             |
| *T. corticola*  | *Umbilicaria muehlenbergii*                                                      | Cao et al. (2015)                      |
| *T. crenulata*  | *Ramalina capitata*                                                              | Tschakner et al. (2007)                |
| *T. crenulata*  | *Xanthoria parietina*                                                            | Beck & Mayr (2012)                     |
|                 | *Caloplaca aurantia,* C. *xerica,* Candelariella medians,* Lecanora swartzii,*  | Voytsekhovich & Beck (2016)            |
|                 | *Leproplaca xantholyta,* Tephromela atr/a,* Xanthoria calicola*                  |                                        |
| *T. crespoana*  | *Parmotrema pseudotinctorum*                                                     | Škaloud et al. (2018)                  |
| *T. cretacea*   | *Aspicilia desertorum,* Rusovskia papillifera*                                   | Voytsekhovich & Beck (2016)            |
| *T. decolorans* | *Buellia zoharyi*                                                                 | Molins et al. (2020)                   |
| *T. decolorans* | *Lecanora rupicola*                                                              | Blaha et al. (2006)                    |
| *T. decolorans* | *Xanthoria parietina*                                                            | Beck & Mayr (2012)                     |
|                 | *Xanthomendoza borealis,* Xm. *fulva,* Xm. *hasseana,* Xanthoria candelaria,*    | Nyati et al. (2013, 2014)              |
|                 | *X. elegans,* X. *parietina,* X. *polycarpa*                                     |                                        |
| *T. decolorans* | *Ramalina menziesii*                                                              | Werth & Sork (2014)                    |
| *T. decolorans* | *Caloplaca orthoclada*                                                           | Vargas Castillo & Beck (2012)          |
| *T. decolorans* | *Ramalina fraxinea*                                                              | Catalá et al. (2016)                   |
| *T. decolorans* | *Anaptychia ciliaris,* Xanthoria parietina*                                      | Dal Grande et al. (2014a)              |
| *T. decolorans* | *Anaptychia setifera,* Candelariella medians*                                   | Voytsekhovich & Beck (2016)            |
| *Trebouxia*     |                                                                                  |                                        |
| *clade G*       |                                                                                   |                                        |
| *clade G*       |                                                                                   |                                        |
| *galapagensis*  |                                                                                   |                                        |
| *usneae group*  |                                                                                   |                                        |
|                 | *Species of Parmotrema and Xanthoparmelia*                                       | Leavitt et al. (2015)                  |
| *T. gelatinosa* |                                                                                  |                                        |
| *T. gelatinosa* | *Caloplaca spp., Hymenelia sp., Lecanora subimergens,*                            | Watanabe et al. (1997). Maritime lichens. id: LM. |
|                 | *Lecidella enteroleucella,* Ochrolechia parellula,* Rinodina sp., Verrucaria sp.*|                                        |
| *T. gelatinosa* | *Physcia semipinnata*                                                            | Helms et al. (2001)                    |
| *T. gelatinosa* | *Flavoparmelia caperata,* Punctelia subrudecta,* Teloschistes sp., Xanthoria sp.*| Doering & Piercey-Normore (2009)       |
| *T. gelatinosa* | *Josepoeltia parva,* Teloschistes chrysophthalmus,* T. *hasseuianus,* Xanthomendoza novozeelandica,* Xm. weberi*| Nyati et al. (2013, 2014)              |
| *T. gelatinosa* | *Rhizocarpon geographicum*                                                       | Voytsekhovich & Beck (2016)            |
| *T. gigantea*   | *Parmelia submarinera*                                                            | Watanabe et al. (1997). Maritime. id: LM. |
| *T. gigantea*   | *Rinodinella controversa*                                                          | Helms et al. (2001)                    |
| *T. gigantea*   | *Protoparmeliopsis muralis*                                                       | Guzow-Krzemińska (2006)                |
| *T. gigantea*   | *Caloplaca orthoclada*                                                            | Vargas Castillo & Beck (2012)          |
| *T. gigantea*   | *Caloplaca erythrocarpia,* Candelariella medians*                                 | Voytsekhovich & Beck (2016)            |
| *T. glomerata*  | *Species of Polyblastia,* Rinodina and Verrucaria*                               | Watanabe et al. (1997). Maritime lichens. id: LM. |
| *T. higginsiae* | *Aspicilia sp., Buellia stellulata,* Caloplaca kobeana,* Hymenelia sp., Lecidella enteroleucella,* Parmelia congensis,* Rhizocarpon sp., Rinodina sp., Rinodinella sp.* | Watanabe et al. (1997). Maritime lichens. id: LM. |
| *T. hypogymniae*| *Hypogymnia physodes*                                                             | Hauck et al. (2007)                    |
| *T. hypogymniae*| *Evernia divaricata,* E. mesomorpha*                                              | Piercey-Normore (2009)                 |
