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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).

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 phycological 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 *Trebouxiophyceae* (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 'trebouxioid' or 'chlorococcalean', 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.
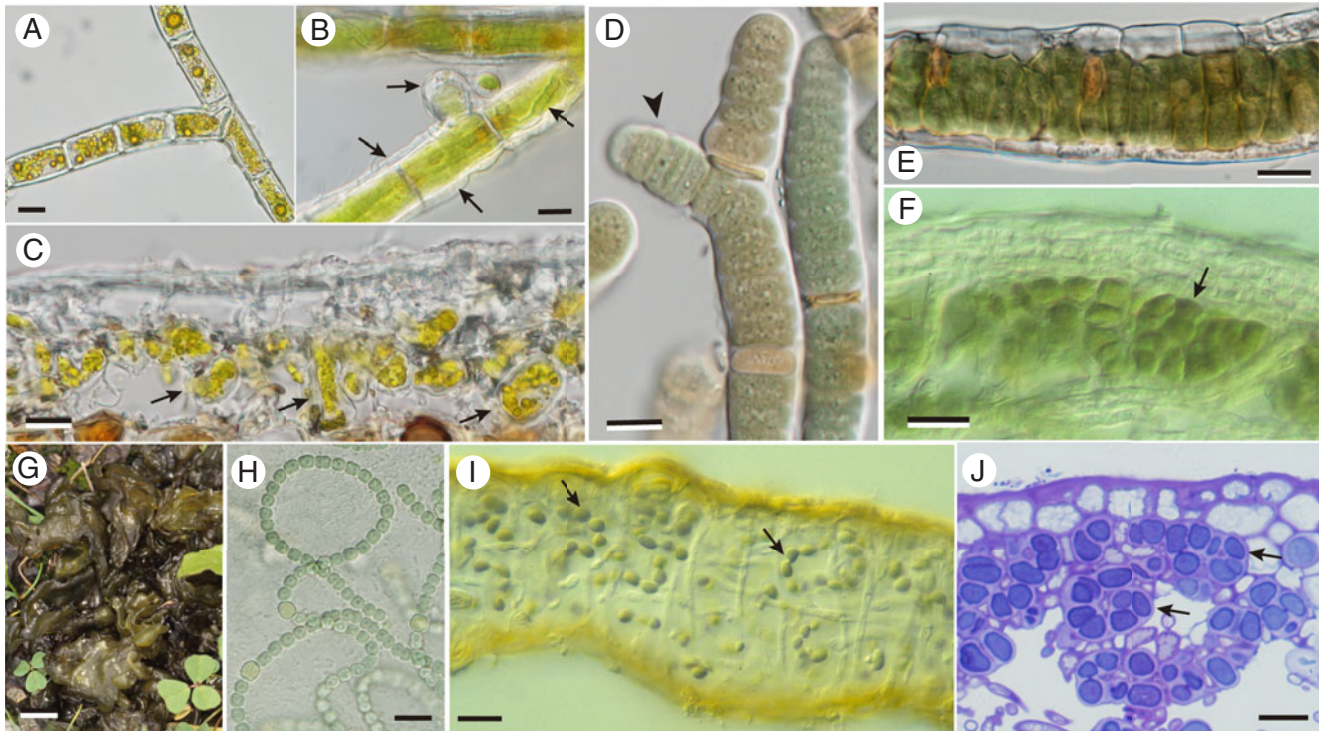
The Major Algal Groups Involved

Lichen algae are diverse. This may contribute to the distinct distributions and climatic preferences of the symbiotic thalli that

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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 rubro-cincta*; 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 *Coccocarpia palmicola*. G–J. *Nostoc*. G, free-living thallus-like macrocolony on soil. H, cultured strain. I, more or less intact filaments (arrows) within thallus of *Collema furfuraceum*. J, contorted or broken up into cell groups (arrows) within cyanomorph of *Sticta canariensis*. Scales: A–F, H–J = 10 µm; G = 1 cm.

enclose them (Marini *et al.* 2011). Most are green algae, a para-phyletic 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 phaeo-phyte) 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, poten-tially suitable algae may be pre-adapted to coping with hydric stresses and high radiation loads (Lange *et al.* 1990; Gustavs *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 pro-tists, plants and animals (Adams *et al.* 2012; Grube *et al.* 2017*b*).

Algal partners in lichen symbioses were termed phycobionts by Scott (1957). Subsequently, Ahmadjian (1982) proposed that *photo-biont* 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.* 2017*b*), while others con-sider 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 polyphyletic 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 algae to encompass all non-embryophyte lineages that inherited oxygenic photosynthesis. Phycobiont and photobiont are considered synonymous terms.

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 CO_2-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 (Geitler 1934; Tschermak 1941*a*; 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 asco-lichens (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 funnelling carbohydrate released by the alga to the fungus (Honegger 1991; Trembley *et al.* 2002*a*). 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*, *Coccomyxa*, *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).
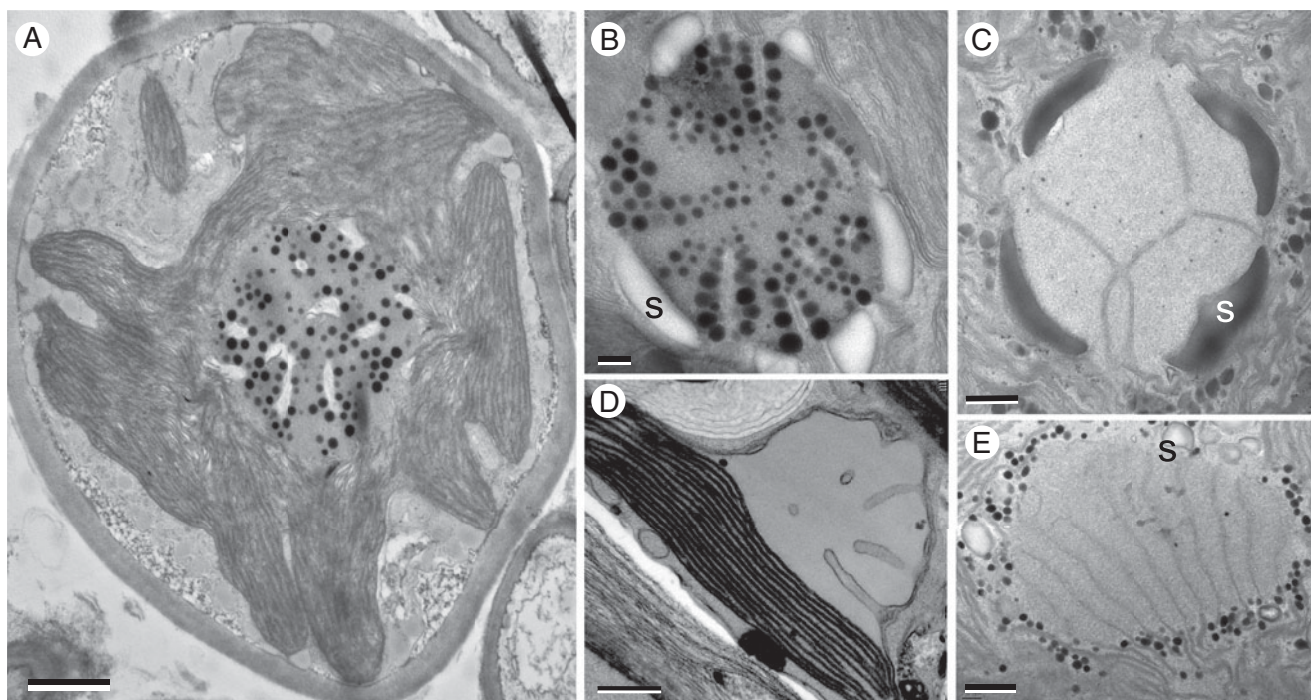
Fig. 2. TEM micrographs of some photobiont pyrenoids, with plastoglobuli (round black dots) and penetrating membranes in various positions and orientations. A, *Trebouxia*, within thallus of *Lasallia pustulata*. Note pyrenoid structure here more closely resembles that of distantly related *Heveochlorella* (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; Kranner et al. 2008; Kosugi et al. 2009; Asplund & Wardle 2013; Gauslaa et al. 2017; Míguez 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. 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 resynthesize 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 micro-organisms separately (Thomas 1939; Scott 1960; Ahmadjian 1962; Stocker-Wörgötter 2001; but see Marton & Galun 1976). It therefore seems logical to view the lichen symbiosis as a more or less mutualistic response to conditions that permit neither partner to thrive independently.

Although both partners may derive benefits, the lichen symbiosis is clearly not symmetrical (Hill 2009). The heterotrophic mycobionts, with their elaborate structural adaptations for algal cultivation, are more fully committed to symbiosis than their trophically autonomous photobionts. The mycobiont frees itself of symbiosis only in spore dispersal, seeking algal partners again immediately upon germination. To carry out sexual reproduction, it must be in symbiosis, whereas its photobiont appears to need aposymbiotic freedom to do so. From the alga's point of view, whenever unfavourable conditions reduce its possibilities of aposymbiotic success, the benefits of lichenization may begin to outweigh any disadvantages. Photobionts may rely on lichen symbioses for long-term persistence in habitats periodically subject to adverse conditions, while needing intervals of independence under favourable conditions to complete their life cycles. Thus, mycobiont and photobiont life histories do not fully coincide, but produce a lichen where they intersect compatibly. To varying degrees, natural selection has optimized the mycobiont principally for symbiosis, the photobiont for autonomy as well as symbiosis. The trade-off is that greater adaptation to symbiotic compatibility is likely to constrain the possibilities for competitive success in the aposymbiotic state. However, the lingering notion that certain photobionts may not ever occur free-living is probably attributable to insufficient sampling, and the conflation of invisibility with absence. Unsurprisingly, those photobionts that are macroscopically visible (*Nostoc*, *Cephaleuros*, *Phycopeltis*, *Trentepohlia*, *Prasiola*, *Petroderma*) have not had their aposymbiotic occurrence disputed.

