Mycorrhiza (2020) 30:23–49
https://doi.org/10.1007/s00572-020-00938-y

REVIEW

The distribution and evolution of fungal symbioses in ancient lineages of land plants

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Received: 15 November 2019 / Accepted: 5 February 2020 / Published online: 4 March 2020

Abstract
An accurate understanding of the diversity and distribution of fungal symbioses in land plants is essential for mycorrhizal research. Here we update the seminal work of Wang and Qiu (Mycorrhiza 16:299-363, 2006) with a long-overdue focus on early-diverging land plant lineages, which were considerably under-represented in their survey, by examining the published literature to compile data on the status of fungal symbioses in liverworts, hornworts and lycophytes. Our survey combines data from 84 publications, including recent, post-2006, reports of Mucoromycotina associations in these lineages, to produce a list of at least 591 species with known fungal symbiosis status, 180 of which were included in Wang and Qiu (Mycorrhiza 16:299-363, 2006). Using this up-to-date compilation, we estimate that fewer than 30% of liverwort species engage in symbiosis with fungi belonging to all three mycorrhizal phyla, Mucoromycota, Basidiomycota and Ascomycota, with the last being the most widespread (17%). Fungal symbioses in hornworts (78%) and lycophytes (up to 100%) appear to be more common but involve only members of the two Mucoromycota subphyla Mucoromycotina and Glomeromycotina, with Glomeromycotina prevailing in both plant groups. Our fungal symbiosis occurrence estimates are considerably more conservative than those published previously, but they too may represent overestimates due to currently unavoidable assumptions.

Keywords Arbuscular mycorrhizas · Ericoid mycorrhizas · Mucoromycota · Hornworts · Liverworts · Lycophytes

Introduction

Fungi colonize plants and interact with their living tissues in a variety of ways; these interactions can be detrimental (parasitic), neutral (symptomless) or beneficial (mutualistic) to the host plant. More than 85% of vascular plant species are considered to form mutually beneficial symbioses in their roots, termed mycorrhizas, with soil fungi (Brundrett and Tedersoo 2018). This percentage is only an estimate because investigating every plant species is neither practical nor currently possible given that not all species are known and ca. 2000 new vascular plants species are described each year (Pimm and Raven 2017). For the most part, fungal symbiosis occurrence rate estimates are lacking for early-diverging plant lineages as little effort has been directed towards compiling the data required to allow these estimations to be made. This also reflects an overall paucity of data available on these groups, including information on the type of interaction formed, i.e. whether the interaction is mycorrhizal or mycorrhizal-like in plants such as liverworts and hornworts that lack true roots. However, in the last decade, there has been an increased research focus on the diversity and distribution of fungal associations in liverworts, hornworts and lycophytes, largely driven by the discovery of Mucoromycotina fungi in association with these plants (Bidartondo et al. 2011; Desirò et al. 2013; Rimington et al. 2015) and the demonstration that at least some of these associations are mycorrhizal or mycorrhizal-like—i.e. those between lycophytes and Mucoromycotina (Hoysted et al. 2019); between liverworts and Glomeromycotina (Field

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00572-020-00938-y) contains supplementary material, which is available to authorized users.

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et al. 2012), Mucoromycotina (Field et al. 2015) and Glomeromycotina and Mucoromycotina together (Field et al. 2016b); and between liverworts and Ascomycota (Kowal et al. 2018). We address this lacuna by compiling published fungal symbiosis status for these early-diverging plant lineages with the caveat that some of the reported symbioses, e.g. those in hornworts, are considered such on the basis of morphology and/or involvement of fungi known to be mycorrhizal with other plant lineages but are yet to be confirmed experimentally. A comprehensive list of which plant species enter into fungal symbioses and with which fungi not only serves as a useful resource for future studies but also provides insight into the origins and distribution of these relationships and how they evolved across plant lineages (Wang and Qiu 2006). This is particularly pertinent today as recent studies are finally providing much improved resolution on the phylogenetic relationships among the earliest-diverging bryophytes (liverworts, mosses and hornworts) and vascular plants, which have been contested for decades (e.g. Puttick et al. 2018; de Sousa et al. 2019). Within bryophytes, mosses are the only group not known to harbour symbiotic fungi in their living cells (Pressel et al. 2010). On the other hand, liverworts engage in remarkably diverse symbioses with Mucoromycotina, Glomeromycotina, Ascomycota or Basidiomycota fungi (Pressel et al. 2010; Bidartondo et al. 2011). Hornworts appear intermediate between liverworts and mosses by forming associations with Mucoromycotina and Glomeromycotina but not with members of the Dikarya (Desirò et al. 2013). Both liverworts and hornworts can also be fungus-free (non-symbiotic). Liverworts have undergone a number of gains and losses of symbiosis during their evolution; the early-diverging groups Haplomitriopsida, Marchantiopsida and Pelliidae are symbiotic with Mucoromycotina and/or Glomeromycotina (Rimington et al. 2019) while more derived lineages associate with Basidiomycota (Metzgeriidae, Jungermanniidae) and Ascomycota (Jungermanniidae) (Pressel et al. 2010). Ascomycota and Basidiomycota are both members of the subkingdom Dikarya, the latest diverging fungal lineage (Hibbett et al. 2007). Molecular analysis has indicated that the Basidiomycota symbionts of liverworts are members of the genera *Serendipita* (*Sebacina*) and *Tulasnella* (Bidartondo and Duckett 2010), while Ascomycota symbioses are formed by *Hyaloscypha* (*Pezoloma* or *Rhizoscyphus*) *ericae* (Upson et al. 2007; Fehrer et al. 2019).

Hornworts and some liverworts also form endosymbioses with cyanobacteria (*Nostoc* sp.) (Adams and Duggan 2008). In hornworts, these associations are ubiquitous (Renzaglia et al. 2007), while in liverworts, they occur only in two Marchantiopsida species that lack fungal symbionts, *Blasia pusilla* and *Cavicularia densa* (Rikkinen and Virtanen 2008). Associations with cyanobacteria have also been reported in some moss species; however, these are exclusively epiphytic or endophytic in the dead hyaline cells in *Sphagnum* leaves (Kostka et al. 2016; Warshan et al. 2017).

Recently, it has been shown that lycophytes also form associations with Mucoromycotina and Glomeromycotina fungi (Rimington et al. 2015), with emerging evidence of carbon-for-nutrient exchanges between these early-diverging vascular plants and their Mucoromycotina symbionts (Hoysted et al. 2019). A better understanding of fungal associations in lycophytes is important when considering the early evolution of land plant-fungus symbiosis. Lycophytes, which comprise ca. 1360 species (Hassler and Schmitt 2018), are the earliest branching lineage of vascular plants (tracheophytes) and represent the transition from non-vascular to seed plants (Kenrick and Crane 1997). They are of particular importance because putative transitional 'pre-vascular' plants, including Rhynie Chert fossils such as *Aglaophyton*, are all extinct (Remy et al. 1994). As such, extant lycophytes are considered the best modern analogues for the first vascular plants (Kenrick and Crane 1997).

Lists detailing the fungal symbiosis status of plants have been published for many years; for example, the first list of fungal symbiosis in liverworts was produced 70 years ago (Stahl 1949). Such lists require regular updating as the number of studies increases and so does our knowledge of the diversity of symbioses within and across plant clades. Earlier compilations usually focused on a local scale and only on certain, almost invariably vascular, plant groups (Harley and Harley 1987). It was not until 2006 that a worldwide literature survey of fungal symbioses across all land plant groups was performed (Wang and Qiu 2006). This landmark publication by Wang and Qiu (2006) captured the status of over 3000 species (143 of which were bryophytes) and, unsurprisingly, has been highly influential ever since. In the 13 years since its publication, this paper has been one of the most cited on mycorrhizas (over 1500 citations as of January 2020) and has provided important insights on the evolution of mycorrhizas; for example, evidence that arbuscular mycorrhizas (AM) are found throughout the land plant phylogeny has been used as a key argument for Glomeromycotina symbiosis being an ancestral trait of land plants (Rimington et al. 2018). However, Wang and Qiu's survey (Wang and Qiu 2006) is now considerably outdated, especially with regard to early-diverging plant lineages. Since its publication there has been much interest in the diverse fungal symbioses of early-diverging plants (e.g. Ligrone et al. 2007; Duckett and Ligrone 2008; Bidartondo and Duckett 2010; Pressel et al. 2010; Desirò et al. 2013; Rimington et al. 2015; Rimington et al. 2018; Rimington et al. 2019) together with the discovery by Bidartondo et al. (2011) of symbioses involving Mucoromycotina fungi in liverworts, hornworts and a fern.