| *T. impressa*   | *Parmelia mexicana*                                                                | Watanabe et al. (1997). Maritime lichens. id: LM. |
| *T. impressa*   | *Phaeophyscia arbuscularis,* Physcia adscendens,* P. *tenella*                     | Beck et al. (1998); Helms et al. (2001).|
| *T. impressa*   | *Dimelaena oreina,* Physcia aipola,* Physconia perisidiosa,* Rinodina capersis,* R. milvina* | Helms et al. (2001)                    |
| Alga                  | Fungal symbionts                                                                 | References & comments                        |
|----------------------|---------------------------------------------------------------------------------|----------------------------------------------|
| *Trebouxia impressa* | *Phaeophyscia orbicularis, Physcia caesia, P. tenella, Physconia distorta*     | Dahlkild et al. (2001)                       |
| *T. impressa*        | *Umbilicaria kappenii*                                                          | Romeike et al. (2002)                        |
| *T. impressa*        | *Melanelia glabra, Parmelia carpophorhiza, P. tiliae*, *Phaeophyscia orbicularis, Physcia caesia, P. stellaris, P. tenella* | Doering & Piercey-Normore (2009)             |
| *T. impressa*        | *Xanthomendoza fallax, X. ulophyllodes*                                        | Nyati et al. (2014)                          |
| *T. impressa*        | *Lecanora rupicola*                                                             | Blaha et al. (2006)                          |
| *T. impressa*        | *Lecanora fuscosbrunnea, Lecidea andersonii, L. atrobrunnea, L. cancriformis, L. tesselata, Lecidella carpathica* | Ruprecht et al. (2012)                       |
| *T. impressa*        | *Thamnolia vermicularis*                                                        | Onuţ-Brännström et al. (2017)                 |
| *T. impressa/T. gelatinosa* | *Cladonia cariosa, C. rei, Diploschistes muscorum*                             | Oszczka et al. (2021)                        |
| Clade I (impressa/gelatinosa group) | *Species of Melanelixia, Melanohalea, Montanelia, Oropagon, Parmelia, Protoparmeliopsis, Rhizoplaca and Xanthoparmelia* | Leavitt et al. (2015)                       |
| *T. impressa/T. potteri* | *Ramolina americana, R. sinensis*                                               | Francisco de Oliveira et al. (2012)          |
| *T. impressa/T. potteri* | *Pleurosticta koflerae*                                                        | Voytsekhovich & Beck (2016)                  |
| *Trebouxia clade including T. impressa, T. flava and T. potteri* | *Physconia distorta, P. grisea*                                                  | Wornik & Grube (2010)                        |
| *T. incrustata*      | *Xanthoria candelaria*                                                           | Aoki et al. (1998), Antarctica. id: LM, culture. |
| *T. incrustata*      | *Rinodina atrocinerea*                                                           | Helms et al. (2001)                          |
| *T. incrustata*      | *Acarospora bullata, Lecanora muralis, L. stenotropa, Neofuscelia stygiodes, Protoparmelia badia, Rhizocarpon cf. cyanescens, R. cf. viridiatrum* | Beck (2002)                                  |
| *T. incrustata*      | *Lecanora rupicola*                                                             | Blaha et al. (2006)                          |
| *T. incrustata*      | *Protoparmelia incrustans*                                                      | Muggia et al. (2013)                         |
| *T. incrustata*      | *Protoparmeliopsis muralis*                                                     | Guzow-Krzemińska (2006)                      |
| *T. incrustata*      | *Caloplaca crenulatella, C. squamulosa, Circinaria contorta, Lecanora muralis, Staurothele sp., Xanthoparmelia pullo, X. stenophylla* | Voytsekhovich & Beck (2016)                  |
| *T. irregularis*     | *Diploschistes muscorum*                                                        | Friedl (1989), Photobiont taken from parasitized Cladonia; later substituted by *T. showmanii*. id: LM. |
| *T. jamesii*         | *Candelaria concolor, Candelariella sp.*                                        | Beck et al. (1998)                           |
| *T. jamesii*         | *Tremolecia atrata*                                                             | Beck & Koop (2001)                           |
| *T. jamesii*         | *Chenotheca subroscida*                                                         | Tibell & Beck (2002)                         |
| *T. jamesii*         | *Umbilicaria antarctica, U. decussata, U. kappenii, U. umbilicanoides*          | Romeike et al. (2002)                        |
| *T. jamesii*         | *Evernia mesomorpha, Melanelia exasperatula*                                    | Piercey-Normore (2006, 2009), Multiple clades within. |
| *T. jamesii*         | *Evernia divericata, E. prunastri, Ramolina fraxinea, R. siliquosa*             | Tschäkler et al. (2007)                      |
| *T. jamesii*         | *Ramolina farinacea*                                                            | Casano et al. (2011); Moya et al. (2017).    |
| *T. jamesii*         | *Ramolina fraxinea*                                                             | Catalá et al. (2016)                         |
| *T. jamesii*         | *Carbona vorticosa, Lecanora fuscosbrunnea, L. physciella, Lecidea auriculata, L. cancriformis, L. lapicida, L. oblundata, Lecidella greenii, L. siplei* | Ruprecht et al. (2012)                      |
| *T. jamesii*         | *Lecidea cancriformis*                                                          | Pérez-Ortega et al. (2012), Hap4, well-supported clade. |