Both fungus and alga must adapt, at least to some extent, to be compatible symbionts. For some authors, such mutual adaptation constitutes coevolution (Ahmadjian 1987; Saini et al. 2019); for others, coevolution supposes parallel cladogenesis in partners' phylogenies, a criterion not generally met by lichen symbioses analyzed in this regard (Piercey-Normore & DePriest 2001; Stenroos et al. 2006). However, it has been argued that focusing exclusively on this fine scale ignores broader patterns of co-adaptation, whereby 'guilds' of different mycobionts share common pools of photobionts to mutual advantage (Rikkinen 2003, 2013). According to Hill (2009), photobionts cannot coevolve with their mycobionts because they lack sexual reproduction in the thallus, are not subject to natural selection from one lichen to the next, and are not perpetuated when a lichen thallus dies. Yet photobionts are continually escaping from lichen thalli by means of soredia, isidia, thallus fragments, co-dispersed hymenial, epithecial or conidiomal algae (Fig. 3), and the excreta of lichenivorous invertebrates (Fröberg et al. 2001; Meier et al. 2002; Boch et al. 2011). Such diaspores afford many chances of finding microconditions where independent algal growth is favoured; aposymbiotic, potentially sexual populations may then develop, be they brief or enduring. Selection among genotypes for compatibility (or resistance) will occur when the opportunity for relichenization next presents itself. Compatible genotypes incorporated into a developing lichen may then be subject to further winnowing selection in the course of thallus growth.

Patterns of Symbiont 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 converse, 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 pin-lichen genus *Chaenotheca* (*Coniocybomycetes*) includes species associating with *Trebouxia*, *Trentepohlia*, *Symbiochloris* or *Tritostichococcus* (Tibell 2001; Škaloud et al. 2016; Pröschold & Darienko 2020). The fruticose lichen genus *Stereocaulon* may harbour thallus photobionts of either *Asterochloris*, *Vulcanochloris* or *Chloroidium* (Vančurová et al. 2018). Species of *Sticta* may partner with chlorobionts of *Symbiochloris*, *Coccomyxa*, *Elliptochloris*, *Heveochlorella* or *Chloroidium* (Lindgren et al. 2020). Squamulose *Psora decipiens* is reported to partner with either *Asterochloris*, *Trebouxia*, *Chloroidium* (Ruprecht et al. 2014) or *Myrmecia* 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-
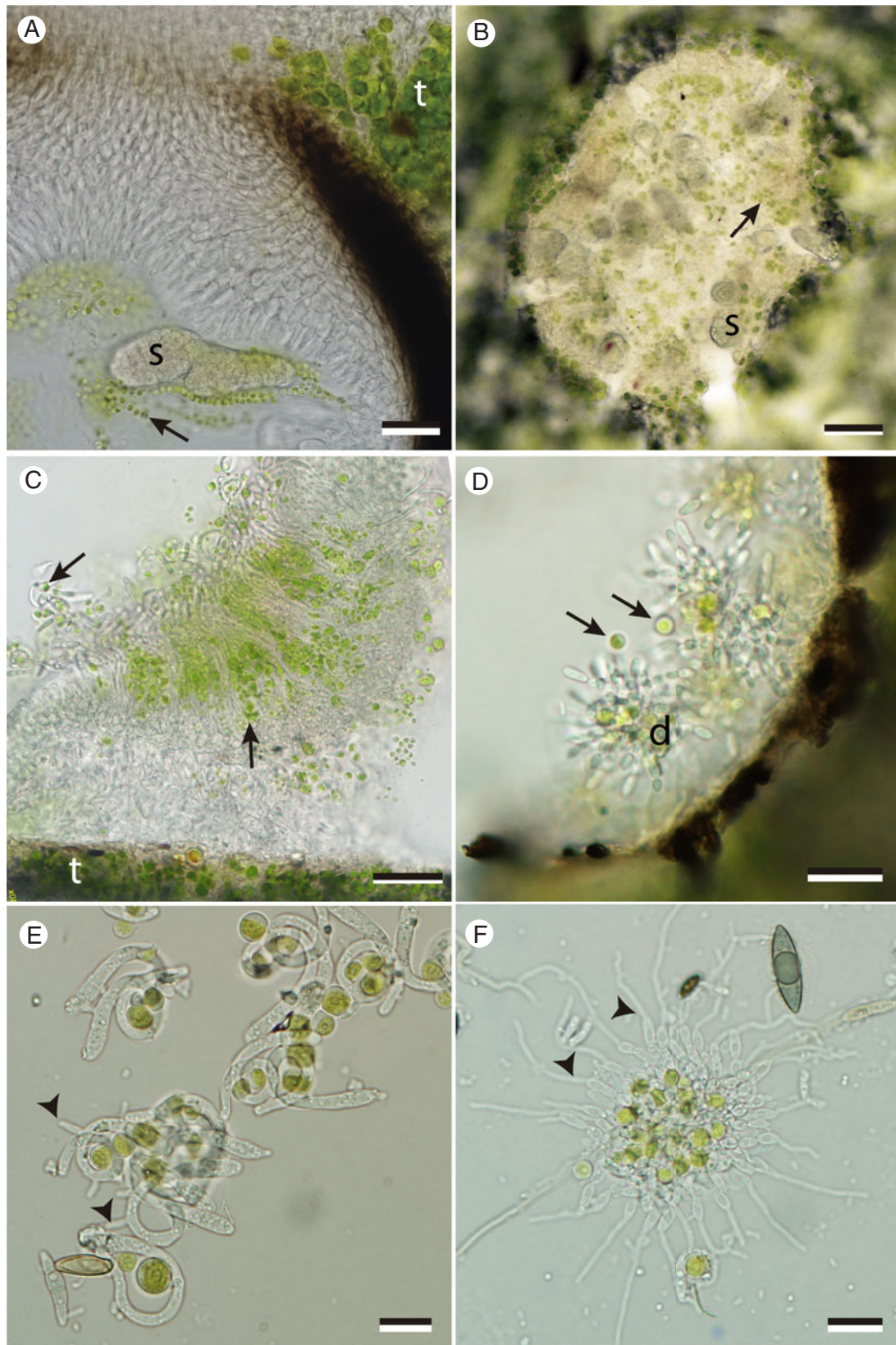
Fig. 3. Liberation and potential co-dispersal of photobionts from the spore-producing structures of certain mycobionts. A, *Diplosphaera* photobiont (arrows) within perithecium of *Endocarpon pusillum*; note much smaller size compared to photobiont cells within thalline tissue (t); s = ascospore. B, apothecial surface of folii-colous lichen colonizing plastic cover slip; note epithecial 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 pro-pagules (bundles of conidial chains dispersed as a unit) with adhering or intermixed *Heveochlorella* photobionts (arrows). E, campylidial 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.
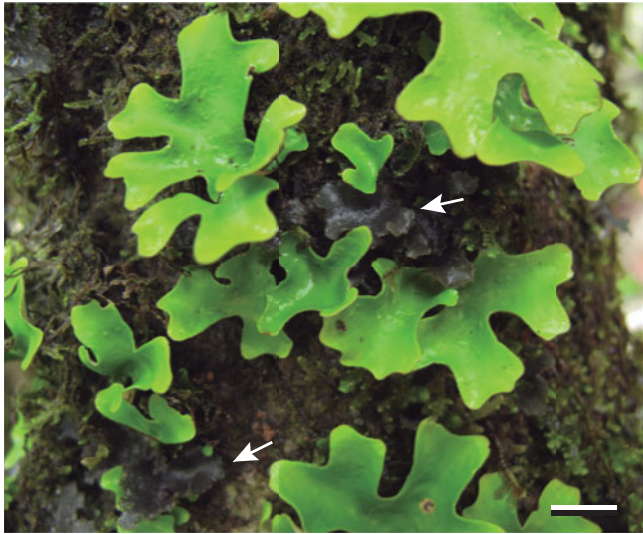
Fig. 4. Dichotomously lobed chloromorphs of *Sticta canariensis* emerging from lower surfaces of cyanomorph thalli (arrows). Scale = 5 mm.

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 *Cyphellostereum* (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 CO_2 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 *Lecanographa 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 chrysoleuca* (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 mycobiont 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 liberality 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 (Piercey-Normore 2004; Yahr et al. 2004; Otálora et al. 2010; Onuț-Brännström et al. 2017). Some studies have correlated symbiont selection patterns with environmental parameters, such as latitude (Singh et al. 2017), climate (Řidká 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; Jüriado 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; Onuț-Brännström 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 (Helms et al. 2001), 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; Otálora 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, prothallic hyphae extending outward along the substratum from the

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.

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 Galløe 1927: p. 40, 1932: p. 78; Letrouit-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 prothallic 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 & Letrouit-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 cephalodia 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 germlings 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; Řidka et al. 2014; Onuţ-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; Osyczka 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
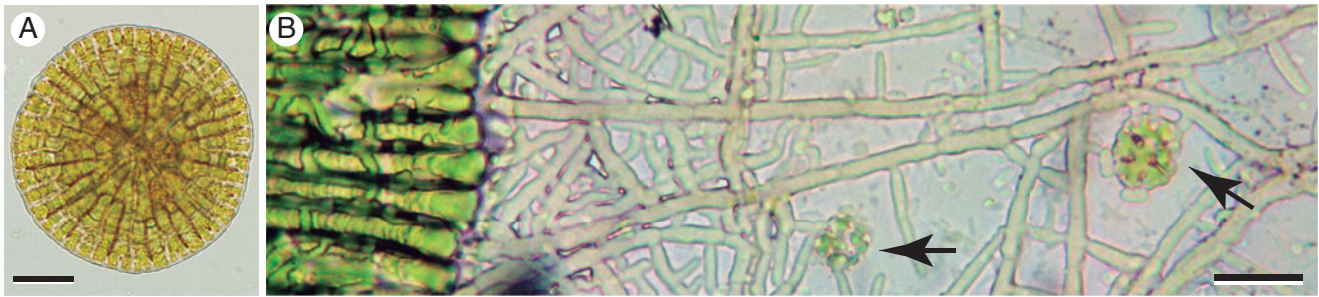
Fig. 6. *Phycopeltis* free-living and in stages of lichenization. A, free-living. B, edge of developed *Phycopeltis* thallus (left) lichenized by a network of hyphae (probably foliicolous *Porina* sp.) that extend over substratum and capture additional young *Phycopeltis* germlings (arrows). Scales: A = 20 µm; B = 10 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 *et al.* 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. Catalá *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 minority 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. *Coccomyxa*, *Elliptochloris*, *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.* 2017*a*). 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). Tschermak-Woess (1988*a*) 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 spheriodal-celled taxa such as *Gloeocapsa* and *Chroococcus*. The much-studied 'Anacystis nidulans' is usually treated now under *Synecococcus*; 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

Stereocaulon (see Tschermak-Woess 1988*a*); 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 filaments morphologically similar to *Scytonema* but only rarely showing false branching. A recent paper reported new species of both *Brasilonema* and *Chroococcidiopsis* 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 1988*a*). 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 *Rhizonema* (see Geitler 1934). The circumscription of *Calothrix* and *Dichothrix* with respect to lichen photobionts currently remains unresolved.