Fungal symbiosis occurrence rate estimates are commonly used to highlight the near-ubiquity of these relationships. For instance, few publications concerning AM fail to mention that at least 80% of plant species form these symbioses, most commonly citing the reference book 'Mycorrhizal Symbiosis' (Smith and Read 1997, 2008). These estimates are useful for emphasizing the importance of mycorrhizas to broad audiences and to highlight the diversity of these relationships between fungi and plants. These estimates are useful starting points for more refined estimates; recently, re-examination has shown that 80% may be an overestimation for AM symbioses, with the true value probably closer to 71% (Brundrett and Tedersoo 2018). Fungal symbiosis occurrence estimations for early-diverging plants have been more sporadic and highly variable including Glomeromycotina symbioses occurring in 60% and 100% of liverwort and hornwort species, respectively (Brundrett 2009) and 25% of bryophytes forming fungal associations, the majority of which involve Glomeromycotina (Brundrett and Tedersoo 2018). The last figure fails to take on board the fact that mosses, the most speciose group of bryophytes with ca. 12,000 species, lack fungal symbionts.

We present a new global compilation of the fungal symbiosis status of liverworts, hornworts and lycophytes. Our compilation more than triples the number of early-diverging plant species listed in Wang and Qiu (2006) and is the first to focus on early-diverging plant lineages on a global scale.

Methods

Literature survey

A survey of the published literature on fungal symbioses in liverworts, hornworts and lycophytes was performed. Re-examination of Wang and Qiu's survey (Wang and Qiu 2006) revealed that some key references for these plants were missing and that fungal symbiosis status was often reported only as 'fungal association' without specifying the fungus involved; thus, a full search was performed, including studies prior to 2006. In trying to capture all available references, several keywords were used as search terms in Google Scholar. In each search, one of the following plant terms was used: 'liverwort', 'hornwort', 'lycopod' and 'lycophyte'. Each plant term was combined with one of the following fungal terms: 'fungi', 'fungus', 'Glomeromycotina', 'Mucoromycotina', 'Glomeromycota', '*Glomus tenue*' and 'fine endophyte'. Additionally, for liverworts, which are known to form more diverse fungal symbioses than the other two lineages, the following terms were also used: 'Ascomycota', 'Basidiomycota', '*Rhizoscyphus*', '*Pezoloma*', '*Sebacina*' and '*Tulasnella*'. Using these criteria, a total of 34 searches were performed. The titles and abstracts of all references returned by the searches were scrutinized to identify reports of the fungal status of any liverwort, hornwort or lycophyte species. Where the search terms returned more than 500 hits (e.g. 'lycopod fungi' returned 14,600 hits), only the first 500 results were investigated. Fungal symbiosis status was recorded as Glomeromycotina, Mucoromycotina, Ascomycota, Basidiomycota or non-symbiotic. Additionally, the presence of dark septate endophytes (DSE) was recorded for lycophytes. For some liverwort and hornwort species, only the presence of a 'fungal association' was recorded as the fungal lineage could not be assigned. As well as recording the fungal status, the identification method (microscopy and/or DNA sequencing) was noted for all species. The publications found through Google Scholar that were deemed relevant to the investigation were read and any literature found within those publications, but not returned directly by Google Scholar, was also included. This secondary search method returned exclusively microscopy studies published prior to 1990 (and dating back to 1891); thus, we are confident that all relevant molecular studies were found with our main search method. Additionally, information on the fungal symbiosis status of some liverwort species was obtained either from the liverwort flora of Paton (1999) or from our own unpublished microscopy observations (25 species; see Table S2).

Plant nomenclature

Nomenclature for liverworts and hornworts follows the most recent floras (Söderström et al. 2016; Stotler and Crandall-Stotler 2017) and the Tropicos database (www.tropicos.org); taxonomic rankings above genus level follow Söderström et al. (2016). For lycophytes, nomenclature follows the Checklist of Ferns and Lycophytes of the World by Hassler and Schmitt (2018). When currently accepted names differ from those in the original reports, both are given in Table 1, with the latter appearing in parentheses.

Estimating symbiosis occurrence rates

Fungal symbiosis occurrence rates were estimated for each of the three early diverging plant lineages: liverworts, hornworts and lycophytes. The number of species per genus or family and the total number of species per lineage were based on Söderström et al. (2016) for liverworts and hornworts and on Hassler and Schmitt (2018) for lycophytes. When making estimates for hornworts and lycophytes, if a species within a genus was colonized by a fungal lineage, then it was assumed that all members of the genus have the potential to be colonized by that fungal lineage. Underlining this assumption was the finding of fungi by our own observations on fresh specimens of the same genera. The total number of species potentially colonized in a plant lineage was divided by the total number of species in that lineage and multiplied by 100 to produce an estimate for the fungal symbiosis occurrence rate. In instances where the fungal status of a genus was unknown or reported only as 'fungal association', the genus was not included in the calculations and the total number of species was reduced accordingly. The same method was applied to liverworts but using the family level rather than the genus,

Table 1 The fungal symbionts of early-diverging plants. Mucoro - Mucoromycotina, Glom - Glomeromycotina, Asco - Ascomycota, Basid - Basidiomycota, FA - Fungal association with unidentified fungi, NS - non-symbiotic, DSE - dark septate endophytes. Species labelled 'Mucoro (FRE)' were reported only as being colonized by fine root endophytes (i.e. *Glomus tenue*). A question mark after 'Mucoro' signifies it was not reported in the original publication but microscopy images are indicative of Mucoromycotina colonization. Checks indicate whether DNA sequencing and/or microscopy were used for fungal identification. An asterisk specifies our unpublished personal observations. In the column labelled Fungi, a hash indicates a report considered incorrect as a result of further studies. A cross signifies a likely incorrect report that is discussed in the main text. Species in bold had conflicting reports of symbiotic status. Where appropriate, the species names used in original reports are provided in parentheses. Reference numbers are listed below the table

Species	Fungi	DNA	Microscopy	Reference
Marchantiophyta				
Haplomitriopsida				
Haplomitriidae				
Calobryales				
Haplomitriaceae				
Haplomitrium				
Haplomitrium (*Calobryum*) *blumei*	Mucoro		✓	1–3
Haplomitrium chilensis	Glom[×]	✓	✓	1
Haplomitrium dentatum	Mucoro	✓	✓*	4, 5
Haplomitrium gibbsiae	Mucoro	✓	✓	1, 2, 4–7
Haplomitrium hookeri	Mucoro	✓	✓	1–5, 8
Haplomitrium intermedium	FA		✓	1
Haplomitrium mnioides	Mucoro	✓	✓*	4, 5
Haplomitrium ovalifolium	Mucoro	✓	✓	1, 2, 6
Treubiidae				
Treubiales				
Treubiaceae				
Treubia				
Treubia insignis	FA		✓	3, 9, 10
Treubia lacunosa	Mucoro	✓	✓	1, 2, 4, 5, 7, 11, 12
Treubia pygmaea	Mucoro	✓	✓	1, 2, 4, 5, 11
Treubia tasmanica	Mucoro	✓	✓	2, 12
Marchantiopsida				
Blasiidae				
Blasiales				
Blasiaceae				
Blasia				
Blasia pusilla	NS (*Nostoc*)	✓	✓	1, 3, 13–16
Cavicularia				
Cavicularia densa	NS (*Nostoc*)	✓	✓	13
Marchantiidae (complex thalloid)				
Lunulariales				
Lunulariaceae				
Lunularia				
Lunularia cruciata	Glom, Mucoro	✓	✓	1, 3–5, 16–18
Marchantiales				
Aytoniaceae				
Asterella				
Asterella australis	Glom	✓	✓	1, 4, 5
Asterella bachmannii	Glom, Mucoro	✓	✓	1, 4, 5
Asterella bolanderi	Glom, Mucoro	✓		4, 5
Asterella (*Fimbriaria*) *blumeana*	NS		✓	3
Asterella californica	Mucoro	✓		4, 5
Asterella drummondii	NS	✓		4, 5
Asterella grollei	NS	✓		4, 5
Asterella khasyana	Glom, Mucoro	✓		4, 5
Asterella (*Fimbriaria*) *lindenbergiana*	NS	✓	✓	3–5
Asterella muscicola	Glom, Mucoro	✓	✓	1, 4, 5
Asterella pringlei	Mucoro	✓		4, 5
Asterella sp.	Glom, Mucoro	✓		4, 5
Asterella (*Fimbriaria*) sp.	FA		✓	3
Asterella tenera	Glom, Mucoro	✓	✓	1, 2, 4, 5
Asterella wilmsii	Glom, Mucoro	✓	✓	1, 4, 5, 19
Cryptomitrium				
Cryptomitrium himalayense	NS	✓		4, 5
Cryptomitrium oreades	NS	✓	✓	1, 4, 5
Mannia				
Mannia angrogyna (*Grimaldia dichotoma*)	NS		✓	1, 3
Mannia fragrans	NS		✓	1
"	Mucoro (FRE)		✓	20
Mannia gracilis	NS	✓		4, 5
Mannia sp	Glom	✓		4, 5
Plagiochasma				
Plagiochasma eximium	Glom		✓	1