| *T. jamesii*         | *Lepraria borealis*                                                             | Engelen et al. (2010), Maritime Antarctica.   |
| Alga                                         | Fungal symbionts                                                                 | References & comments                        |
|----------------------------------------------|---------------------------------------------------------------------------------|----------------------------------------------|
| Trebouxia jamesii                           | Ramalina menziesii                                                              | Werth & Sork (2014). Only 6% of sampled thalli; majority had T. decolorans. |
| T. jamesii                                   | Candelariella vitellina, Lecanora frustulosa, Lecidea sp., Protoparmelia psorophana, Ramalina calicaris, R. capitata, R. pollinaria, R. pontica, Ramalina sp., Rhizocarpon geographicum, Rhizoplaca sp., Umbilicaria grisea | Voytsekhovich & Beck (2016)                  |
| T. jamesii                                   | Protoparmelia badia, P. montagnei                                               | Singh et al. (2017)                          |
| T. jamesii clade ‘T. letharii’                | Letharia barbata, L. gracilis, L. lucida, L. lupina, L. rugosa                  | Kroken & Taylor (2000)                       |
| T. jamesii clade ‘T. vulpinae’                | Letharia vulpina                                                                | Kroken & Taylor (2000)                       |
| T. jamesii clade ‘T. vulpinae’                | Cetraria aculeata                                                               | Fernández-Mendoza et al. (2011); Onu-Brännström et al. (2018). |
| T. jamesii and Trebouxia clades A, I, S, G    | Thamnolia vermicularis                                                          | Nelsen & Gargas (2009)                        |
| T. jamesii ‘group A’                         | Boreoplaca ultrafrigida, Umbilicaria esculenta, U. muehlenbergii                | Cao et al. (2015)                            |
| T. jamesii ‘group B’                         | Boreoplaca ultrafrigida, U. muehlenbergii                                       | Cao et al. (2015)                            |
| T. jamesii ssp. angustiobata                 | Acarospora sinopica, Lecidea lapicida                                            | Beck (1999)                                  |
| T. jamesii ssp. jamesii                      | Acarospora rugulosa, Bellemerea diamorpha, Lecanora polytropa, L. subaurea, Lecidea silacea, Rhizocarpon geographicum, Umbilicaria cylindrica | Beck (1999)                                  |
| T. potteri                                  | Pertussaria spp.                                                                | Takeshita et al. (1989). id: LM, culture.   |
| T. potteri/flava                            | Lecanora rupicola                                                              | Blaha et al. (2006)                          |
| T. showmanii                                 | Caloplaca spp.                                                                 | Watanabe et al. (1997). Maritime lichens. id: LM, culture. |
| T. showmanii                                 | Diploschistes muscorum                                                         | Friedl (1989), id: LM.                      |
| T. simplex                                  | Acarospora rugulosa, A. sinopica, A. smaragdula, Bellemerea alpina, B. cinereorufescens, B. subsorediza, Carbonea vorticosa, Lecidea confluentus, L. epanora, L. handelli, L. lapicida, L. psaupercula, L. polytrapa, L. silacea, L. subaurea, L. tesselata, Miriquidica atrafulva, M. garovagii, Pleopsidium chlorophanum, Porphia tuberculosa, Rhizocarpon geographicum, R. lecanorinum, R. norvegicum, R. polycarpum, R. ridescens, R. simuliform, Sparastasia testudinaria, Tremolecia atrata, Umbilicaria cristafula, U. cylindrica, U. torrefacta | Beck (2002)                                  |
| T. simplex                                  | Lecanora rupicola                                                              | Blaha et al. (2006)                          |
| T. simplex                                  | Lecanora conizaeoides                                                          | Hauck et al. (2007)                          |
| T. simplex                                  | Evenia mesomorpha, Evenniastrum catawbiense, Imshaugia aleurites, Pseudevernia consocians | Piercey-Normore (2009)                      |
| T. simplex                                  | Evenia mesomorpha, Imshaugia placorodia, Lecanora conizaeoides, Pseudevernia cladoniae, P. consocians | Doering & Piercey-Normore (2009)             |
| T. simplex                                  | Bryoria americana, B. bicolor, B. capillaris, B. fremontii, B. furcellata, B. glabra, B. implexa, B. lanestris, B. nadervinkiana, B. nitida, B. simplicior, B. smithii, B. subconca, B. tenui, Bryoria sp. | Lindgren et al. (2014)                      |
| T. simplex                                  | Protoparmelia hypotrempella, P. ochrococca, P. oleaginosa                        | Singh et al. (2017)                          |
| T. simplex                                  | Thamnolia vermicularis                                                         | Onu-Brännström et al. (2017)                 |
| T. simplex/jamesii                          | Lasallia pulsatula, L. hispanica, Umbilicaria spodochroa                        | Hestmark et al. (2016); Dal Grande et al. (2018). |
| Clade S (simplex/letharii/jamesii group)     | Species of Cetraria, Letharia, Melanohalea, Motanella, Rhizoplaca and Xanthoparmelia | Leavitt et al. (2015)                        |
### Table 1. (Continued)