Chroococcidiopsis 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 to produce four or more autospore-like products known as baeocytes, initially contained within the sheath-like, fibrous outer wall layer of the mother cell (Waterbury & Stanier 1978). The baeocytes of *Myxosarcina*, unlike those of *Chroococcidiopsis*, have a brief stage of gliding motility; the genera are said to be otherwise indistinguishable morphologically. The baeocyte-forming cyanobacteria were formerly grouped together in the order *Pleurocapsales* (Waterbury & Stanier 1978), but SSU sequence analysis has shown this trait to be a convergence shared by a number of lineages of quite different origin (Fewer *et al.* 2002). In that study, several photobionts isolated from *Lichinaceae* appear within the same clade as *Chroococcidiopsis thermalis*, sister to the heterocyte-forming *Stigonematales* and *Nostocales*, and distant from *Myxosarcina* as well as other morphologically similar taxa formerly attributed to *Chroococcidiopsis* (Fewer *et al.* 2002). Sequences obtained from photobionts of several *Peltula* species collected in Vietnam also suggested affinities within a broad 'Chroococcidiopsidales' clade (Võ 2016). Other algal partners of *Lichinaceae* have been attributed to *Chroococcidiopsis* based on morphology and the production of baeocytes observed in cultured isolates (Büdel & Henssen 1983). Tschermak-Woess (1988*a*) suggested that some taxa identified as *Chroococcidiopsis* might actually belong to *Gloeocapsa* and require study in culture. Most photobiont isolates attributed to *Chroococcidiopsis* and *Myxosarcina* await more detailed molecular scrutiny.

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 (1988*a*), 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 *Rhizonema*, 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 1988*a*). 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 baeocytes 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 *Collemopsidium* (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 *Collemopsidium* [=*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 *Stigonema*. 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 *Hapalosiphonaceae* (Komárek *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). Phenotypically defined at present, taxa attributed to *Nostoc* fall within several distinct clades of the *Nostocales*, making the genus polyphyletic (Rajaniemi *et al.* 2005; Gagunashvili & 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 microplasmodesmatal connections with neighbouring vegetative cells (Giddings & Staehelin 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).

Nostoc, like many filamentous cyanobacteria, has a motile phase. Short filament segments known as hormogonia are produced by multiple divisions of the vegetative cells between two heterocytes, then break free (Boissière *et al.* 1987; Paulsrud 2001). The segments disperse or migrate directionally by a gliding motion that involves secretion of polysaccharide, against which proteinaceous pili appear to push or pull the trichome (Khayatan *et al.* 2015). Under favourable conditions, the hormogonia lose motility and differentiate heterocytes as they transition to vegetative filaments (Paulsrud 2001). It is conceivable that motile hormogonia might facilitate symbiont encounters in the formation of cyanolichens, as also suspected of flagellate stages in eukaryotic photobionts, but direct evidence is lacking. In the establishment of plant-*Nostoc* symbioses, the role of hormogonia as infective agents is well known (Adams *et al.* 2012), and genes related to hormogonial function have been identified in lichen-symbiotic strains (Gagunashvili & Andrésson 2018). *Nostoc* may also disperse temporally by forming akinetes, a kind of resistant spore that develops from a vegetative cell and endures adverse conditions.

Nostoc is photobiont in the majority of cyanophilic lichens. In the *Peltigerales*, *Nostoc* serves as principal thallus photobiont, or as secondary photobiont specialized for nitrogen fixation within discrete structures known as cephalodia; these are formed upon or within a thallus that has a green alga as principal photobiont. In a number of cases, *Nostoc* may serve as both principal and secondary photobiont of a single mycobiont species or individual; this results in cyanomorph and cephalodiate chloromorph thalli that may be either separate or conjoined (James & Henssen 1976; Brodo & Richardson 1978; Tønsberg & Holtan-Hartwig 1983; Armaleo & Clerc 1991; Stenroos *et al.* 2003; Moncada *et al.* 2013; Simon *et al.* 2018). The same strain of *Nostoc* may occur in both morphs (Paulsrud *et al.* 1998, 2001). In many such instances, chloromorph and cyanomorph are both foliose, but in some species

of *Lobaria* and *Sticta*, the *Nostoc*-containing cyanomorph is a branching, fruticose growth that bears no resemblance to the foliose chloromorph (Jordan 1972; James & Henssen 1976; Tønsberg & Goward 2001; Magain *et al.* 2012); when growing separately, the two morphs were long presumed to represent very different taxa. Thallus morphology would appear to be influenced by the distinct photobionts in such cases. In certain species of *Pseudocyphellaria* on the other hand, the independently growing 'cyanomorphs' include numerous clusters of the green algal symbiont (probably *Symbiochloris*) spread among the *Nostoc* within the algal layer (Henskens *et al.* 2012), with no visible alterations to thallus morphology. Even when *Nostoc* serves as a secondary (cephalodial) photobiont in a mature lichen, it may be acquired at a very early stage of lichen formation through contact and capture by the developing mycobiont prothallus (Ott 1988; de los Ríos *et al.* 2011). Once organized, thallus lobes containing green algae may secondarily encounter and incorporate compatible *Nostoc* on the lower surface (Jordan 1970; Jordan & Rickson 1971), or either the upper or lower surface (Cornejo & Scheidegger 2013). Mycobiont selectivity for particular strains of *Nostoc* can be very high (Paulsrud *et al.* 2001). The *Nostoc*-containing cyanomorph may in turn capture compatible green algal symbionts that contact the tomentum hyphae of the lower cortex, from which chloromorph lobes arise (Sanders 2001).

In most lichens where it is primary photobiont, *Nostoc* is confined to a discrete algal layer; its filaments are often broken up or contorted into cell clusters with little secretion of mucilaginous sheath material (Fig. 1J). When isolated into culture, it reverts to the morphology and growth pattern typical of its free-living state (Kardish *et al.* 1989). However, in many of the so-called gelatinous lichens, the form of the *Nostoc* is not fundamentally altered in lichenization; it maintains the necklace-like filaments and extensive surrounding gelatinous sheath, through which the mycobiont hyphae penetrate (Fig. 1I). In such cases, the photobiont constitutes the main structural component of the lichen, which may maintain an appearance and texture rather similar to that of free-living *Nostoc* macrocolonies. A recent study suggests that these differences in phenotypic expression, leading to stratified versus gelatinous lichens, may be associated with different genetic strains of *Nostoc* (Magain & Sérusiaux 2014). This would appear to be another example where major differences in thallus structure may be correlated with photobiont identity.

Cyanophilic mycobionts can be highly selective of their *Nostoc* partner strains, often overriding geographical factors (Paulsrud *et al.* 1998, 2000; Stenroos *et al.* 2006; Myllys *et al.* 2007), although a considerably lower selectivity was observed in lichen communities in maritime Antarctica (Wirtz *et al.* 2003). Within a single clade of *Peltigera*, both highly selective and less discriminating generalist species can be recognized (Magain *et al.* 2017, 2018). A study of temperate and boreal communities reported genetically distinct terricolous and epiphytic pools of *Nostoc*, from which *Peltigera* and *Nephroma* spp. colonizing those respective substrata select their photobionts (Rikkinen *et al.* 2002). Using a larger data set, Stenroos *et al.* (2006) found *Nostoc* photobiont strains to be correlated with mycobiont identity rather than ecological guild. However, fungal preference for the *Nostoc* photobiont strains of other community members over those sampled from the substratum has been reported in other lichen communities (Cardós *et al.* 2019). In other studies, involving

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 arbuscular mycorrhizal fungi make the *Geosiphon-Nostoc* symbiosis quite distinct from fungal-algal symbioses treated under the lichen concept (Kluge *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 nitrogen, usually in the form of ammonium, is supplied to the host from the numerous heterocytes that differentiate in the symbiotic state (Meeks 1998). In hornworts and the liverwort *Blasia*, hormogonia enter and inhabit specialized, 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*; Svenning *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 Võ (2016) observed paired false branching in photobionts of Vietnamese *Cyphellostereum* and *Dictyonema*, she concluded

that the algae were *Scytonema* rather than *Rhizonema*, apparently without corroborating molecular data. However, recent observations of *Rhizonema*, isolated into culture from *Dictyonema* and identified with genetic sequence comparisons, show branching that appears distinctly false (Fig. 1D). Interestingly, a 19th century illustration of a *Dictyonema sericeum* 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* (*Peltigerales*), and the basidiomycetes *Acantholichen, Dictyonema, 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; Tschermak-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 (Bhâradwâja 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 (Võ 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 radically 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 *Rhizonema*. 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 *Rhizonema*). 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 multiseriate 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 'primitively lichenized' *Thermutopsis jamesii* based on morphology in collected material (Henssen 1990). Molecular sequences obtained from cephalodia of *Placopsis* placed the cyanobionts in or near *Tolypothrix* (Raggio *et al.* 2012).

Green algae (Viridiplantae – Archaeplastida)

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 *Scoliciosporum* (Beck 2002) and *Fuscidea* species (Zahradníková *et al.* 2017). Cells are spherical with alternating perpendicular planes of division, producing cuboidal packets of transiently adherent daughter cells. Autospores and biflagellate zoospores are also formed (Ettl & Gärtner 2014). Autospores may be of unequal size within a sporangium (Gärtner & Ingolić 1989), as also occurs in Watanabalean 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 Ahmadjian'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*, *Stereocaulaceae*, 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. Puncochárová — 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 *Verrucariaceae* (Nyati *et al.* 2007; Thüs *et al.* 2011). Unlike *Chlorella*, *Auxenochlorella* lacks a pyrenoid. The genus also includes 'zoochlorellae' symbionts of the cnidarian *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 *Sulzbacheromyces* in the *Lepidostromatales* (Hodkinson *et al.* 2014; Masumoto 2020).