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
"	NS	✓		4, 5
Plagiochasma rupestre	Glom, Mucoro	✓	✓	1, 4, 5, 21
"	NS		✓	3
Plagiochasma sp.	Glom, Mucoro	✓		4, 5
Plagiochasma sp.	FA		✓	3
Reboulia				
Reboulia hemisphaerica	Glom	✓	✓	1, 3–5
Cleveaceae				
Athalamia				
Athalamia pinguis	Glom	✓	✓	1, 4, 5
Clevea				
Clevea (*Athalamia*) *hyalina*	Glom	✓	✓	1, 4, 5
Clevea spathysii (*rousseliana*)	NS		✓	3
Peltolepis				
Peltolepis quadrata (*grandis*)	NS		✓	1, 3
Sauteria				
Sauteria alpina	NS	✓	✓	1, 3–5
Conocephalaceae				
Conocephalum				
Conocephalum conicum (*Fegatella conica*)	Glom	✓	✓	1–5, 14, 16, 22, 23
Conocephalum japonicum	Glom	✓		4, 5
Conocephalum salebrosum	Glom	✓	✓	1, 4, 5, 14
Corsiniaceae				
Corsinia				
***Corsinia coriandrina* (*marchantioides*)**	Glom		✓	1
"	NS	✓	✓	3–5
Cronisia				
Cronisia fimbriata	NS		✓	1
Cyathodiaceae				
Cyathodium				
Cyathodium aureonitens	NS	✓		4, 5
Cyathodium cavernarum	NS	✓	✓	1, 4, 5
Cyathodium foetidissimum	NS		✓	1
"	FA#		✓	3
Cyathodium sp.	NS	✓		4, 5
Cyathodium tuberosum	NS	✓		4, 5
Dumortieraceae				
Dumortiera				
Dumortiera hirsuta (*irrigua/velutina*)	Glom	✓	✓	1, 3–5
Exormothecaceae				
Aitchisoniella				
Aitchisoniella himalayensis	NS		✓	1
Exormotheca				
Exormotheca holstii	NS		✓	1, 3
Exormotheca pustulosa	NS		✓	1
Stephensoniella				
Stephensoniella brevipedunculata	NS		✓	1
Marchantiaceae				
Marchantia				
Marchantia berteroana	Glom	✓	✓	1, 4, 5
Marchantia breviloba	Glom	✓		4, 5
Marchantia chenopoda	Glom	✓		4, 5
Marchantia debilis	Glom	✓		4, 5
Marchantia foliacea	Glom	✓	✓	1, 2, 4, 5, 24, 25
Marchantia geminata	FA		✓	3
Marchantia paleacea	Glom	✓	✓	3–5, 26, 27
Marchantia papillata	Glom	✓		4, 5
Marchantia pappeana	Glom	✓	✓	1, 4, 5
Marchantia pileata	Glom	✓		4, 5
Marchantia polymorpha subsp. *montivagans*	Glom		✓	1
Marchantia polymorpha subsp. *polymorpha*	NS	✓	✓	1, 3–5
Marchantia polymorpha subsp. *ruderalis*	NS	✓	✓	1, 4, 5, 14
Marchantia (*Bucegia*) *romanica*	NS		✓	1
Marchantia wallisii (*grisea*)	FA		✓	3
Preissia				
Preissia (*Marchantia*) *quadrata*	Glom	✓	✓	1, 3–5, 26
Monocleaceae				
Monoclea				
Monoclea forsteri	Glom, Mucoro	✓	✓	1, 3–5
Monoclea gottschei	NS	✓		4, 5
"	Glom	✓	✓	1
Monoclea sp.	FA		✓	3
Monosoleniaceae				

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Monosolenium				
Monosolenium tenerum	NS		✓	1
Oxymitraceae				
Oxymitra				
Oxymitra cristata	NS		✓	1
Oxymitra incrassata	NS	✓	✓	1, 4, 5
Ricciaceae				
Riccia				
Riccia albolimbata	NS		✓	1
Riccia beyrichiana	NS		✓	1
Riccia canaliculata	NS		✓	1
Riccia cavernosa	NS		✓	1
Riccia ciliata	NS		✓	3
Riccia crozalsii	NS		✓	1
Riccia crystallina	NS		✓	1
Riccia fluitans	NS		✓	1, 3, 14, 16
Riccia glauca	NS	✓	✓	1, 3, 14, 28
Riccia huebeneriana	NS		✓	1
Riccia montana	NS		✓	1
Riccia nigrella	NS		✓	1
Riccia okahandjana	NS		✓	1
Riccia sorocarpa	NS		✓	1
Riccia stricta	NS		✓	1
Riccia subbifurca	NS		✓	1
Ricciocarpus				
Ricciocarpos natans	NS		✓	1, 3
Targioniaceae				
Targionia				
Targionia hypophylla	Glom, Mucoro	✓	✓	1, 3–5
Wiesnerellaceae				
Wiesnerella				
Wiesnerella denudata	NS		✓	1
"	FA		✓	3
Neohodgsoniales				
Neohodgsoniaceae				
Neohodgsonia				
Neohodgsonia mirabilis	Glom, Mucoro	✓	✓	1, 2, 4, 5, 29
Sphaerocarpales				
Monocarpaceae				
Monocarpus				
Monocarpus sphaerocarpus	NS		✓	1
Riellaceae				
Riella				
Riella americana	NS		✓	1
Riella helicophylla	NS		✓	1
Sphaerocarpaceae				
Geothallus				
Geothallus tuberosus	NS		✓	1
Sphaerocarpos				
Sphaerocarpos michelii	NS		✓	1
Sphaerocarpos texanus	NS		✓	1
Sphaerocarpos sp.	NS		✓	3
Jungermanniopsida				
Pelliidae (simple thalloid I)				
Fossombroniales				
Calyculariaceae				
Calycularia				
Calycularia crispula	Glom, Mucoro	✓	✓*	4, 5
Allisoniaceae				
Allisonia				
Allisonia cockaynei	Glom, Mucoro	✓	✓	1, 2, 4, 5, 29
Fossombroniaceae				
Fossombronia				
Fossombronia angulifolia	Glom, Mucoro	✓	✓*	4, 5
Fossombronia angulosa	Glom		✓	1, 3
Fossombronia australis	Glom, Mucoro	✓	✓	1, 2, 4, 5
Fossombronia caespitiformis	Glom, Mucoro	✓	✓	1, 4, 5
Fossombronia echinata	Glom, Mucoro	✓	✓	1, 4, 5
Fossombronia foveolata	Glom, Mucoro	✓	✓	4, 5, 14
Fossombronia husnotii	Glom	✓	✓	4, 5
Fossombronia hyalorhiza	Glom, Mucoro	✓		4, 5
Fossombronia incurva	Glom, Mucoro	✓		4, 5
Fossombronia indica	Glom	✓		4, 5