| Alga Fungal symbionts | References & comments |
|-----------------------|-----------------------|
| Clade S (Trebouxiopsis/leptarii/jamesii group) | Pseudephebe minuscula, P. pubescens |
| T. simplex/suecica (S clade) | Cetraria aculeata, C. ericetorum, C. islandica, C. muricata, C. sepincola, Flavocetraria cucullata, F. nivalis, Melanelia agnata, M. hepatizon, M. stygia, Tuckermannopsis chlorophylla, Vulpicida pinastri |
| T. simplex s. lat. | Tephromela atrata s. str. |
| T. simplex subclades 1 and 2 | Cetraria aculeata, C. islandica, Thamnolia subuliformis |
| Trebouxiopsis solaris | Aspicilia cinerea, Caloploca aractina, Candelariella vittelina, Circinaria contorta, Ramalina capitata, Rhizocarpon geographicum |
| T. aff. solaris | Chrysothrix candelaris |
| T. aff. solaris | Lecanographa amylacea (‘Buellia violaceofusca’) |
| T. suecica | Acanthospora sinopica, Candelariella vitellina, Immersaria athroocarpa, Lecanora polytropa, Miriquidica atrofulva, Protoparmelia atriseda, P. badia, Rhizocarpon geographicum |
| T. suecica | Protoparmelia badia, P. memnonia |
| T. vagua | Candelariella vitellina, Circinaria contorta, Diploschistes diacapsis, Pseudoparmelia tomentosa |
| T. vagua | Thamnolia vermicularis |
| Near T. vagua | Caloplaca tubelliana, Dirina massiliensis [Arthoniomycetes!], Lecanora albescens |
| Trebouxiopsis clade IV (including T. corticola, T. galapagensis, T. higginsiae and T. usneae) | Tropical Ramalina anceps, R. complanata, R. dendroides, R. gracilis, R. peruviana, R. sorediosa, R. sprengeli |
| Trebouxiopsis A 02 | Austrolechia sp., Buellia frigida, Carborea vorticosa, Huea sp., Lecidea cancriformis, L. polypycnidophora, Lecidella greenii, Rhizoplaca macleanii |
| Trebouxiopsis sp. clade 1 | Fulgensia bracteata, F. fulgens, Toninia sedifolia |
| Trebouxiopsis sp. ‘D11’ | Buellia frigida, endolithic Lecidea sp., Umbilicaria aprina |
| Trebouxiopsis TR9 | Ramalina farinacea |
| Trebouxiopsis sp. ‘URa1’ | Carborea vorticosa, Lecidea cancriformis |
| Trebouxiopsis sp. ‘URa2’ | Carborea vorticosa, Lecidea andersonii, L. atrobrunnea, L. cancriformis, L. fuscoatra, L. lapicida, Lecidea sp., Lecidella greenii, L. siplei, Rhizoplaca macleanii |
| Trebouxiopsis sp. ‘URa3’ | Carborea vorticosa, Lecanora phylisciella, Lecidea andersonii, L. cancriformis, L. lapicida, L. polypycnidophora, Lecidella greenii, L. patavina, L. siplei, Rhizoplaca macleanii |
| Trebouxiopsis sp. ‘URa4’ | Lecidea andersonii, Lecidella stigmatea |
| Trebouxiopsis sp. | Buellia papillata, Caloplaca johnstonii, C. lewis-smithii, Candelariella flavida, Lecidella patavina, Lepraria coccusumin, Pseudopehebe minuscula, Psoroma sp., Tephromela atrata, T. disciformis, Usnea lambii, Xanthoria elegans |
| Trebouxiopsis sp. | Bagliettoa marmorea |
| Trebouxiopsis sp. | Lasallia pustulata |
| Trebouxiopsis sp. | Cetraria aculeata |