Cephaleuros Kunze ex E. M. Fries — These foliicolous relatives of *Trentepohlia* form macroscopic, multicellular thalli visible as

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.* 2006; 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 into a short-stalked, dwarf sporophyte bearing a putative meiosporangium. Flagellate meiospores presumably develop into new gametophytic thalli. The *Cephaleuros* gametophyte is the phase known to serve as phycobiont for the fungus *Strigula*. Whether or not the sporophytes can also be lichenized is unknown. Perhaps they are too highly reduced or short-lived, but the question does not seem to have been explored. On gametophyte thalli, two distinct structures produce flagellate zoospores or gametes (often called zoïds, or swarmers, when their function is uncertain or polyvalent). Zoosporangia are elevated in groups upon vertical stalks; they produce quadriflagellate zoospores that have been observed to round off, germinate and reproduce the gametophyte thallus asexually (Ward 1884; Thompson & Wujek 1997). The mature sporangia detach readily as units of dispersal, for which both wind and insects act as vectors. On the horizontal filament system, single, usually terminal cells may enlarge to become what are referred to as gametangia; these produce biflagellate cells that may fuse sexually (Thompson & Wujek 1997). However, other authors have been unable to observe any instances of sexual fusions in the taxa they studied, instead reporting that the biflagellate zoïds germinate directly as zoospores to form new gametophyte thalli (Suto & Ohtani 2013).

Ward (1884) described in detail the course of lichenization of *Cephaleuros* by *Strigula*. Young germlings of *Cephaleuros* are often quickly overrun by the mycelium of *Strigula*, suppressing algal reproduction, while individuals contacted at more 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 & Gärtner 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 (1988*a*) review of phycobionts as 'facultatively lichenized'. However, Skuja (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 hyphae 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 1988*b*) are among those taxa moved to other genera, especially *Chloroidium*; others await re-examination. At present, only a couple of lichen-forming fungal species have photobionts of corroborated placement within *Chlorella* (*Porpidia crustulata*; Li *et al.* 2013) or *Chlorellales*. The genus has also been long identified with endosymbiotic algal symbionts of diverse protists and invertebrates. Molecular sequences confirm that true *Chlorella* occur 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 versatile* is a true *Chlorella* (Forsberg & Lindblad 1996). However, the phylogenetic affinities of other 'zoochlorellae' symbionts appear to fall elsewhere in the

Trebouxiophyceae (Lewis & Muller-Parker 2004; Kovačević *et al.* 2010; Pröschold *et al.* 2011), while many have yet to be explored with molecular sequence comparisons.

Chloroidium Nadson — Resurrected to accommodate segregates from *Chlorella* s. lat. (Darienko *et al.* 2010), *Chloroidium* 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, *Chloroidium* includes photobiont partners of a growing number of lichen-forming fungi, including some species of *Gomphillaceae*, *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.

Coccobotrys Chodat (now *Uvulifera* Molinari-Novoa) — This green alga forms irregular cuboidal cell packages or branched multiseriate filaments in culture (Neustupa 2015). The genus *Coccobotrys* 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. *Coccobotrys verrucariae* was also cited among algae isolated from soil crusts (Flechtner *et al.* 2009), and a photobiont identified with microscopy as 'probably *Coccobotrys*' (Canals *et al.* 1997) was isolated from *Botrylepraria lesdainii*, another member of the *Verrucariales* (Kukwa & Pérez-Ortega 2010). A second species of *Coccobotrys* was described by Warén (1920) as the photobiont of *Lecidea fuliginosa*, but Tschermak-Woess (1988a) expressed doubt that the alga he described belongs in *Coccobotrys*. The photobiont status of species in this genus should be corroborated. Genetic sequence analyses place *Coccobotrys* in the *Trebouxiophyceae* (e.g. Thüs *et al.* 2011; Mikhailyuk *et al.* 2020), but its affinities among the defined clades within this class remain uncertain. Molinari-Novoa (2016) recently found *Coccobotrys* 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.* 2015) 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*, *Peltigera*, *Solorina*, the stalked-apotheciate genera *Baeomyces*, *Dibaeis* and *Phyllobaeis*, and the basidiomycete *Lichenomphalia* (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 parasitoid 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).

Deuterostichococcus Pröschold & Darienko — A recent segregate of *Stichococcus* s. lat. (Pröschold & Darienko 2020), this trebouxiophycean genus currently includes, in addition to free-living isolates, 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).

Dictyochloropsis Geitler — See *Symbiochloris*.

Dilabifilum Tschermak-Woess — Polymorphic, unicellular to sarcinoid 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

phylogenies. A number of photobionts previously contained therein are now distributed in *Halofilum*, *Lithotrichon*, *Paulbroadya* and *Pseudendoclonium*, while others await reassessment.

Diplosphaera Bialosuknia — This prasiolalean genus 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 & Gärtner 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 *Staurothele*, *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 aposymbiotically; 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 Gomphillaceae and Pilocarpaceae (see *Heveochlorella*). Dispersal of liberated photobionts can thereby provide a direct connection between lichenized and free-living populations of the alga.

Elliptochloris Tschermak-Woess — Like its sister genus *Coccomyxa*, *Elliptochloris* has subspherical to ellipsoidal unicells with a parietal chloroplast, bearing two opposed indentations in the type species *E. bilobata* (Tschermak-Woess 1980*b*). 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 1980*b*; 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* (Coppins 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 *Protothelenella* 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 (Gustavs 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 *Bryoclavula* and *Multiclavula* (see Table 1). They also occur as endosymbionts of the marine anemone *Anthopleura* (Letsch et al. 2009).

Gloeocystis 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 *Gloeocystis* as photobiont of *Cryptodiscus* [*Bryophagus*] *gloeocapsa* and *Epigloea bactrospora* were cited by Ahmadjian (1967) and Tschermak-Woess (1988*a*). There is doubt as to whether *Epigloea* is lichenized (Kirk et al. 2001; not included in Lücking et al. (2017*a*)), although distinctly symbiotic contacts with living, unicellular green algae were illustrated by Jaag & Thomas (1934) and Döbbler (1984).

According to Neustupa (2015), the algal genus *Gloeocystis* 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 *Dilabifilum* (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 striatula* (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 *Jaagichlorella*. These algae belong to the trebouxiophyceaen 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. 2014*b*). Soon thereafter, the 'trebouxioid' photobionts associated with foliicolous

Gomphillaceae 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 foliicolous 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 (Metz *et al.* 2019) were also attributed to *Heveochlorella*.

In many foliicolous 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 campylidia 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 sarcinoid 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 Voytsekhovich *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. Borzì — This photobiont grows as unicells 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 trebouxiophycean 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 terrestre*' (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 terrestris, 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 rheitrophila* (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 autospores (Ettl & Gärtner 2014). Gene-based phylogenies consistently place *Myrmecia* in the *Trebouxiales*, sister to *Trebouxia* (Muggia *et al.* 2020) or to the *Asterochloris* + *Vulcanochloris* clade (Vančurová *et al.* 2015). *Myrmecia* occurs free-living as well as in lichen symbiosis. An aerophilic alga, originally described as *Friedmannia* 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 autospores. 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 normandinae* as the photobiont partner of lichen-forming *Normandina pulchella*; 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 *Normandina* thalli they examined and, more recently, Pröschold & Darienko (2020) reduced *Nannochloris normandinae* 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 trebouxiophycean genus produce mucilaginous colonies of spherical to ellipsoidal or crescent-shaped cells that reproduce by autospores (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,

genetically distinct but morphologically plastic species (Eliáš *et al.* 2013). An alga identified as *Neocystis* sp. was cited as 'additional photobiont' of *Micarea misella*, in thalli having *Elliptochloris bilobata* as principal photobiont (Voytsekhovich *et al.* 2011).

Paulbroadya Darienko & Pröschold — This recently recognized clade in the *Ulvales* is distinguished by SSU-ITS sequences from other taxa previously treated under *Dilabifilum* (Darienko & Pröschold 2017). The species *Paulbroadya petersii* occurs as photobiont of the marine intertidal lichen *Wahlenbergiella mucosa* (Darienko & Pröschold 2017).

Phycopeltis Millardet — 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 *Cephaleuros*, *Phycopeltis* thalli are supracuticular, non-pathogenic, and at least some species readily colonize other favourably displayed plant substrata besides leaves. Sporangia are usually borne erect on a very short stalk, and release quadriflagellate 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 *Cephaleuros* 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 intertwined phylogenetically (Zhu *et al.* 2015, 2017; Grube *et al.* 2017*a*). *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 foliicolous 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 phyllosphere, species of *Phycopeltis* are important photobionts in foliicolous lichen communities, where they partner with diverse leaf-dwelling mycobionts including species of *Arthonia*, *Chroodiscus*, *Mazosia*, *Opegrapha*, *Porina*, *Trichothelium*, and supracuticular taxa of *Strigulaceae*, among others (Santesson 1952; Lücking 2008). Multiple *Phycopeltis* thalli may occur edge-to-edge within a single foliicolous 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 (Kovačik & 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 *Ascophyllum* (Xu *et al.* 2008), or *Turgidosculum* upon *Blidingia* (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.

Pseudendoclonium Wille — These ulvalean 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 *Dilabifilum*, recognizing the photobiont of *Arthopyrenia kelpii* as *Pseudendoclonium arthopyreniae*, and the photobiont of *Hydropunctaria maura* as *P. commune*, which is also widespread as a free-living alga on intertidal rocks. *Pseudendoclonium arthopyreniae* has a pyrenoid surrounded by thick plates of starch and traversed by several narrow, thylakoid-derived membranes lacking pyrenoglobuli (Namba & Nakayama 2021).

Pseudochlorella 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 *Pseudochlorella* the photobionts of certain *Micarea*, *Placynthiella* and *Stereocaulon* species (see Tschermak-Woess 1988*a*; 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* (Hodač *et al.* 2016) in the *Verrucariaceae*.

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 prasiolalean clades. Some seven to nine clades have now been recognized within *Stichococcus* s. lat. (Hodač *et al.* 2016; Pröschold & Darienko 2020). All *Stichococcus*-like photobionts examined in a study of the *Verrucariaceae* by Thüs *et al.* (2011), were shown to belong in *Diplosphaera*. Others now appear to fall within *Pseudostichococcus*, *Deuterostichococcus* or *Tritostichococcus* (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.* (2014*b*). *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*, *Chaenotheca, 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 lecanoromycetid 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 (Peveling 1968, 1969; Fisher & Lang 1971; Friedl 1989). CO_2-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 (Škaloud & 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; Uher 2008; Neustupa & Štifterová 2013), with the notable exception of Degelius (1964). Clearly, the germinating spores of trebouxiophilic mycobionts 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 scepticism 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 appressorial hyphae (Honegger 1990). In aposymbiotic culture, by contrast, the production and release of *Trebouxia* zoids 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 *Arthoniomycetes*, *Coniocybomycetes*, *Dothidiomycetes*, *Eurotiomycetes* (*Pyrenulales*) 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: phragmoplastic 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.*

2014*a*, *b*; Kosecka *et al.* 2020). Due to its visible and widespread presence in the free-living state, *Trentepohlia* is an excellent subject for studying the relationship between lichenized and aposymbiotic populations in nature (Fig. 1A–C). So far, however, the genus has been the focus of relatively few modern phylogenetic studies, despite its visibility and primary importance in lichen symbioses.