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Fossombronia kashyapii	Glom, Mucoro	✓		4, 5
Fossombronia maritima	Glom	✓	✓	1, 4, 5
Fossombronia porphyrorhiza	NS	✓		4, 5
Fossombronia pusilla	Glom, Mucoro	✓	✓	1, 3–5, 16
Fossombronia reticulata	NS	✓		4, 5
Fossombronia sp.	Glom, Mucoro	✓		4, 5
Fossombronia wondraczekii	Glom, Mucoro	✓	✓	1, 3–5
Petalophyllaceae				
Petalophyllum				
Petalophyllum ralfsii	Glom		✓	1
Sewardiella				
Sewardiella tuberifera	Glom, Mucoro	✓	✓	4, 5
Pallaviciniales				
Hymenophytaceae				
Hymenophyton				
Hymenophyton flabellatum	Glom	✓	✓	1, 3–5
Moerckiaceae				
Moerckia				
Moerckia blyttii	Glom, Mucoro	✓	✓	1, 3–5
Moerckia hibernica	NS		✓	1
Moerckia flotoviana	NS		✓*	
Pallaviciniaceae				
Greeneothallus				
Greeneothallus gemmiparus	Glom		✓	1
Jensenia				
Jensenia connivens	Glom	✓	✓	1, 2
Jensenia crassifrons	Glom	✓		4, 5
Jensenia wallisii	Glom		✓	1
Pallavicinia				
Pallavicinia connivens	Glom		✓	1
Pallavicinia indica	NS		✓	1
Pallavicinia lyellii	NS		✓	1
Pallavicinia sp.	FA		✓	3
Pallavicinia xiphoides	Glom, Mucoro	✓	✓	4, 5
"	NS#		✓	1
Podomitrium				
Podomitrium phyllanthus	Glom	✓	✓	1, 2, 4, 5
Symphyogyna				
Symphyogyna brasiliensis	Glom	✓	✓	1, 4, 5
Symphyogyna brongniartii	Glom	✓	✓	1, 4, 5
Symphyogyna hochstetteri	Glom, Mucoro	✓		4, 5
Symphyogyna hymenophyllum	Glom, Mucoro	✓	✓	1, 2, 4, 5
"	NS#	✓		30
Symphyogyna podophylla	Glom	✓		2
Symphyogyna prolifera	Glom	✓		2
Symphyogyna sp.	NS	✓		30
Symphyogyna sp.	FA		✓	3
Symphyogyna subsimplex	Glom	✓	✓	1, 2
Symphyogyna (*Pallavicinia*) *tenuinervis*	NS		✓	1
Symphyogyna undulata	Glom		✓	1
Xenothallus				
Xenothallus vulcanicola	Glom		✓	1, 25
Phyllothalliaceae				
Phyllothallia				
Phyllothallia nivicola	NS	✓	✓	1, 4, 5, 25
Pelliales				
Noterocladaceae				
Noteroclada				
Noteroclada (*Androcryphia*) *confluens*	Glom	✓	✓	1, 3–5
Pelliaceae				
Pellia				
Pellia endiviifolia (fabbroniana)	Glom	✓	✓	1, 4, 5, 14, 31
"	Mucoro (FRE)		✓	23
Pellia epiphylla	Glom, Mucoro	✓	✓	1, 3–5, 16
Pellia neesiana	NS	✓		4, 5
"	Glom		✓	1, 3
Metzgeriidae (simple thalloid II)				
Metzgeriales				
Aneuraceae				
Aneura				
Aneura lobata	Basid		✓	1
Aneura maxima	Basid	✓	✓	1, 3, 28
Aneura mirabilis	Basid	✓	✓	1, 28, 31–33

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Aneura novaguineensis	Basid		✓	1, 32, 34
Aneura pellioides	NS	✓	✓	28
Aneura pinguis	Basid	✓	✓	1, 3, 15, 16, 28, 31, 32, 34–37
Aneura pseudopinguis	Basid		✓	1
Aneura sp.	Basid	✓		28
Lobatiriccardia				
Lobatiriccardia (*Aneura*) *alterniloba*	FA		✓	34
Lobatiriccardia coronopus subsp. *australis* (*Aneura lobata* subsp. *australis*)	Basid		✓	32
Lobatiriccardia (*Aneura*) *lobata*	Basid	✓	✓	28, 34
Lobatiriccardia sp.	Basid	✓		28
Riccardia				
Riccardia aequicellularis	NS		✓	34
Riccardia aequitexta	FA		✓	34
Riccardia alba	NS		✓	34
Riccardia alcicornis	NS		✓	34
Riccardia asperulata	NS		✓	34
Riccardia australis	FA		✓	34
Riccardia bipinnatifda	NS		✓	34
Riccardia breviala	FA		✓	34
***Riccardia chamedryfolia* (*Aneura sinuata*)**	NS	✓	✓	1, 28
"	FA		✓	3
Riccardia cochleata	NS		✓	1, 34
"	Basid		✓	38
Riccardia colensoi	NS		✓	34
Riccardia crassa	NS		✓	34
Riccardia eriocaula	NS		✓	1, 34
Riccardia furtiva	FA		✓	34
Riccardia incurvata	NS		✓	1
Riccardia intercellula	Basid		✓	1, 34
Riccardia latifrons	NS		✓	1, 33
"	Basid	✓	✓	37
Riccardia lobulata	NS		✓	34
Riccardia marginata	NS		✓	34
Riccardia metzgeriiformis	Basid	✓		39
Riccardia multicorpora	FA		✓	34
Riccardia (Aneura) multifida	NS	✓	✓	1, 30, 33
"	Basid	✓	✓	3, 37
Riccardia nitida	NS		✓	34
Riccardia pallidevirens	FA		✓	34
Riccardia* (*Aneura*) *palmata	NS		✓	1, 3, 33
"	Basid	✓	✓	37
Riccardia papulosa	FA		✓	34
Riccardia pennata	Basid		✓	1, 34, 38
Riccardia perspicua	FA		✓	34
Riccardia pseudodendroceros	NS		✓	34
Riccardia pusilla	FA		✓	34
Riccardia smaragdina	Basid	✓		35
Riccardia sp.	Basid	✓		35
Riccardia umida	NS		✓	34
Riccardia wattsiana	FA		✓	34
Verdoornia				
Verdoornia succulenta	Basid		✓	1, 25, 32
Metzgeriaceae				
Metzgeria				
Metzgeria conjugata	NS		✓	1, 33
Metzgeria decipiens	NS		✓	1
Metzgeria furcata	NS	✓	✓	1, 3, 30, 33
Metzgeria leptoneura	NS		✓	33
Metzgeria pubescens	NS		✓	1, 3, 33
Metzgeria temperata	NS	✓	✓	1, 30, 33
Metzgeria violacea (*fruticulosa*)	NS		✓	1, 33
Pleuroziales				
Pleuroziaceae				
Pleurozia				
Pleurozia gigantea	NS		✓	1
Pleurozia purpurea	NS	✓	✓	1, 28
Jungermanniidae (leafy)				
Jungermanniales				
Acrobolbaceae				
Acrobolbus				
Acrobolbus cinerascens	NS	✓		30