(Continued)
| Alga                | Fungal symbionts                                                                 | References & comments                                                                 |
|---------------------|---------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|
| Trebouxia sp.       | Austrolechia spp., Buellia frigida, Caloplaca cf. citrina, C. sublobata, Caloplaca sp., Carbonea vorticosa, Huaa sp., Lecanora cancriformis, L. natowiana, L. fuscobrunnea, Lecidella greenii, Rhizoplaca macleani, Rhizoplaca sp., Umbilicaria aprina | Pérez-Ortega et al. (2012). Crustose lichens of McMurdo Dry Valleys, probably representing at least two undescribed clades. |
| Trebouxia sp.       | Austrolechia spp., Buellia frigida, Caloplaca cf. citrina, C. sublobata, Caloplaca sp., Carbonea vorticosa, Huaa sp., Lecanora cancriformis, L. natowiana, L. fuscobrunnea, Lecidella greenii, Rhizoplaca macleani, Rhizoplaca sp., Umbilicaria aprina | Pérez-Ortega et al. (2012). Crustose lichens of McMurdo Dry Valleys, probably representing at least two undescribed clades. |
| Trebouxia sp. B     | Boreoplaca ultrafrigida, Parmelia omphalodes                                    | Cao et al. (2015)                                                                      |
| Trebouxia sp.       | Rhizoplaca spp., Protoparmeliopsis spp.                                          | Leavitt et al. (2016). Some 15 spp., collected worldwide.                             |
| Vulcaochloris sp.   | Stereocaulon vesuvianum                                                          | Vančurová et al. (2015). From La Palma.                                               |
| Vulcaochloris sp.   | Stereocaulon pteryzans                                                          | Kosecka et al. (2021)                                                                  |
| Class Trebouxiophyceae, Order Prasiolales, Elliptochloris clade | (Coccomyxa greatwallensis) Isolated from Psoroma hypnorum                         | Cao et al. (2018). Symbiotic status not established.                                   |
| Coccomyxa sp.       | Dibaeis baemycetes                                                               | Beck (2002)                                                                            |
| Coccomyxa sp.       | Peltigera variolosa, Solarina bispora, S. crocea, S. saccata                     | Malavasi et al. (2016)                                                                |
| Coccomyxa sp.       | Lichenomphalia ericeratum, L. griselina, L. hudsoniana, L. luteovitellina, L. velutina, Lichenomphalia sp. | Zoller & Lutzoni (2003)                                                               |
| Coccomyxa sp.       | Lichenomphalia hudsoniana, L. meridionalis, L. umbellifera                       | Masumoto et al. (2019); Gasulla et al. (2020); Masumoto (2020).                      |
| Coccomyxa sp.       | Dacampia hookeri                                                                  | Henssen (1995). id: LM.                                                               |
| Coccomyxa sp.       | Nephroma arcticum, N. expallidum, Peltigera ophthosa, P. britannica, P. leucophlebia | Lohtander et al. (2003)                                                              |
| Coccomyxa sp.       | Peltigera variolosa, Solarina bispora, S. crocea, S. saccata                     | Darienko et al. (2015). Photobionts not monophyletic, related to free-living C. subellipsoidea. |
| Coccomyxa sp.       | Micarea byssacea, M. denigrata, M. leposula, M. lignaria, M. micrococcum, M. nitschkeana, M. peliocarpa, M. prasina (Pilocarpaceae) | Yahr et al. (2015)                                                                   |
| Coccomyxa sp.       | Icmadophilus diversus, I. ericeratum, I. japonica, I. splachnirima                | Ludwig (2015)                                                                         |
| Coccomyxa sp.       | Lichenomphalia oreades                                                            | Lucking et al. (2017b)                                                                |
| Coccomyxa sp.       | Sticta laciniosa from Cuba                                                        | Lindgren et al. (2020)                                                                |
| Related to Coccomyxa and Pseudococcomyxa | Schizoxylon albescens (Stictidaceae)                                               | Muggia et al. (2011)                                                                  |
| Elliptochloris bilobata | Fuscoidea cyatheo var. japonica                                                  | Watanabe et al. (1997). Maritime. id: LM, culture.                                    |
| E. bilobata         | Species of Buellia and Leproloma                                                   | Aoki et al. (1998). Antarctic. id: LM, culture.                                       |
| E. bilobata         | Boeomyces rufus                                                                   | Trembley et al. (2002b)                                                              |
| E. bilobata         | Verrucaria sublubulata                                                             | Thús et al. (2011)                                                                   |
| E. bilobata         | Micarea misella, M. prasina                                                       | Voytsekhovich et al. (2011). id: LM, culture.                                        |
| E. bilobata         | Micarea prasina                                                                   | Yahr et al. (2015)                                                                   |
| E. bilobata         | Catolechia wahlenburgii                                                            | Darienko et al. (2016)                                                               |
| E. parasphaerica ad int. | Multiclavula petricola, M. vernalis                                              | Reported by H. Masumoto & S. Handa in Masumoto (2020).                                 |
| E. perforata        | Micarea prasina                                                                   | Darienko et al. (2016)                                                               |
| E. reiformis         | Fuscoidea cyathoides var. japonica, Leproloma sp., Ochrolechia perequella         | Watanabe et al. (1997); Darienko et al. (2016). Maritime. id: LM, culture.            |
| E. reiformis         | Micarea peliocarpa                                                                 | Voytsekhovich et al. (2011). id: LM, culture.                                        |
| E. subsphaerica     | Aspicilla sp., Fuscoidea cyathoides var. japonica                                 | Watanabe et al. (1997). Maritime. id: LM, culture.                                    |
| E. subsphaerica     | Micarea melanobola, M. prasina, M. subnigrata                                    | Voytsekhovich et al. (2011). id: LM, culture.                                         |
Table 1. (Continued)