The pigments characteristic of the *Trentepohliaceae*, called 'haematochrome' in the older literature, are carotenoids that occur abundantly as lipidic globules in the cytoplasm. Some authors have attributed the colour to astaxanthin (Thompson & Wujek 1997; Grube *et al.* 2017*a*), a deep red carotenoid known from other chlorophytes such as *Haematococcus* and the snow alga *Chlamydomonas nivalis*. However, analyses of *Trentepohlia* haematochrome show principally beta-carotenes (Czeczuga & Maximov 1996; Mukherjee *et al.* 2010; Kharkongor & Ramanujam 2015; Chen *et al.* 2016). Located outside the plastids, these secondary carotenoids do not participate in photosynthetic light-harvesting but are hypothesized to filter excess light and suppress any damaging reactive oxygen species thereby generated (Solovchenko 2013). This may contribute to the visible success of *Trentepohlia* in colonizing exposed substrata in diverse environments.

The sporangia of *Trentepohlia* are themselves units of dispersal, easily detached when mature and vectored by wind, rain or insects. They then initiate a second round of shorter-distance dispersal by releasing quadriflagellate zoospores (Thompson & Wujek 1997). *Trentepohlia* also produces putative gametangia that are morphologically distinct from sporangia. However, the biflagellate zoïds released have most often been observed germinating as spores rather than fusing as gametes (Rindi & Guiry 2002).

Cellular contacts between mycobionts and their trentepohliaceous photobionts often appear to be superficial. However, most of these lichens, when carefully examined microscopically, reveal haustorial penetration, often deeply into the algal cells (Tschermak 1941*a*; Withrow & Ahmadjian 1983; Matthews *et al.* 1989; but see Meier & Chapman 1983).

Trentepohlia photobionts have been occasionally reported to grow out from the algal layer and emerge as free filaments projecting from the lichen thallus or thalline apothecial margin (Zahlbruckner 1907: p. 126; McGee 2002). In one case, such a filament was seen bearing a sporangium (Tschermak 1941*a*: p. 289). However, some authors have expressed scepticism about this interpretation, suggesting that epiphytic *Trentepohlia* might instead develop upon, and then grow into, an already formed thallus (Henssen & Jahns 1974: p. 196). More detailed observations are clearly required, but either explanation could represent another potentially significant mechanism by which exchange may occur between lichenized and free-living populations.

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 1941*b*). *Trochiscia* currently appears to be placed among the *Chlorophyceae*, in or near *Sphaeropleales* (Fučíková *et al.* 2019). It was identified as photobiont of *Polyblastia amota* and *P. hyperborea* (Tschermak 1941*b*; 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* (Vančurová *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* (Vančurová *et al.* 2018). *Vulcanochloris* has also been recently reported as a minority photobiont in thalli of *Ramalina farinacea* (Moya *et al.* 2017).

Stramenopila (Heterokontae)

Heterococcus Chodat — The yellow-green (xanthophyte) algae lack fucoxanthin, the golden brownish plastidial 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 rheitrophila*, *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 *Xanthonema*; Silva 1979) was identified via light microscopy as photobiont of *Staurothele clopimoides* (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 unilocular and/or plurilocular sporangia (zoidangia) 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

thylakoids, as in *Trebouxia* and *Heveochlorella*); the position of the pyrenoid may be laminar, protruding to exserted, or enfolded by chloroplast lobes (Sanders *et al.* 2005). The alga was first brought to the attention of lichenologists by a footnote in a phycology dissertation (Wynne 1969) that reported it in symbiosis with a *Verrucaria* species on intertidal rocks in northern California. The lichen was not studied further until Moe (1997) re-collected it and formally described the fungal symbiont as *Verrucaria tavaresiae* (now *Wahlenbergiella tavaresiae*; Gueidan *et al.* 2011). When lichenized, the *Petroderma* 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 verrucariacean 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 places where emphasis might be useful. id = procedures used in the study to identify the photobiont. LM = light microscopy, TEM = transmission electron microscopy. See table 1 in Tschermak-Woess (1988*a*) for a comprehensive list of photobiont reports prior to 1988. Taxon names follow those used in the original articles.

Alga	Fungal symbionts	References & comments
Domain *Bacteria*, Phylum *Cyanobacteria*		
[***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 (1988*a*)
Chroococcidiopsis sp.	*Anema nummularium, Peccania cerebriformis, Psorotichia 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. placodizans*	Võ (2016)
Gloeocapsa sp.	Species of *Anema, Edwardiella, Gonohymenia, Heppia, Jenmania, Peccania, Phylliscum, Psorotichia, Pyrenopsis, Synalissa* and *Thyrea*; cephalodia of *Amygdalaria* and *Stereocaulon* spp.	Numerous LM reports summarized by Tschermak-Woess (1988*a*). Friedl & Büdel (2008); Brodo *et al.* (2001). id: LM.
Hyella 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 multipartitum*	Oksanen *et al.* (2002)
Nostoc sp.	*Nephroma*, numerous spp.	Lohtander *et al.* (2003)
Nostoc sp.	*Leptogium puberulum, Massalongia carnosa, Placopsis contortuplicata, P. parellina, 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. degenii, P. didactyla, P. horizontalis, P. lepidophora, P. membranacea, P. neopolydactyla, P. rufescens, Sticta 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. athroophila, P. conoplea, P. durietzii, P. elixii, P. euphylla, P. farinosa, P. fulvescens, P. isabellina, P. lobulifera, P. mosenii, P. obscura, P. pallida, P. patagonica, P. rubiginella, P. rubiginosa, P. sphinctrina, P. tavaresii*	Elvebakk *et al.* (2008)
Nostoc sp.	*Degelia atlantica, D. plumbea*	Otálora *et al.* (2013)

(*Continued*)

Table 1. (*Continued*)

Alga	Fungal symbionts	References & comments
Nostoc sp.	*Polychidium muscicola*	Jayalal *et al.* ([2012](#))
Nostoc sp.	Species of *Fuscopannaria*, *Kroswia*, *Pannaria*, *Parmeliella* and *Physma*	Magain & Sérusiaux ([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 andinum	*Cora arachnodavidea, 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. ciferrii, C. crispoleslia, C. galapagoensis, C. hymenocarpa, C. melvinii, C. paraciferrii, C. reticulifera, C. smaragdina, C. soredavidia, C. squamiformis, C. strigosa, C. suturifera, C. terrestris, C. viliewoa, Cora* sp. *Cyphellostereum* sp., *Dictyonema aeruginosum, D. barbatum, D. darwinianum, D. hernandezii, D. interruptum* [= *D. coppinsii*], *D. phyllogenum, D. sericeum, D. schenkianum, Dictyonema* sp.; cephalodia of *Stereocaulon ramulosum*	Dal Forno *et al.* ([2020](#))
R. neotropicum	*Acantholichen pannarioides, Coccocarpia palmicola, Cora gigantea, C. leslactuca, C. rubrosanguinea, Corella* sp., *Dictyonema* sp.	Dal Forno *et al.* ([2020](#))
Rhizonema sp.	*Acantholichen pannarioides, Coccocarpia filiformis, C. palmicola, C. stellata, Dictyonema aeruginosulum, 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 phycophila*	Jülich ([1972](#)). Reported as *Scytonema. Athelia poeltii* also said to associate with filamentous cyanobacteria; Jülich ([1978](#)).
Rhizonema sp.	*Coccocarpia palmicola, Erioderma pedicellatum, E. sorediatum, Leptogidium* sp., *Lichinodium* sp., *Moelleropsis nebulosa, Parmeliella parvula*	Cornejo & Scheidegger ([2016](#)); Cornejo *et al.* ([2016](#)). Boreal env. (Newfoundland). Also symbiotic among liverwort *Frullania asagrayana.*
Rhizonema sp.	*Lichinodium ahlneri, 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 Võ ([2016](#)) concerning *Heppia*.
Scytonema sp.	*Heppia lutosa*	Võ ([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.	*Thermutopsis* sp.	Henssen ([1990](#))
cf. *Tolypothrix*	Cephalodia of *Placopsis perrugosa* and *P. stenophylla*	Raggio *et al.* ([2012](#))
Domain *Eukarya*, Eukaryote supergroup *Archaeplastida*, Kingdom *Plantae*, Division *Chlorophyta* Class *Trebouxiophyceae*, Order *Chlorellales*		
Auxenochlorella	*Psoroglaena stigonemoides*	Thüs *et al.* ([2011](#))
Near *A. protothecoides*	*Psoroglaena stigonemoides*	Nyati *et al.* ([2007](#)). Strain P-1015.