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Acrobolbus ochrophyllus	NS		✓	25
Acrobolbus wilsonii	Basid#		✓	40
Goebelobryum				
Goebelobryum unguiculatum	NS		✓	25
Lethocolea				
Lethocolea pansa	FA		✓	25
Saccogynidium				
Saccogynidium australe	NS		✓	25
Adelanthaceae				
Adelanthus				
Adelanthus bisetulus	NS	✓		30
Adelanthus falcatus	FA		✓	25
Adelanthus lindenbergianus	NS		✓*	
Biantheridion				
Biantheridion undulifolium	NS		✓	33, 40
Pseudomarsupidium				
Pseudomarsupidium (*Adelanthus*) *decipiens*	NS		✓*	
Syzygiella				
Syzygiella autumnalis	NS		✓	40
"	FA#		✓	33
Syzygiella (*Jamesoniella*) *colorata*	NS	✓		30
Syzygiella jacquinotii	Asco	✓		28
Syzygiella sonderi (*Cryptochila grandiflora*)	NS		✓	25
Syzygiella (*Herzogobryum*) *teres*	NS		✓	25
Wettsteinia				
Wettsteinia schusteriana	NS	✓		30
Anastrophyllaceae				
Anastrepta				
Anastrepta orcadensis	NS		✓	40
Anastrophyllum				
Anastrophyllum alpinum	NS		✓*	
Anastrophyllum donnianum	NS		✓	40
Anastrophyllum joergensenii	NS		✓*	
Anastrophyllum sp.	NS	✓		30
Barbilophozia				
Barbilophozia barbata	Basid	✓	✓	28, 40
"	Asco#		✓	15
Barbilophozia hatcheri	Basid	✓	✓	28, 40–42
"	NS#	✓	✓	30, 33
Barbilophozia (*Lophozia*) *kunzeana*	Basid		✓	40
"	FA		✓	43, 44
Barbilophozia lycopodioides	Basid	✓	✓	28, 40
Barbilophozia (*Lophozia*) *sudetica*	Basid	✓	✓	15, 28, 40
Crossocalyx				
***Crossocalyx* (*Sphenolobus*) *hellerianus* (*Anastrophyllum hellerianum*)**	NS#		✓	33
"	Asco	✓		28
"	Basid#		✓	40
Gymnocolea				
Gymnocolea inflata	NS		✓	40
Gymnocolea inflata subsp. *acutiloba*	NS		✓	40
Isopaches				
Isopaches (*Lophozia*) *alboviridis*	FA		✓	44
Isopaches bicrenatus (*Lophozia bicrenata*)	Basid	✓	✓	28, 40, 43, 44
Neoorthocaulis				
Neoorthocaulis (*Barbilophozia*) *attenuatus*	Basid	✓	✓	28, 40
Neoothocaulis (*Barbilophozia*) *floerkei*	Basid	✓	✓	28, 40
Orthocaulis				
Orthocaulis (*Barbilophozia*) *atlanticus*	Basid		✓*	
Schljakovia				
Schljakovia (*Barbilophozia*) *kunzeana*	Basid		✓*	
Schljakovianthus				
Schljakovianthus (*Barbilophozia*) *quadrilobus* (*Lophozia quadriloba*)	Basid	✓	✓	28, 40, 44
Sphenolobopsis				
Sphenolobopsis pearsonii	NS		✓	40
Sphenolobus				
***Sphenolobus minutus* (*Anastrophyllum minutum*)**	NS		✓	33, 40
"	Asco#		✓	15
Sphenolobus (*Anastrophyllum*) *saxicola*	NS		✓	40
Tetralophozia				
Tetralophozia setiformis	NS	✓	✓	25, 30, 40
Antheliaceae				

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Anthelia				
Anthelia julacea	NS	✓		30
Anthelia juratzkana	NS	✓	✓	25, 30
Balantiopsidaceae				
Balantiopsis				
Balantiopsis diplophylla	NS	✓		30
Balantiopsis rosea	FA		✓	25
Isotachis				
Isotachis montana	NS	✓		30
"	FA		✓	25
Isotachis (*Eoisotachis*) *stephanii*	FA		✓	25
Blepharostomataceae				
Blepharostoma				
Blepharostoma trichophyllum	NS		✓	33
Brevianthaceae				
Brevianthus				
Brevianthus flavus	NS	✓		30
Calypogeiaceae				
Calypogeia				
Calypogeia arguta	FA		✓	33
Calypogeia azurea	Asco		✓	15, 40
Calypogeia fissa	Asco	✓	✓	16, 28, 33, 40, 45
Calypogeia integristipula	Asco		✓	15, 40
Calypogeia muelleriana	Asco		✓	15, 16, 28, 33, 40
"	NS#	✓		30
Calypogeia neesiana (*trichomanis*)	Asco		✓	33, 40
Calypogeia sphagnicola	Asco		✓	25, 33
Mizutania				
Mizutania riccardioides	Asco		✓	46
Cephaloziaceae				
Cephalozia				
Cephalozia ambigua	Asco		✓*	
Cephalozia bicuspidata	Asco	✓	✓	16, 33, 45, 47, 48
Cephalozia sp.	NS	✓		30
Cephalozia sp.	Asco		✓	25
Fuscocephaloziopsis				
Fuscocephaloziopsis (*Pleurocladula*) *albescens*	FA		✓	49
Fuscocephaloziopsis* (*Cephalozia*) *catenulata	NS#		✓	33
"	Asco		✓*	
Fuscocephaloziopsis (*Cephalozia*) *connivens*	Asco	✓	✓	16, 28, 31, 33, 45, 48
Fuscocephaloziopsis (*Cephalozia*) *leucantha*	FA		✓	33
Fuscocephaloziopsis (*Cephalozia*) *loitlesbergeri*	Asco		✓	16, 33
Fuscocephaloziopsis (*Cephalozia*) *lunulifolia*	FA		✓	33
Fuscocephaloziopsis (*Cephalozia*) *macrostachya*	FA		✓	33
Fuscocephaloziopsis (*Schofieldia*) *monticola*	NS#	✓		30
Fuscocephaloziopsis (*Cephalozia*) *pleniceps*	FA		✓	33
Nowellia				
Nowellia curvifolia	Asco		✓	16, 33
Odontoschisma				
Odontoschisma denudatum	Asco		✓	16, 45
"	NS#		✓	33
Odontoschisma elongatum	NS		✓	33
Odontoschisma fluitans	NS#		✓	33
Odontoschisma francisci	FA		✓	33
Odontoschisma macounii	FA		✓*	
Odontoschisma prostratum	NS#	✓		30
Odontoschisma sp.	NS#	✓		30
Odontoschisma sphagni	FA		✓	16, 33
Cephaloziellaceae				
Anastrophyllopsis				
Anastrophyllopsis subcomplicata (*Anastrophyllum schismoides*)	NS		✓	25
Cephaloziella				
Cephaloziella baumgartneri	NS#		✓	33
Cephaloziella divaricata	Asco		✓	16, 33
Cephaloziella exiliflora	Asco	✓		50
Cephaloziella hampeana	FA		✓	33
Cephaloziella massalongi	NS#		✓	33
Cephaloziella rubella	FA		✓	33
"	NS#	✓		30
Cephaloziella sp.	Asco		✓	25
Cephaloziella turneri	Asco		✓*	
Cephaloziella (*Cephalozia*) *varians*	Asco	✓	✓	51, 52