| Alga | Fungal symbionts | References & comments |
|------|------------------|-----------------------|
| Elliptochloris subsphaerica | Multiclavula mucida | Masumoto (2020) |
| Elliptochloris sp. | Stictis urceolatum | Thüs et al. (2011) |
| Elliptochloris sp. | Catillaria chalybeia | Dal Grande et al. (2014b) |
| Elliptochloris sp. | Ramolina farinacea | Moya et al. (2017). Minority photobiont. |
| Elliptochloris sp. | Bryocladula phycophila | Masumoto (2020) |
| Elliptochloris sp. | Sticta filix, S. menziesii, S. stipitata, S. subcaperata | Lindgren et al. (2020) |
| Pseudococcomyxa simplex | Leproloma sp. | Watanabe et al. (1997). Maritime. id: LM, culture. |
| Pseudococcomyxa sp. | Micarea prasina | Voytsekhovich et al. (2011). id: LM, culture. |

**Class Trebouxiophyceae, Order Watanabeales**

| Chloroidium angustoellipsoideum | Stereocaulon nanodes, S. spathuliferum | Vančurová (2012); Vančurová et al. (2018). Darienko et al. (2018): C. ellipsoideum now C. lichenum. |
| C. ellipsoideum | Trapelia obtegens | Beck (2002) |
| C. ellipsoideum | Stereocaulon nanodes, S. pileatum, S. vesuvianum, S. spathuliferum, Stereocaulon sp. | Vančurová (2012); Vančurová et al. (2018). Stereocaulon vesuvianum also hosts Asterochloris and Vulcanochloris. |
| Near C. ellipsoideum | Trapeliopsis flexuosa, T. granulosa | Schmitt & Lumbsch (2001). Amplified unintentionally with non-specific primers. 'Chlorella ellipsoidea sequence X63520. Known photobionts of other Trapeliaceae are in Prasiolales. |
| C. saccharophilum | Trapelia coarctata | Tschermak-Woess (1988b) |
| C. saccharophilum | Lecidea inops, Psilocheila leprosa, Stereocaulon nanodes | Beck (2002) |
| C. saccharophilum | Psora decipiens | Rupprech et al. (2014). One record; all other thalli had Asterochloris or Trebouxiella. Contrast Williams et al. (2017). |
| C. viscosum | Bacidina [Woessia] fusarioides | Tschermak-Woess (1988b); Darienko et al. (2018). |
| Chloroidium sp. | Verrucaria proterminsa | Thüs et al. (2011). Possibly an accessory alga rather than main photobiont. |
| Chloroidium sp. | Verrucaria nigrescens, Verrucaria sp. | Voytsekhovich & Beck (2016). id: LM. |
| Chloroidium sp. | Species of Gomphillus and Gyalidea | Sanders et al. (2016) |
| Chloroidium sp. | Sticta latifrons, S. subcaperata | Lindgren et al. (2020) |
| Near Chloroidium and Parachloroidium | Bapalmuia lineata | Sanders et al. (2016) |
| Heveochlorella sp. (Jaagichlorella | Pseudocystellaria sp., Sticta sp. | Dal Grande et al. (2014b). Three specimens; authors confident alga is photobiont. |
| Heveochlorella sp. | Psorocladus cinerascens, A. fugiens, A. guminparum (Thelenellaceae); Aderkomyces heterellus, Echinoplaca spp., Gyrolecidium appendiculatum, G. floridease, G. imperfecta, G. poioae, G. uliceae, Gyroleciopsis sessilis, Gyroleciopsis sps. (Gomphillaceae); Byssoloma discords, Colopadua fusca, C. perpallida, C. puiggarii (Pilocarpaceae) | Sanders et al. (2016). Mainly foliicolous. |
| Heveochlorella sp. | Sticta caperata, S. dichotoma, S. latifrons, S. squamata, S. subcaperata, S. subcaperata, S. variabilis, Sticta spp. | Lindgren et al. (2020) |
| [unidentified, falling “near” Heterochlorella] | Psoroglaena epiphylla | Nyati et al. (2007); Thüs et al. (2011). |

**Class Trebouxiophyceae, incertae sedis**

| Apatococcus lobatus | Caloplaca sp., Fusidemia cyathoides var. japonica, Lecanora subtergallum, Pyrenopsis sp., Verrucaria sp. | Watanabe et al. (1997). Maritime. id: LM. |
| A. lobatus | Scoliciosporum umbrinum | Beck (2002) |
| A. fusidemiae | Fusidemia arboricola, F. cyathoides, F. kochiana, F. pusilla | Zahradníková et al. (2017) |
| Apatococcus sp. | Fusidemia lightfootii | Zahradníková et al. (2017) |