(*Continued*)

Table 1. (*Continued*)

Alga	Fungal symbionts	References & comments
Near **Chlorella** *sorokiniana*	*Porpidia crustulata*	Li *et al.* ([2013](#))
Nannochloris *normandinae*	*Normandina pulchella*	Tschermak-Woess ([1988*a*](#)). 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. diffractellum, E. pallidulum, E. pusillum, Flakea papillata, Neocatapyrenium rhizinosum, Normandina acroglypta, N. pulchella, Placidiopsis cartilaginea, Placopyrenium bucekii, Polyblastia cupularis, P. viridescens, Staurothele areolata, S. clopima, S. clopimoides, S. drummondii, 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.	*Ramalina farinacea*	Moya *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 ([1988*a*](#)).
P. signiensis	*Trapelia coarctata*	Darienko *et al.* ([2016](#))
Pseudochlorella sp.	*Stereocaulon strictum*	Brunner & Honegger ([1985](#)). Pyrenoid ultrastructure suggests this strain might be *Chloroidium*, as indicated by DNA sequences from other *Stereocaulon* photobionts.
Pseudochlorella sp.	*Placynthiella dasaea*	Voytsekhovich *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 rhizinosum*	Hodač *et al.* ([2016](#)); Pröschold & Darienko ([2020](#)).
Tritostichococcus *coniocybes*	*Chaenotheca* sp.	Pröschold & Darienko ([2020](#))
Class *Trebouxiophyceae*, Order *Trebouxiales*		
Asterochloris *antarctica*	*Cladonia* sp.	Kim *et al.* ([2020](#))
Asterochloris clade I1	*Cladonia corymbescens, C. furcata, C. pyxidata, C. rangiferina*	Řidká *et al.* ([2014](#))
Asterochloris clade I2	*Cladonia furcata*	Řidká *et al.* ([2014](#))
Asterochloris clade II	*Cladonia subtenuis*	Yahr *et al.* ([2006](#))
Asterochloris clade 9	*Cladonia cariosa, C. coniocraea, C. delavayi, C. fruticulosa, C. praetermissa, C. scabriuscula, C. verticillata*	Řidká *et al.* ([2014](#))
Asterochloris clade 12	*Cladonia pyxidata*	Řidká *et al.* ([2014](#))
Asterochloris clade 16	*Cladonia fruticulosa*	Řidká *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*)

Table 1. (Continued)

Alga	Fungal symbionts	References & comments
Asterochloris excentrica	*Lepraria caesioalba, L. neglecta, L. rigidula*	Škaloud & Peksa (2010)
A. friedlii	*Lepraria caesioalba, L. lobificans*	Škaloud et al. (2015)
A. friedlii	*Lepraria achariana, L. finkii*	Kosecka et al. (2021)
A. friedlii	*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	*Diploschistes muscorum*	Škaloud & Peksa (2010)
A. glomerata	*Stereocaulon pileatum, S. saxatile, Stereocaulon* sp.	Peksa & Škaloud (2011)
A. glomerata	*Cladonia coniocraea, C. squamosa, Stereocaulon evolutoides, S. pileatum*	Řidká 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. submitis, C. subulata, C. uncialis*	Pino-Bodas & Stenroos (2020)
A. glomerata/irregularis clade	*Cladonia cariosa, C. cervicornis* ssp. *verticillata, C. phyllophora*	Rola et al. (2021)
A. irregularis	*Squamarina lentigera*	Beck et al. (2002)
A. irregularis	*Cladonia furcata, Lecidea fuscoatra, L. plana, Lepraria caesioalba, Porpidia crustulata, P. flavocaerulescens, P. macrocarpa, Porpidia* 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. apocalypticum, 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. ecmocyna, C. gracilis, C. granulans, C. kanewskii, C. labradorica, C. macrophylla, C. uliginosa, C. uncialis*	Pino-Bodas & Stenroos (2020)
A. italiana	*Cladonia capitellata, C. scabriuscula*	Škaloud et al. (2015)
A. italiana	*Cladonia coccifera, C. diversa*	Steinová et al. (2019)
A. italiana	*Stereocaulon condensatum*	Vančurová (2012)
A. italiana	*Cladonia bellidiflora, C. borbonica, C. brevis, C. callosa, C. capitellata, C. ciliata, C. foliacea, C. groenlandica, C. islandica, C. lepidophora, C. mawsonii, C. merochlorophaea, C. neozelandica, C. pleurota, C. portentosa, C. prolifica, C. pulvinata, C. rappi, C. rigida, C. subcervicornis, C. subsubulata, C. ustulata, C. weymouthii*	Pino-Bodas & Stenroos (2020)
A. italiana clade	*Diploschistes muscorum*	Rola et al. (2021)
A. leprarii	*Lepraria caesioalba, L. neglecta*	Škaloud et al. (2015)
A. lobophora	*Cladonia* cf. *bacillaris, Diploschistes 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)

Table 1. (*Continued*)

Alga	Fungal symbionts	References & comments
Asterochloris lobophora/ 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*a*); 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. vulcanii, 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. nigrocinta, 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*s 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*	Moya *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 acuata, C. aggregata, C. andesita, C. arbuscula* 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. vouauxii, Lepraria cryptovouauxii, L. hodkinsoniana, Stereocaulon myriocarpum, 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. nigrocincta, 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. evansii, C. fimbriata, C. perforata, C. rangiferina, Lepraria atromentosa, L. caesiella, L. caesioalba, L. incana, L. lobificans, L. nigrocincta, 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)

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Table 1. (*Continued*)

Alga	Fungal symbionts	References & comments
Asterochloris spp.	Species of *Lepraria* and *Stereocaulon*	Peksa & Škaloud (2011)
Asterochloris spp.	*Cladonia furcata*	Řidká *et al.* (2014)
Myrmecia *biatorellae*	*Catapyrenium rufescens, Dermatocarpon hepaticum, D. tuckermani, D. velebiticum, Lecidea berengeriana, Lobaria linita, Polysporina simplex, Psora decipiens, P. globifera, Psoroma hypnorum, Sarcogyne privigna, Verrucaria submersella*	Tschermak-Woess (1988*a*)
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. angustilobata	*Acarospora sinopica, Porpidia tuberculosa, Tremolecia atrata*	Beck (2002)
T. angustilobata	*Protoparmelia badia*	Singh *et al.* (2017)
T. angustilobata	*Pseudephebe* 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. siliquosa*	Tschaikner *et al.* (2007). id: LM, cultures.
T. arboricola	*Caloplaca fernandeziana, C. orthoclada*	Vargas Castillo & Beck (2012)
T. arboricola	*Xanthoria aureola, X. calcicola, X. capensis, X. ectaneoides, X. flammea, X. hirsuta, X. karrooensis, X. ligulata, X. parietina, X. polycarpa, X. turbinata*	Nyati *et al.* (2013, 2014)
T. arboricola	*Ochrolechia* sp., *Xanthoria calcicola, X. parietina*	Voytsekhovich & Beck (2016)
T. arboricola clade	*Acarospora conafii, Ramalina thrausta*	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, Rhizoplaca* 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, Circinaria contorta*	Voytsekhovich & Beck (2016)
T. asymmetrica	*Circinaria* spp.	Molins *et al.* (2018)
T. asymmetrica clade	*Placidium* sp.	Jung *et al.* (2019)
T. australis	*Lecanora farinacea, L. polytropa, Rhizocarpon geographicum*	Beck (2002)

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Table 1. (*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*	Tschaikner *et al.* (2007)
T. crenulata	*Xanthoria parietina*	Beck & Mayr (2012)
T. crenulata	*Caloplaca aurantia, C. xerica, Candelariella medians, Lecanora swartzii, Leproplaca xantholyta, Tephromela atra, Xanthoria calcicola*	Voytsekhovich & Beck (2016)
T. crespoana	*Parmotrema pseudotinctorum*	Škaloud *et al.* (2018)
T. cretacea	*Aspicilia desertorum, Rusavskia papillifera*	Voytsekhovich & Beck (2016)
T. cretacea	*Buellia zoharyi*	Molins *et al.* (2020)
T. decolorans	*Lecanora rupicola*	Blaha *et al.* (2006)
T. decolorans	*Xanthoria parietina*	Beck & Mayr (2012)
T. decolorans	*Xanthomendoza borealis, Xm. fulva, Xm. hasseana, Xanthoria candelaria, X. elegans, X. parietina, X. polycarpa*	Nyati *et al.* (2013, 2014)
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.* (2014*a*)
T. decolorans	*Anaptychia setifera, Candelariella medians*	Voytsekhovich & Beck (2016)
Trebouxia clade G (*galapagensis/usneae* group)	Species of *Parmotrema* and *Xanthoparmelia*	Leavitt *et al.* (2015)
T. gelatinosa	*Caloplaca* spp., *Hymenelia* sp., *Lecanora subimmergens, Lecidella enteroleucella, Ochrolechia parellula, Rinodina* sp., *Verrucaria* sp.	Watanabe *et al.* (1997). Maritime lichens. id: LM.
T. gelatinosa	*Physcia semipinnata*	Helms *et al.* (2001)
T. gelatinosa	*Flavoparmelia caperata, Punctelia subrudecta, Teloschistes* sp., *Xanthoria* sp.	Doering & Piercey-Normore (2009)
T. gelatinosa	*Josefpoeltia parva, Teloschistes chrysophthalmus, T. hosseusianus, Xanthomendoza novozelandica, Xm. weberi*	Nyati *et al.* (2013, 2014)
T. gelatinosa	*Rhizocarpon geographicum*	Voytsekhovich & Beck (2016)
T. gigantea	*Parmelia subramigera*	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 orbicularis, Physcia adscendens, P. tenella*	Beck *et al.* (1998); Helms *et al.* (2001).
T. impressa	*Dimelaena oreina, Physcia aipola, Physconia perisidiosa, Rinodina capensis, R. milvina*	Helms *et al.* (2001)

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Table 1. (*Continued*)

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, Parmelina carporrhizans, P. tiliacea, 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 fuscobrunnea, 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*	Osyczka *et al.* (2021)
Clade I (*impressa/gelatinosa* group)	Species of *Melanelixia, Melanohalea, Montanelia, Oropogon, Parmelia, Protoparmeliopsis, Rhizoplaca* and *Xanthoparmelia*	Leavitt *et al.* (2015)
T. impressa/T. potteri	*Ramalina 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 pulla, 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	*Chaenotheca subroscida*	Tibell & Beck (2002)
T. jamesii	*Umbilicaria antarctica, U. decussata, U. kappenii, U. umbilicarioides*	Romeike *et al.* (2002)
T. jamesii	*Evernia mesomorpha, Melanelia exasperatula*	Piercey-Normore (2006, 2009). Multiple clades within.
T. jamesii	*Evernia divaricata, E. prunastri, Ramalina fraxinea, R. siliquosa*	Tschaikner *et al.* (2007)
T. jamesii	*Ramalina farinacea*	Casano *et al.* (2011); Moya *et al.* (2017).
T. jamesii	*Ramalina fraxinea*	Catalá *et al.* (2016)
T. jamesii	*Carbonea vorticosa, Lecanora fuscobrunnea, L. physciella, Lecidea auriculata, L. cancriformis, L. lapicida, L. obluridata, 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.