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Nothogymnomitrion				
Nothogymnomitrion (*Marsupella*) *erosum*	NS		✓	25
Obtusifolium				
Obtusifolium (*Lophozia*) *obtusum*	NS		✓	40
Oleolophozia				
Oleolophozia (*Lophozia*) *perssonii*	Basid		✓	40
Protolophozia				
Protolophozia (*Lophozia*) *crispata*	Basid	✓		28
Protolophozia herzogiana	FA		✓	43
Geocalycaceae				
Geocalyx				
Geocalyx graveolens	Asco	✓		28
“	Basid[#]		✓	40
“	FA		✓	33
Gymnomitriaceae				
Gymnomitrion				
Gymnomitrion (*Marsupella*) *adustum*	NS		✓	33, 40
Gymnomitrion (*Marsupella*) *alpinum*	NS		✓	33
Gymnomitrion concinnatum	NS	✓	✓	30, 33, 40
Gymnomitrion corallioides	NS		✓*	
Gymnomitrion crenulatum	NS		✓	33
Gymnomitrion incompletum (*cuspidatum*)	NS		✓	25
Gymnomitrion obtusum	NS		✓	33, 40
Gymnomitrion sp.	NS	✓		30
Marsupella				
Marsupella emarginata	NS	✓	✓	30, 33, 40
Marsupella stableri	NS		✓	33, 40
Nardia				
Nardia breidleri	Basid		✓	33, 40
Nardia compressa	NS		✓	40
Nardia geoscyphus	Basid	✓	✓	28, 40
Nardia scalaris	Basid	✓	✓	16, 28, 40, 45
“	NS[#]	✓		30
Harpanthaceae				
Harpanthus				
Harpanthus flotovianus	NS		✓	33, 40
Harpanthus scutatus	Basid		✓	33, 40
Herbertaceae				
Herbertus				
Herbertus aduncus	NS	✓		30
Herbertus alpinus	NS	✓	✓	25, 30
Herbertus borealis	NS		✓	33
Triandrophyllum				
Triandrophyllum subtrifidum	NS		✓	25
Hygrobiellaceae				
Hygrobiella				
Hygrobiella laxifolia	NS		✓*	
Jungermanniaceae				
Eremonotus				
Eremonotus myriocarpus	Asco	✓	✓*	28
“	Basid[#]		✓	40
Jungermannia				
Jungermannia atrovirens	NS		✓	33, 40
Jungermannia borealis	NS		✓	33
Jungermannia exsertifolia	NS		✓	33
Jungermannia exsertifolia subsp. *cordifolia*	NS	✓		30
Jungermannia gracillima	NS		✓	16, 33, 40, 45
Jungermannia hyalina	NS		✓	40
Jungermannia obovata	NS		✓	33, 40
Jungermannia polaris	NS		✓	40
Jungermannia pumila	NS		✓	33, 40
Mesoptychia				
Mesoptychia (*Leiocolea*) *badensis*	NS		✓*	
Mesoptychia (*Leiocolea*) *bantriensis*	NS		✓	40
Mesoptychia (*Leiocolea*) *heterocolpos*	NS		✓	40
Mesoptychia (*Leiocolea*) *rutheana*	NS		✓	40
Mesoptychia (*Leiocolea*) *turbinata*	NS		✓	33, 40
Lepicoleaceae				
Lepicolea				
Lepicolea attenuata	NS		✓	25
Lepicolea scolopendra	NS	✓	✓	25, 30
Lepidoziaceae				
Acromastigum				

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Acromastigum colensoanum	FA		✓	25
Bazzania				
Bazzania adnexa	NS	✓		30
"	FA#		✓	25
Bazzania denudata	NS	✓		30
Bazzania flaccida	NS		✓	15
Bazzania sp.	NS	✓		30
Bazzania tayloriana	NS	✓		30
Bazzania tricrenata	NS		✓	33
Bazzania trilobata	Asco#		✓	45
"	NS	✓	✓	15, 30, 33
Hygrolembidium				
Hygrolembidium australe	Asco		✓	25
Isolembidium				
Isolembidium anomalum	Asco		✓	25
Kurzia				
Kurzia pauciflora	Asco		✓	16, 33, 45
Kurzia sp.	Asco		✓	25
Kurzia sylvatica	FA		✓	33
Kurzia trichoclados	FA		✓	33
Lembidium				
Lembidium (*Chloranthelia*) *berggrenii*	Asco		✓	25
Lembidium nutans	Asco		✓	25
Lepidozia				
Lepidozia reptans	Asco	✓	✓	16, 28, 33, 45
"	NS	✓		30
Lepidozia sp.	NS	✓		30
Lepidozia sp.	Asco		✓	25
Megalembidium				
Megalembidium insulanum	Asco		✓	25
Neogrollea				
Neogrollea notabilis	Asco		✓	25
Pseudocephalozia				
Pseudocephalozia lepidozioides	Asco		✓	25
Psiloclada				
Psiloclada clandestina	Asco		✓	25
Telaranea				
Telaranea europaea	Asco		✓*	
Telaranea nematodes	Asco		✓*	
"	FA		✓	33
Telaranea sp.	Asco		✓	25
Tricholepidozia				
Tricholepidozia (*Telaranea*) *murphyae*	Asco		✓*	
"	FA		✓	33
Tricholepidozia (*Telaranea*) *tetradactyla*	Asco		✓*	
Zoopsidella				
Zoopsidella caledonica	Asco		✓	25
Zoopsis				
Zoopsis sp.	Asco		✓	25
Lophocoleaceae				
Chiloscyphus				
Chiloscyphus pallescens	NS		✓	33, 40
Chiloscyphus polyanthos	NS		✓	33, 40
Chiloscyphus sp.	NS		✓	25
Clasmatocolea				
Clasmatocolea sp.	NS		✓	25
Heteroscyphus				
Heteroscyphus billardierei	NS	✓		30
Heteroscyphus sp.	NS		✓	25
Leptoscyphus				
Leptoscyphus cuneifolius	NS		✓	33, 40
Leptoscyphus sp.	NS		✓	25
Lophocolea				
Lophocolea bidentata	NS	✓	✓	30, 33, 40
Lophocolea bispinosa	NS		✓*	
Lophocolea brookwoodiana	NS		✓*	
Lophocolea cuspidata	NS		✓	33
Lophocolea fragrans	NS		✓*	
Lophocolea (*Lophozia*) *heteromorpha*	FA#		✓	44
Lophocolea heterophylla	Asco#		✓	15
"	NS		✓	16, 33, 40
Lophocolea semiteres	NS		✓*	
Lophocolea sp.	NS	✓		30

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Lophoziaceae				
Lophozia				
Lophozia ascendens	FA		✓	44
Lophozia sp.	NS#	✓		30
Lophozia sp.	Basid		✓	25
Lophozia ventricosa	Basid	✓	✓	16, 28, 40, 43–45
"	NS#	✓		30
Lophozia wenzelii	Basid	✓	✓	28, 44
Lophoziopsis				
Lophoziopsis (*Lophozia*) *excisa*	Basid	✓	✓	28, 40, 43, 44, 53
Lophoziopsis (*Lophozia*) *latifolia*	FA		✓	44
Lophoziopsis (*Lophozia*) *longidens*	Basid	✓	✓	28, 40
Lophoziopsis (*Lophozia*) *pellucida*	FA		✓	44
Trilophozia				
Trilophozia (*Tritomaria*) *quinquedentata*	Basid		✓*	
Tritomaria				
Tritomaria* (*Lophozia*) *capitata	Basid		✓*	
"	NS		✓	40
Tritomaria exsecta	Basid		✓	40
Tritomaria exsectiformis	Basid	✓	✓	28, 40
Tritomaria quinquidentata	Basid	✓	✓	28, 40, 43, 44
Mastigophoraceae				
Dendromastigophora				
Dendromastigophora flagellifera	NS	✓	✓	25, 30
Myliaceae				
Mylia				
Mylia anomala	Asco		✓	33, 40
Mylia taylorii	NS		✓	40
Plagiochilaceae				
Pedinophyllum				
Pedinophyllum interruptum	Basid		✓	40
"	NS#		✓	33
"	FA		✓	43
Plagiochila				
Plagiochila asplenioides	NS	✓	✓	30, 33, 40
Plagiochila bifaria	NS		✓*	
Plagiochila britannica	NS		✓*	
Plagiochila caduciloba	NS	✓		30
Plagiochila carringtonii	NS		✓	40
Plagiochila incurvicolla	NS	✓		30
Plagiochila porelloides	NS	✓	✓	30, 33, 40
Plagiochila punctata	FA#		✓	33
"	NS		✓*	
Plagiochila ramosissima	NS	✓		30
Plagiochila sp.	NS	✓		30
Plagiochila sp.	NS		✓	25
Plagiochila spinulosa	NS		✓	33
Plagiochila virginica	NS	✓		30
Plagiochilion				
Plagiochilion conjugatum	NS		✓	25
Pseudolepicoleaceae				
Archeophylla				
Archeophylla schusteri	NS		✓	25
Temnoma				
Temnoma quadrifidum	NS		✓	25
Saccogynaceae				
Saccogyna				
Saccogyna viticulosa	Basid	✓	✓	28, 33, 40
Scapaniaceae				
Diplophyllum				
Diplophyllum albicans	Basid	✓	✓	15, 28, 40, 43
"	NS#	✓	✓	16, 30, 33
Diplophyllum apiculatum	Basid	✓	✓	28
"	NS#	✓		30
Diplophyllum dioicum	Basid	✓	✓	25, 28
"	NS#	✓		30
Diplophyllum obtusifolium	Basid	✓	✓	28, 40, 43
"	Asco#		✓	15
Diplophyllum obtusatum	Basid		✓*	
Diplophyllum taxifolium	NS	✓	✓	28, 40
Douinia				
Douinia ovata	NS	✓	✓	28, 33, 40
Saccobasis				