(Continued)
| Alga          | Fungal symbionts                                                                 | References & comments                                      |
|--------------|----------------------------------------------------------------------------------|-----------------------------------------------------------|
| **Coccobotrys verrucariae** | Verrucaria nigrescens                                                            | Chodat (1913); Vischer (1960).                           |
| Coccobotrys sp. (?)              | Botryolepraria lesdainii                                                          | Canals et al. (1997). id: LM, culture.                   |
| **Dictyochloropsis splendida**   | Phlyctis argena                                                                  | Tschermak-Woess (1995). id: LM.                           |
| D. symbiontica                     | Sphaerophorus diplopyrus, S. fragilis, S. melanocarpus, S. melaphorus              | Ihda et al. (1997). id: LM, culture.                      |
| D. symbiontica                     | Species of Calaplaica and Leproloma                                               | Watanabe et al. (1997). Maritime. id: LM.                |
| D. symbiontica                     | Leccania naegelii                                                                | Beck et al. (1998)                                        |
| **Dictyochloropsis clade 2**      | brigantiaea ferruginea, B. leucoxantha (Brigantiaeaceae); Crocodia aurata, Lobaria oregana, L. patinafera, L. pulmonaria, Lobariaella crenulata, L. pallidocrenulata, Lobariaella sp., Pseudocyphellaria faurieata, P. homeophylla, P. lindsayi, P. lividofusca, P. multiforma, Sticta canariensis, S. latifrons, S. pulmonarioi, S. subcaperrata, Sticta spp. (Lobariaceae); Megaspora sulphurata (Megasporaceae); Chaothecopsis consociata (Myxocaliciaceae); Phlyctis argena (Phlyctidaceae); Biota sp. (Ramalinaeaceae); Chaothecopsis brunneoia (Coniothyriomycetes) | Dal Grande et al. (2014b). Dictyochloropsis. clade 2 = Symbiochloris; Škaloud et al. (2016). |
| **Leptosira terestris**            | Vezaea eutilus                                                                     | Tschermak-Woess & Poelt (1976). id: LM, culture.          |
| L. thrombii                           | Thrombium epigaeum                                                                | Tschermak-Woess (1953). id: LM, culture.                  |
| **Neocystis sp.**                   | Micarea misella                                                                   | Voytsekhovich et al. (2011). Reported as an ‘additional photobiont’ to Elliptochloris. id: LM, culture. |
| **Symbiochloris sp.**               | Brigantiaea ferruginea, B. leucoxantha (Brigantiaeaceae); Crocodia aurata, Dendriscosticta platyphylla, D. wrightii; Lobaria macaronesia, L. oregana, L. patinafera, L. pulmonaria, Lobariaella crenulata, L. pallidocrenulata, Lobariaella sp., Pseudocyphellaria faurieata, P. homeophylla, P. lindsayi, P. lividofusca, P. multiforma, Sticta canariensis, S. latifrons, S. pulmonarioi, S. subcaperrata, Sticta spp. (Lobariaceae); Megaspora sulphurata (Megasporaceae); Chaothecopsis consociata (Myxocaliciaceae); Phlyctis argena (Phlyctidaceae); Biota sp. (Ramalinaeaceae); Chaothecopsis brunneoia (Coniothyriomycetes) | Škaloud et al. (2016). All known photobionts previously included in Dictyochloropsis s. lat. |
| **Symbiochloris sp.**               | Sticta ainoae, S. cinereoglauca, S. granatensis, S. laciniosa, S. puracensis, Sticta spp. | Lindgren et al. (2020)                                   |
| **Class Ulvophyceae, Order Trentepohliales** |                                                                                 |                                                           |
| **Cephaleuros sp.**                | Strigula smaragdula                                                               | Green (2012)                                              |
| **Cephaleuros sp.**                | Strigula smaragdula                                                               | Jiang et al. (2020)                                      |
| **Phycopeltis sp.**                | Tenuitholiascus porinoides                                                        | Jiang et al. (2020)                                      |
| **Trentepohlia lagenifera**         | Graphina cleistophlebra, G. inabensis, G. inortoest, G. mendax, G. undulata, Graphis aperiens, G. aphanes, G. batanensis, G. cognata, G. connectans, G. dupaxana, G. handelii, G. intricata, G. prosperps, G. rikuzensis, G. rufta, G. scripta, G. subdura, G. subtropica, G. subvirginia, G. tenella, Phaeographina chlorocarpoides, P. endofusca, Phaeographis aterifomis, P. exaltata, P. pruinosa | Nakano (1988). id: LM, culture. |
| T. lagenifera                       | Pyrenula japonica                                                                 | Nakano & Ihda (1996). id: LM, culture.                   |
| **Trentepohlia/’Printzina’**        | Acanthothecis sp., Anthracothecium sp., Astrothelium cinnamomeum, A. galbineum, A. leucoconicum, A. versicolor, Astrothelium sp., Coenogoniium linkii, Cryptothecia assimilis, Cryptothelium pulchrum, Cryptothelium sp., Dendrographa alectoroi, Dichosporidium baschianum, Graphis scripta, Graphis sp., Laurera megasperma, Myriotrema peninsulorum, Porina histrix, P. dolichophora, P. luteissema, P. tetracerae, Porina spp., Racodium rupestre, Thalidroma hypeleptum, Thelotrema pachyphorum, Trypethelium oenium, T. nitiduscumul, Trypethelium spp. | Nelsen et al. (2011). ’Printzina’ clades occur scattered throughout Trentepohlia. Mycobionts represent Arthoniomycetes, Dothideomycetes and Lecanoromycetes. |