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Table 1. (*Continued*)

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 psarophana, 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. lethariae*'	*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); Onuț-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. *angustilobata*	*Acarospora sinopica, Lecidea lapicida*	Beck (1999)
T. jamesii ssp. *jamesii*	*Acarospora rugulosa, Bellemerea diamartha, Lecanora polytropa, L. subaurea, Lecidea silacea, Rhizocarpon geographicum, Umbilicaria cylindrica*	Beck (1999)
T. potteri	*Pertusaria* 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 confluens, L. epanora, L. handelii, L. lapicida, L. paupercula, L. polytropa, L. silacea, L. subaurea, L. tesselata, Miriquidica atrofulva, M. garovaglii, Pleopsidium chlorophanum, Porpidia tuberculosa, Rhizocarpon geographicum, R. lecanorinum, R. norvegicum, R. polycarpum, R. ridescens, R. simillimum, Sporastatia testudinea, Tremolecia atrata, Umbilicaria crustulosa, U. cylindrica, U. torrefacta*	Beck (2002)
T. simplex	*Lecanora rupicola*	Blaha *et al.* (2006)
T. simplex	*Lecanora conizaeoides*	Hauck *et al.* (2007)
T. simplex	*Evernia mesomorpha, Everniastrum catawbiense, Imshaugia aleurites, Pseudevernia consocians*	Piercey-Normore (2009)
T. simplex	*Evernia 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. nadvornikiana, B. nitidula, B. simplicior, B. smithii, B. subcana, B. tenuis, Bryoria* sp.	Lindgren *et al.* (2014)
T. simplex	*Protoparmelia hypotremella, P. ochrococca, P. oleagina*	Singh *et al.* (2017)
T. simplex	*Thamnolia vermicularis*	Onuț-Brännström *et al.* (2017)
T. simplex/jamesii	*Lasallia pustulata, L. hispanica, Umbilicaria spodochroa*	Hestmark *et al.* (2016); Dal Grande *et al.* (2018).
Clade S (*simplex/lethariii/jamesii* group)	Species of *Cetraria, Letharia, Melanohalea, Motanelia, Rhizoplaca* and *Xanthoparmelia*	Leavitt *et al.* (2015)

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Table 1. (*Continued*)

Alga	Fungal symbionts	References & comments
Clade S (*Trebouxia simplex/letharii/jamesii* group)	*Pseudephebe minuscula, P. pubescens*	Garrido-Benavent *et al.* (2020)
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*	Xu *et al.* (2020)
T. simplex s. lat.	*Tephromela atra* s. str.	Muggia *et al.* (2008). *Tephromela* photobionts also found in two other *Trebouxia* clades.
T. simplex subclades 1 and 2	*Cetraria aculeata, C. islandica, Thamnolia subuliformis*	Onuț-Brännström *et al.* (2018)
Trebouxia solaris	*Aspicilia cinerea, Caloplaca aractina, Candelariella vittelina, Circinaria contorta, Ramalina capitata, Rhizocarpon geographicum*	Voytsekhovich & Beck (2016)
T. aff. *solaris*	*Chrysothrix candelaris*	Ertz *et al.* (2018)
T. aff. *solaris*	*Lecanographa amylacea* ('*Buellia violaceofusca*')	Ertz *et al.* (2018). Same mycobiont produces morphologically distinct, sexual thallus with *Trentepohlia* sp.!
T. suecica	*Acarospora sinopica, Candelariella vitellina, Immersaria athroocarpa, Lecanora polytropa, Miriquidica atrofulva, Protoparmelia atriseda, P. badia, Rhizocarpon geographicum, Tremolecia atrata, Umbilicaria torrefacta*	Beck (2002)
T. suecica	*Protoparmelia badia, P. memnonia*	Singh *et al.* (2017)
T. suecica	*Pseudephebe* sp.	Garrido-Benavent *et al.* (2020)
T. vagua	*Candelariella vitellina, Circinaria contorta, Diploschistes diacapsis, Porpidia crustulata*	Voytsekhovich & Beck (2016)
T. vagua	*Thamnolia vermicularis*	Onuț-Brännström *et al.* (2017)
Near *T. vagua*	*Caloplaca tubelliana, Dirina massiliensis [Arthoniomycetes!], Lecanora albescens*	Voytsekhovich & Beck (2016)
Trebouxia 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. sprengelii*	Cordeiro *et al.* (2005)
Trebouxia A 02	*Austrolechia* sp., *Buellia frigida, Carbonea vorticosa, Huea* sp., *Lecidea cancriformis, L. polypycnidophora, Lecidella greenii, Rhizoplaca macleanii*	Wagner *et al.* (2020). Antarctic Dry Valleys.
Trebouxia sp. clade 1	*Fulgensia bracteata, F. fulgens, Toninia sedifolia*	Schaper & Ott (2003). Götland, Sweden.
Trebouxia sp. 'D11'	*Buellia frigida,* endolithic *Lecidea* sp., *Umbilicaria aprina*	de los Ríos *et al.* (2005). Continental Antarctic.
Trebouxia TR9	*Ramalina farinacea*	Casano *et al.* (2011); Moya *et al.* (2017).
Trebouxia sp. 'URa1'	*Carbonea vorticosa, Lecidea cancriformis*	Ruprecht *et al.* (2012)
Trebouxia sp. 'URa2'	*Carbonea vorticosa, Lecidea andersonii, L. atrobrunnea, L. cancriformis, L. fuscoatra, L. lapicida, Lecidea* sp., *Lecidella greenii, L. siplei, Rhizoplaca macleanii*	Ruprecht *et al.* (2012)
Trebouxia sp. 'URa3'	*Carbonea vorticosa, Lecanora physciella, Lecidea andersonii, L. cancriformis, L. lapicida, L. polypycnidophora, Lecidella greenii, L. patavina, L. siplei, Rhizoplaca macleanii*	Ruprecht *et al.* (2012)
Trebouxia sp. 'URa4'	*Lecidea andersonii, Lecidella stigmatea*	Ruprecht *et al.* (2012)
Trebouxia sp.	*Buellia papillata, Caloplaca johnstonii, C. lewis-smithii, Candelariella flava, Lecidella pataviana, Lepraria cacuminum, Pseudephebe minuscula, Psoroma* sp., *Tephromela atra, T. disciformis, Usnea lambii, Xanthoria elegans*	Engelen *et al.* (2016). Maritime Antarctic.
Trebouxia sp.	*Bagliettoa marmorea*	Thüs *et al.* (2011)
Trebouxia sp.	*Lasallia pustulata*	Sadowksa-Deś *et al.* (2014)
Trebouxia sp.	*Cetraria aculeata*	Lutsak *et al.* (2016)

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Table 1. (*Continued*)

Alga	Fungal symbionts	References & comments
Trebouxia sp.	*Austrolechia* spp., *Buellia frigida*, *Caloplaca* cf. *citrina*, *C. sublobata*, *Caloplaca* sp., *Carbonea vorticosa*, *Huea* sp., *Lecanora cancriformis*, *L. flotowiana*, *L. fuscobrunnea*, *Lecidella greenii*, *Rhizoplaca macleanii*, *Rhizoplaca* sp., *Umbilicaria aprina*	Pérez-Ortega *et al.* (2012). Crustose lichens of McMurdo Dry Valleys, probably representing at least two undescribed clades.
Trebouxia sp.	*Circinaria* spp.	Molins *et al.* (2018)
Trebouxia sp. B	*Boreoplaca ultrafrigida*, *Parmelia omphalodes*	Cao *et al.* (2015)
Trebouxia lineages lacking formal recognition	*Rhizoplaca* spp., *Protoparmeliopsis* spp.	Leavitt *et al.* (2016). Some 15 spp., collected worldwide.
Vulcanochloris sp.	*Stereocaulon vesuvianum*	Vančurová *et al.* (2015). From La Palma.
Vulcanochloris sp.	*Ramalina farinacea*	Moya *et al.* (2017). Minority photobiont.
Vulcanochloris sp.	*Stereocaulon pityrizans*	Kosecka *et al.* (2021)
Class *Trebouxiophyceae*, Order *Prasiolales*, *Elliptochloris* clade		
(**Coccomyxa** *greatwallensis*)	Isolated from *Psoroma hypnorum*	Cao *et al.* (2018). Symbiotic status not established.
C. icmadophilae	*Dibaeis baeomyces*	Beck (2002)
C. solorinae var. *croceae*, var. *saccatae* and *C. peltigerae*	*Peltigera variolosa*, *Solorina bispora*, *S. crocea*, *S. saccata*	Malavasi *et al.* (2016)
C. subellipsoidea	*Lichenomphalia ericetorum*, *L. grisella*, *L. hudsoniana*, *L. luteovitellina*, *L. velutina*, *Lichenomphalia* sp.	Zoller & Lutzoni (2003)
C. subellipsoidea	*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 aphthosa*, *P. britannica*, *P. leucophlebia*	Lohtander *et al.* (2003)
Coccomyxa sp.	*Peltigera variolosa*, *Solorina 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. leprosula*, *M. lignaria*, *M. micrococca*, *M. nitschkeana*, *M. peliocarpa*, *M. prasina* (*Pilocarpaceae*)	Yahr *et al.* (2015)
Coccomyxa sp.	*Icmadophila aversa*, *I. ericetorum*, *I. japonica*, *I. splachnirima*	Ludwig (2015)
Coccomyxa sp.	*Lichenomphalia oreades*	Lücking *et al.* (2017*b*)
Coccomyxa sp.	*Sticta laciniosa* from Cuba	Lindgren *et al.* (2020)
Related to *Coccomyxa* and *Pseudococcomyxa*	*Schizoxylon albescens* (*Stictidaceae*)	Muggia *et al.* (2011)
Elliptochloris *bilobata*	*Fuscidea cyathea* 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	*Baeomyces rufus*	Trembley *et al.* (2002*b*)
E. bilobata	*Verrucaria sublobulata*	Thüs *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 wahlenbergii*	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. reniformis	*Fuscidea cyathoides* var. *japonica*, *Leproloma* sp., *Ochrolechia parellula*	Watanabe *et al.* (1997); Darienko *et al.* (2016). Maritime. id: LM, culture.
E. reniformis	*Micarea peliocarpa*	Voytsekhovich *et al.* (2011). id: LM, culture.
E. subsphaerica	*Aspicilia* sp., *Fuscidea cyathoides* var. *japonica*	Watanabe *et al.* (1997). Maritime. id: LM, culture. (=*Chlorella reisiglii* Watanabe; Darienko *et al.* 2016)
E. subsphaerica	*Micarea melanobola*, *M. prasina*, *M. subnigrata*	Voytsekhovich *et al.* (2011). id: LM, culture.