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Saccobasis (*Tritomaria*) *polita*	Basid	✓	✓	28, 44
Scapania				
Scapania aequiloba	NS		✓	40
Scapania aspera	NS		✓	40
Scapania bolanderi	Basid	✓		54
***Scapania brevicaulis* (*degenii*)**	FA		✓	49
"	NS#		✓	40
Scapania calcicola	Basid	✓	✓	28, 40
"	NS#		✓	33
Scapania compacta	NS		✓	40
Scapania curta (*personnii*)	FA		✓	49
Scapania cuspiduligera	Basid	✓	✓	28, 40
"	NS#		✓	33
Scapania glaucocephala	FA		✓	49
Scapania glaucocephala var. *saxicola*	FA		✓	49
Scapania gracilis	NS		✓	33, 40
Scapania gymnostomophila	Basid		✓✓	40
"	FA		✓	49
Scapania irrigua	Basid	✓	✓	28, 40
Scapania lingulata var. *microphylla*	FA		✓	49
Scapania nemorea	NS	✓	✓	30, 40
Scapania nimbosa	NS		✓	40
Scapania obcordata	FA		✓	49
Scapania obcordata var. *paradoxa*	FA		✓	49
Scapania ornithopodioides	NS		✓	40
Scapania paludicola	NS		✓*	
Scapania scandica	NS		✓	33
Scapania sp.	NS	✓		30
Scapania subaplina	NS		✓*	
Scapania uliginosa	NS		✓	40
Scapania umbrosa	Basid	✓	✓	28, 40
"	NS#		✓	33
Scapania undulata	NS	✓	✓	28, 30, 40
Scapania zemliae (*invisa*)	FA		✓	49
Schistochilopsis				
Schistochilopsis (*Lophozia*) *incisa*	Basid	✓	✓	15, 28, 40
Schistochilopsis incisa var. *opacifolia* (*Lophozia opacifolia*)	Basid	✓	✓	28, 40
Schistochilopsis (*Lophozia*) *hyperarctica*	FA		✓	44
Schistochilaceae				
Schistochila				
Schistochila alata	Asco		✓	55
Schistochila appendiculata	Asco		✓	55
"	NS	✓		30
Schistochila balfouriana	Asco		✓	55
"	NS	✓		30
Schistochila childii	Asco		✓	55
Schistochila glaucescens	Asco		✓	55
Schistochila kirkiana	Asco		✓	55
Schistochila lamellata	Asco		✓	55
Schistochila laminigera	Asco		✓	55
Schistochila muricata	Asco		✓	55
Schistochila nobilis	Asco		✓	25, 55
Schistochila pinnatifolia	Asco		✓	55
Schistochila repleta	Asco		✓	55
Schistochila splachnophylla	Asco	✓	✓	45, 55
Schistochila subimmersa	Asco	✓	✓	45, 55
Schistochila succulenta	Asco		✓	45, 55
Solenostomataceae				
Solenostoma				
Solenostoma (*Jungermannia*) *orbiculata*	NS		✓	25
Southbyaceae				
Gongylanthus				
Gongylanthus ericetorum	Basid		✓	40
"	FA		✓	43
Southbya				
Southbya nigrella	Basid	✓	✓	16, 28, 40, 43
Southbya tophacea	Basid	✓	✓	28, 31, 40, 43
Trichocoleaceae				
Leiomitria				
Leiomitra lanata	NS	✓		30
Trichocolea				
Trichocolea mollissima	NS		✓	25

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Trichocolea rigida	NS	✓		30
Trichocolea tomentella	NS	✓		30
Trichotemnomataceae				
Trichotemnoma				
Trichotemnoma corrugatum	NS		✓	25
Porellales				
Frullaniaceae				
Frullania				
Frullania dilatata	NS		✓	33
Frullania eboracensis	NS	✓		30
Frullania fragilifolia	NS		✓	33
Frullania microphylla	NS		✓	33
Frullania nisquallensis	NS	✓		30
Frullania sp.	NS		✓	25
Frullania tamarisci	NS		✓	33
Frullania teneriffae	NS		✓	33
Goebeliellaceae				
Goebeliella				
Goebeliella cornigera	NS	✓		30
Jubulaceae				
Jubula				
Jubula hutchinsiae	NS		✓	33
Jubula hutchinsiae subsp. *pennsylvanica*	NS	✓		30
Lejeuneaceae				
Cheilolejeunea				
Cheilolejeunea (*Leucolejeunea*) *clypeata*	NS	✓		30
Cheilolejeunea (*Leucolejeunea*) sp.	NS	✓		30
Cololejeunea				
Cololejeunea calcarea	NS		✓	33
Cololejeunea microscopica	NS		✓	33
Colura				
Colura calyptrifolia	NS		✓	33
Drepanolejeunea				
Drepanolejeunea hamatifolia	NS		✓	33
Harpalejeunea				
Harpalejeunea ovata	NS		✓	33
Lejeunea				
Lejeunea cavifolia	NS		✓	33
Lejeunea lamacerina	NS		✓	33
Lejeunea patens	NS		✓	33
Lejeunea ulicina	NS	✓	✓	30, 33
Marchesinia				
Marchesinia mackaii	NS		✓	33
Mastigolejeunea				
Mastigolejeunea anguiformis	NS	✓		30
Myriocoleopsis				
Myriocoleopsis (*Cololejeunea*) *minutissima*	NS		✓	33
Lepidolaenaceae				
Gackstroemia				
Gackstroemia alpina	NS	✓	✓	25, 30
Lepidolaena				
Lepidolaena sp.	NS		✓	25
Lepidolaena taylorii	NS	✓		30
Porellaceae				
Lepidogyna				
Lepidogyna sp.	NS		✓	25
Porella				
Porella arboris-vitae	NS		✓	33
Porella cordaeana	NS		✓	33
Porella elegantula	NS	✓		30
Porella navicularis	NS	✓		30
Porella obtusata	NS		✓	33
Porella pinnata	NS	✓	✓	30, 33
Porella platyphylla	NS	✓	✓	30, 33
Porella sp.	NS		✓	25
Radulaceae				
Radula				
Radula aquilegia	NS		✓	33
Radula complanata	NS		✓	33
Radula lindenbergiana	NS		✓	33
Radula sp.	NS		✓	25
Ptilidiales				
Ptilidiaceae				