(Continued)
| Alga                | Fungal symbionts                                                                 | References & comments                                                                                     |
|---------------------|---------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------|
| Trentepohlia/'Printzina’ | Astrothelium variolusum, Graphis endoxantha, G. pulverulenta, G. scripta, Herpithallon rubriconctum, Phaeographina sp., Phaeographis inusta, P. punctiformis, Pyrenula confinis, P. cruenta, P. pseudobufonia, P. sexlocularis, Strigula subtilissima, Trypethelium vires | Green (2012). Photobiont of one Strigula sp. included.                                                     |
| Trentepohlia ‘Printzina’ | Acrocordia gemmata, Arthoria cinnabarina, A. radiata, Arthothelium ruanum, Cystocoleus ebeneus, Dimerella pinet, Graphis propinqua, G. scripta, G. submarginata, Gyalecta jenensis, Mycoporum sparsellum, Opegrapha atrata, Pyrenula lovegata, Roccella decipiens, R. galapagoensis, R. linears, R. irellina, R. maderensis, R. cf. montagnei, R. phytophis, R. tinctoria, R. tuberculata, Thelotrema lepadinum | Hametner et al. (2014a, b)                                                                                    |
| Trentepohlia sp.     | Lecanographa amylacea                                                             | Ertz et al. (2018). Mycobiont also forms heteromorphic, asexual thalli with Trebouxia sp.                 |
| Trentepohlia sp.     | Dichosporidium sp., Diorygma antillarum, D. confluens, D. nigrocinctum, Diorygma sp., Herpothallon echinatum, H. rubroechinatum, Herpithallon sp., Ocellularia sorediigera, Ocellularia spp., Porina sp., Sagenidiopsis isidiata, Sagenidiopsis sp., Syncesia farinacea | Kosecka et al. (2020)                                                                                     |

**Class Ulvophyceae, Order Ulvales**

**Blidingia minima**
- Turgidosculum ulvae
- Pérez-Ortega et al. (2018). Form ‘borderline lichen’ but mycobiont belongs to lichen-forming clade.
- Thüs et al. (2011)
- Darienko & Pröschold (2017)

**Pseudendoclonium arborpyreniae**
- Species of Caloplaca, Rinodina, Thelidium and Verrucaria
- Watanabe et al. (1997). Maritime lichens. According to This et al. (2011), maritime specimens of Caloplaca etc. may overgrow Verrucariaceae containing Dilabifilum (Pseudendoclonium). id: LM, culture.

**P. incrustans**
- Verrucaria aquatilis
- Tschermak-Woess (1970). Dilabifilum, reclassified in Darienko & Pröschold (2017).

**P. commune**
- Hydrophacuria rheidtophila
- Darienko & Pröschold (2017). Submerged lichen.

**Bracteacoccus sp.**
- ‘Multiclavula clara’ [=Sulzbachromyces sinensis]
- Takeshita et al. (2010). id: LM, culture.
- Hodkinson et al. (2014). rbcl sequences.

**Bracteacoccus sp.**
- Sulzbachromyces coatingae
- Masumoto (2020). ITS and rbcl sequences.

**Chlamydomonas sp.**
- Pyranea
- Skuja (1943). Association doubtfullly lichenic.

**Chlorosarcinopsis minor**
- Lecidea lapicida, L. plana
- Plesl (1963). Genus polyphyletic (Neustupa 2015).

**Gloeocystis sp.**
- Bryophagus gloeocapsa, Epigloea bactrospora
- Tschermak-Woess (1988a). Gloeocystis s. lat. highly polyphyletic (Neustupa 2015).

**Radiococcus signiensis**
- Placynthiella icmalea, P. uliginosa
- Voytekovich et al. (2011). Other photobions found in lesser abundance within same algal layer. id: LM, culture.

**Trochiscia sp.**
- Polyblastia amota, P. hyperborae
- Tschermak (1941b); Ahmadjian (1967); but Ettl & Gärtner (2014) consider ID questionable.

**Domain Eukaryo, Eukaryote supergroup Archeoplastida, Kingdom Plantae, Division Streptophyta (Chlorophyta)**

**Interfilum sp.**
- Micarea prasina; Placynthiella icmalea, P. uliginosa
- Voytekovich et al. (2011). Reported as secondary (less abundant) photobiont within algal layer. id: LM, culture.
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References

| Table 1. (Continued) |
|----------------------|
| **Alga** | **Fungal symbionts** | **References & comments** |
| **Domain Eukarya, Eukaryote supergroup: SAR (Stramenopila Alveolata Rhizaria), Kingdom Stramenopila (Heterokontae)** | **Class Phaeophyceae** | |
| Petrolithon maculiforme | Wahlenbergiella tavaresiae | Moe (1997); Peters & Moe (2001); Gueidan et al. (2011). |
| **Class Xanthophyceae** | | |
| Heterococcus sp. | Verrucaria funckii, V. leuverata | Zeiller (1954); Tschemak-Woess (1988a). |
| Heterococcus sp. | Hydropunctaria maura | Parra & Redon (1977). id: LM. |
| Heterococcus sp. | Hydropunctaria rhitropila; Verrucaria funckii, V. hydrela | Thüs et al. (2011) |
| Xanthonema sp. | Staurothele clopimoides | Pereira Riquelme (1992). id: LM. |

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