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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.* (2014*b*)
Elliptochloris sp.	*Ramalina farinacea*	Moya *et al.* (2017). Minority photobiont.
Elliptochloris sp.	*Bryoclavula 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. angustoellipsoideum* 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 (1988*b*)
C. saccharophilum	*Lecidea inops, Psilolechia leprosa, Stereocaulon nanodes*	Beck (2002)
C. saccharophilum	*Psora decipiens*	Ruprecht *et al.* (2014). One record; all other thalli had *Asterochloris* or *Trebouxia*. Contrast Williams *et al.* (2017).
C. viscosum	*Bacidina [Woessia] fusarioides*	Tschermak-Woess (1988*b*); Darienko *et al.* (2018).
Chloroidium sp.	*Verrucaria praetermissa*	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*** Darienko & Pröschold 2019)	*Pseudocyphellaria* sp., *Sticta* sp.	Dal Grande *et al.* (2014*b*). Three specimens; authors confident alga is photobiont.
Heveochlorella sp.	*Aspidothelium cinerascens, A. fugiens, A. geminiparum* (*Thelenellaceae*); *Aderkomyces heterellus, Echinoplaca* spp., *Gyalectidium appendiculatum, G. floridense, G. imperfectum, G. paolae, G. ulloae, Gyalideopsis sessilis, Gyalideopsis* sp. (*Gomphillaceae*); *Byssoloma discordans, Calopadia 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. 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., *Fuscidea cyathoides* var. *japonica, Lecanora subimmergens, Pyrenopsis* sp., *Verrucaria* sp.	Watanabe *et al.* (1997). Maritime. id: LM.
A. lobatus	*Scoliciosporum umbrinum*	Beck (2002)
A. fuscideae	*Fuscidea arboricola, F. cyathoides, F. kochiana, F. pusilla*	Zahradníková *et al.* (2017)
Apatococcus sp.	*Fuscidea lightfootii*	Zahradníková *et al.* (2017)

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Table 1. (*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 diplotypus, S. fragilis, S. melanocarpus, S. melophorus*	Ihda *et al.* ([1997](#)). id: LM, culture.
D. symbiontica	Species of *Caloplaca* and *Leproloma*	Watanabe *et al.* ([1997](#)). Maritime. id: LM.
D. symbiontica	*Lecania naegelii*	Beck *et al.* ([1998](#))
Dictyochloropsis clade 2	*Brigantiaea ferruginea, B. leucoxantha* (*Brigantiaeaceae*); *Crocodia aurata, Lobaria oregana, L. patinifera, L. pulmonaria, Lobariella crenulata, L. pallidocrenulata, Lobariella* sp., *Pseudocyphellaria fimbriata, P. homeophylla, P. lindsayi, P. lividofusca, P. multifida, Sticta canariensis, S. latifrons, S. pulmonariodes, S. subcaperata, Sticta* spp. (*Lobariaceae*); *Megalospora sulphurata* (*Megalosporaceae*); *Chaenothecopsis consociata* (*Mycocaliciaceae*); *Phlyctis argena* (*Phlyctidaceae*); *Biatora* sp. (*Ramalinaceae*); *Chaenotheca brunneola* (*Coniocybomycetes*)	Dal Grande *et al.* ([2014*b*](#)). *Dictyochloropsis*. clade 2 = *Symbiochloris*; Škaloud *et al.* ([2016](#)).
***Leptosira* terrestris**	*Vezdaea aestivalis*	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 macaronesica, L. oregana, L. patinifera, L. pulmonaria; Lobariella crenulata, L. pallidocrenulata, Lobariella* sp., *Pseudocyphellaria* sp., *Ricasolia amplissima, Sticta canariensis, S. neopulmonaria* (*Lobariaceae*); *Megalospora sulphurata* (*Megalosporaceae*); *Chaenothecopsis consociata* (*Mycocaliciaceae*); *Phlyctis argena* (*Phlyctidaceae*); *Chaenotheca brunneola* (*Coniocybomycetes*).	Škaloud *et al.* ([2016](#)). All known photobionts previously included in *Dictyochloropsis* s. lat.
Symbiochloris sp.	*Sticta ainoae, S. cinereoglauca, S. granatensis, S. laciniata, 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 cleistoblephara, G. inabensis, G. intortura, G. mendax, G. undulata, Graphis aperiens, G. aphanes, G. batanensis, G. cognata, G. connectans, G. dupaxana, G. handelii, G. intricata, G. proserpens, G. rikuzensis, G. rufla, G. scripta, G. subdura, G. subtropica, G. subvirginea, G. tenella, Phaeographina chlorocarpoides, P. endofusca, Phaeographis asteriformis, 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., *Coenogonium linkii, Cryptothecia assimilis, Cryptothelium pulchrum, Cryptothelium* sp., *Dendrographa alectorioides, Dichosporidium boschianum, Graphis scripta, Graphis* sp., *Laurera megasperma, Myriotrema peninsulae, Porina distans, P. dolichophora, P. imitatrix, P. nucula, P. tetracerae, Porina* spp., *Racodium rupestre, Thalloloma hypoleptum, Thelotrema pachysporum, Trypethelium aenum, T. nitidiusculum, Trypethelium* spp.	Nelsen *et al.* ([2011](#)). 'Printzina' clades occur scattered throughout *Trentepohlia*. Mycobionts represent *Arthoniomycetes*, *Dothideomycetes* and *Lecanoromycetes*.

(*Continued*)

Table 1. (*Continued*)

Alga	Fungal symbionts	References & comments
Trentepohlia/'*Printzina*'	*Astrothelium variolosum, Graphis endoxantha, G. pulverulenta, G. scripta, Herpothallon rubrocinctum, Phaeographina* sp., *Phaeographis inusta, P. punctiformis, Pyrenula confinis, P. cruenta, P. pseudobufonia, P. sexlocularis, Strigula subtilissima, Trypethelium virens*	Green ([2012](#)). Photobiont of one *Strigula* sp. included.
Trentepohlia '*Printzina*'	*Acrocordia gemmata, Arthonia cinnabarina, A. radiata, Arthothelium ruanum, Cystocoleus ebeneus, Dimerella pineti, Graphis propinqua, G. scripta, G. submarginata, Gyalecta jenensis, Mycoporum sparsellum, Opegrapha atra, Pyrenula laevegata, Roccella decipiens, R. galapagoensis, R. linearis, R. lirellina, R. maderensis, R.* cf. *montagnei, R. phycopsis, R. tinctoria, R. tuberculata; Thelotrema lepadinum*	Hametner *et al.* ([2014*a*](#), [*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, Herpothallon* 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.
(*Dilabifilum*)	*Hydropunctaria adriatica*	Tschermak-Woess ([1976](#)). id: LM, culture.
(*Dilabifilum*)	*Hydropunctaria maura, H. rheitrophila, Wahlenbergiella striatula, Verrucaria aquatilis*	Thüs *et al.* ([2011](#))
(*Dilabifilum*)	*Verrucaria glaucina*	Voytsekhovich & Beck ([2016](#)). id: LM.
Halofilum *ramosum*	*Hydropunctaria amphibia, H. maura, Wahlenbergiella striatula*	Darienko & Pröschold ([2017](#)); Gasulla *et al.* ([2019](#)).
Lithotrichon *pulchrum*	*Hydropunctaria rheitrophila*	Darienko & Pröschold ([2017](#)). Submerged lichen.
Paulbroadya *petersii*	*Wahlenbergiella mucosa*	Darienko & Pröschold ([2017](#))
Pseudendoclonium *arthopyreniae*	Species of *Caloplaca, Rinodina, Thelidium* and *Verrucaria*	Watanabe *et al.* ([1997](#)). Maritime lichens. According to Thüs *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	*Hydropunctaria maura*	*Dilabifilum,* reclassified in Darienko & Pröschold ([2017](#)).
Class *Chlorophyceae*		
Bracteacoccus sp.	'*Multiclavula clara*' [=*Sulzbacheromyces sinensis*]	Takeshita *et al.* ([2010](#)). id: LM, culture.
Bracteacoccus sp.	*Sulzbacheromyces caatingae*	Hodkinson *et al.* ([2014](#)). *rbc*L sequences.
Bracteacoccus sp.	*Sulzbacheromyces sinensis*	Masumoto ([2020](#)). ITS and *rbc*L sequences.
Chlamydomonas sp.	*Pyronema*	Skuja ([1943](#)). Association doubtfully lichenic.
Chlorosarcinopsis *minor*	*Lecidea lapicida, L. plana*	Plessl ([1963](#)). Genus polyphyletic (Neustupa [2015](#)).
Gloeocystis sp.	*Bryophagus gloeocapsa, Epigloea bactrospora*	Tschermak-Woess ([1988*a*](#)). *Gloeocystis* s. lat. highly polyphyletic (Neustupa [2015](#)).
Radiococcus *signiensis*	*Placynthiella icmalea, P. uliginosa*	Voytsekhovich *et al.* ([2011](#)). Other photobionts found in lesser abundance within same algal layer. id: LM, culture.
Trochiscia sp.	*Polyblastia amota, P. hyperborea*	Tschermak ([1941*b*](#)); Ahmadjian ([1967](#)); but Ettl & Gärtner ([2014](#)) consider ID questionable.
Domain *Eukarya*, Eukaryote supergroup *Archaeplastida*, Kingdom *Plantae*, Division *Streptophyta* (*Charophytes*)		
Interfilum sp.	*Micarea prasina; Placynthiella icmalea, P. uliginosa*	Voytsekhovich *et al.* ([2011](#)). Reported as secondary (less abundant) photobiont within algal layer. id: LM, culture.

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Table 1. (*Continued*)

Alga	Fungal symbionts	References & comments
Domain *Eukarya*, Eukaryote supergroup: SAR (*Stramenopila Alveolata Rhizaria*), Kingdom *Stramenopila* (*Heterokontae*) Class *Phaeophyceae*		
***Petroderma* maculiforme**	*Wahlenbergiella tavaresiae*	Moe (1997); Peters & Moe (2001); Gueidan *et al.* (2011).
Class *Xanthophyceae*		
***Heterococcus* sp.**	*Verrucaria funckii, V. laevata*	Zeitler (1954); Tschermak-Woess (1988*a*).
Heterococcus sp.	*Hydropunctaria maura*	Parra & Redón (1977). id: LM.
Heterococcus sp.	*Hydropunctaria rheitrophila; Verrucaria funckii, V. hydrela*	Thüs *et al.* (2011)
***Xanthonema* sp.**	*Staurothele clopimoides*	Pereira Riquelme (1992). id: LM.

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