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Ptilidium				
Ptilidium ciliare	NS	✓	✓	25, 30
Ptilidium sp.	NS	✓		30
Anthocerotophyta				
Anthocerotopsida				
Anthocerotales				
Anthocerotaceae				
Anthoceros				
Anthoceros agrestis	Glom, Mucoro	✓	✓	14, 56
Anthoceros cristatus	Mucoro	✓	✓	57
Anthoceros fusiformis	Mucoro	✓		56
Anthoceros lamellatus	Glom, Mucoro	✓		56
Anthoceros laminiferus	Glom, Mucoro	✓	✓	2, 25, 56
Anthoceros punctatus	Glom, Mucoro	✓	✓	2, 56, 58
Anthoceros sp.	Glom, Mucoro	✓	✓	56
Folioceros				
Folioceros fuciformis	Glom	✓		56
Folioceros sp.	Glom, Mucoro	✓	✓	56
Dendrocerotales				
Dendrocerotaceae				
Dendroceros				
Dendroceros crispus	NS	✓		56
Dendroceros granulatus	NS		✓	25
Dendroceros validus	NS	✓	✓	25, 56
Megaceros				
Megaceros flagellaris	NS	✓		56
Megaceros denticulatus	NS		✓	25
Megaceros leptohymenius	Glom, Mucoro	✓		56
Megaceros pellucidus	Glom, Mucoro	✓		56
"	NS		✓	25
Megaceros sp.	Glom, Mucoro	✓		56
Nothoceros				
Nothoceros giganteus	NS	✓	✓	25, 56
Nothoceros vincentianus	Glom, Mucoro	✓		56
Phaeomegaceros				
Phaeomegaceros coriaceus	Glom, Mucoro	✓	✓	25, 56
Phaeomegaceros hirticalyx	Mucoro	✓	✓	56
Phaeomegaceros sp.	Glom, Mucoro	✓		56
Phymatocerotales				
Phymatocerotaceae				
Phymatoceros				
Phymatoceros bulbiculosus	FA		✓	3
(*Anthoceros dichotomus*)				
Notothyladales				
Notothyladaceae				
Notothylas				
Notothylas javanica	Glom	✓		56
Notothylas orbicularis	Glom	✓		56
Paraphymatoceros				
Paraphymatoceros coriaceus	Mucoro	✓		2
Paraphymatoceros pearsonii	NS	✓		56
Paraphymatoceros sp.	Mucoro	✓		2
Phaeoceros				
Phaeoceros carolinianus	Glom, Mucoro	✓	✓	2, 25, 56
Phaeoceros dendroceroides	Glom, Mucoro	✓		56
Phaeoceros laevis	Glom, Mucoro	✓	✓	2, 3, 56, 59
Phaeoceros sp.	Glom, Mucoro	✓		56
Leiosporocerotopsida				
Leiosporocerotales				
Leiosporocerotaceae				
Leiosporoceros				
Leiosporoceros dussii	NS	✓		56
Lycopodiophyta				
Lycopodiopsida				
Lycopodiales				
Lycopodiaceae				
Austrolycopodium				
Austrolycopodium (*Lycopodium*) *fastigiatum*	Mucoro	✓		60
Austrolycopodium (*Lycopodium*) *magellanicum*	NS	✓		60
Austrolycopodium (*Lycopodium*) *paniculatum*	DSE, Glom		✓	61
Dendrolycopodium				
Dendrolycopodium dendroideum	NS	✓		60
Dendrolycopodium obscurum	NS	✓		60

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Diphasiastrum				
Diphasiastrum* (*Lycopodium*) *alpinum	Basid[×]	✓	✓	62
"	Glom	✓	✓	62, 63
"	NS	✓	✓	60, 64
Diphasiastrum complanatum	NS		✓	65
Diphasiastrum digitatum (*Lycopodium digitatum/L. flabelliforme*)	Glom		✓	66, 67
Diphasiastrum issleri	Glom		✓	63
Diphasiastrum (*Lycopodium*) *thyoides*	DSE		✓	68
Diphasiastrum (*Lycopodium*) *tristachyum*	Glom		✓	67
Huperzia				
Huperzia appressa	NS	✓		60
Huperzia australiana	NS	✓		60
"	Glom		✓	69
Huperzia lucidula	NS	✓		60
Huperzia* (*Lycopodium*) *selago	NS	✓		60
"	DSE		✓	64
"	Glom		✓	63, 70
Huperzia serrata	NS		✓	71
"	Glom		✓	70
Huperzia serrata var. *longipetiolata*	NS		✓	65
Huperzia sp.	NS		✓	71
Lateristachys				
Lateristachys (*Lycopodiella*) *lateralis*	Mucoro	✓		60
Lycopodiastrum				
Lycopodiastrum casuarinoides	NS		✓	65
Lycopodiella				
Lycopodiella inundata	Mucoro	✓	✓	60, 72
"	Glom		✓	63, 73
Lycopodium				
Lycopodium clavatum	NS	✓	✓	60, 70
"	DSE		✓	64, 74
"	Glom	✓	✓	63, 75–77
"	Mucoro?		✓	76
Lycopodium clavatum subsp. *contiguum*	Glom	✓		77
Lycopodium japonicum	Glom		✓	65
Palhinhaea				
***Palhinhaea cernua* (*Lycopodiella cernua/Lycopodium cernuum*)**	Glom	✓	✓	60, 71, 78–80
"	NS		✓	65, 74
"	Mucoro		✓	78
Phlegmariurus				
Phlegmariurus (*Huperzia*) *affinis*	Glom	✓		77
Phlegmariurus (*Huperzia*) *crassus*	Glom	✓		77
Phlegmariurus (*Huperzia*) *hamiltonii*	Glom		✓	75
Phlegmariurus henryi	NS		✓	65
Phlegmariurus hypogaeus (*Huperzia hypogaea*)	Glom	✓	✓	77
Phlegmariurus phlegmaria (*Huperzia phlegmaria/Lycopodium phlegmaria*)	NS	✓		60
Phlegmariurus phyllanthus (*Huperzia phyllantha*)	Glom		✓	79
Phlegmariurus squarrosus (*Huperzia squarrosa*)	Glom		✓	74
Phlegmariurus tetragonus (*Huperzia tetragona*)	Glom	✓		77
Phlegmariurus urbani (*Huperzia urbanii*)	Glom	✓		77
Pseudodiphasium				
Pseudodiphasium (*Lycopodium*) *volubile*	NS	✓		60
Spinulum				
Spinulum* (*Lycopodium*) *annotinum	Mucoro	✓		60
"	Glom		✓	63
Isoëtales				
Isoëtaceae				
Isoëtes				
Isoëtes coromandelina	Glom		✓	81
Isoëtes echinospora	DSE, Glom		✓	82
"	NS		✓	63
Isoëtes histrix	NS		✓	63
Isoëtes lacustris	DSE, Glom		✓	82
"	NS		✓	63
Selaginellales				
Selaginallaceae				
Selaginella				
Selaginella arbuscula	Glom		✓	79
Selaginella biformis	Glom		✓	65
Selaginella bryopteris	Glom		✓	75

Table 1 (continued)

Species	Fungi	DNA	Microscopy	Reference
Selaginella cataphracta	NS		✓	74
Selaginella chrysocaulos	NS		✓	65
Selaginella davidii	Glom		✓	65, 83
Selaginella delicatula	Glom		✓	65
Selaginella doederleinii	DSE, Glom		✓	75
Selaginella finitima	DSE, Glom		✓	84
Selaginella fissidentoides	DSE, Glom		✓	74
Selaginella frondosa	Glom		✓	65
Selaginella furcillifolia	Glom		✓	71
Selaginella helferi	NS		✓	65
Selaginella intermedia	Glom		✓	71
Selaginella involvens	Glom		✓	65
Selaginella kraussiana	Glom	✓	✓	60, 63
Selaginella mairei	Glom		✓	85
Selaginella martensii	Glom		✓	84
Selaginella minutifolia	Glom		✓	71
Selaginella moellendorffii	Glom		✓	83
Selaginella monospora	NS		✓	65
Selaginella obtusa	Glom		✓	74
Selaginella pallescens	DSE, Glom		✓	68
Selaginella pennata	NS	✓		60
Selaginella picta	Glom		✓	65
Selaginella plana	Glom		✓	71
Selaginella pulvinata	Glom		✓	65, 85
Selaginella remotifolia	Glom		✓	65
Selaginella roxburghii var. *strigosa*	Glom		✓	71
Selaginella sanguinolenta	Glom		✓	65
Selaginella selaginoides	Glom	✓	✓	60, 63
Selaginella sp.	DSE, Glom		✓	75
Selaginella sp.	Glom		✓	80
Selaginella stipulata	Glom		✓	71
Selaginella wightii	Glom		✓	80
Selaginella willdenowii	NS		✓	71

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with a few exceptions where additional considerations were included in our calculations to improve the quality of our estimates:

1) Aneuraceae—This Metzgeriidae family is the most species-rich of the simple thalloid liverworts. Colonization by Basidiomycota is common in the species-poor, early-diverging genera *Aneura*, *Lobatiriccardia* and *Verdoornia* (Rabeau et al. 2017) but less so in the largest, more derived genus *Riccardia* (Pressel et al. 2010). To avoid a considerable overestimation of symbiosis by Basidiomycota in Metzgeriidae, our calculations of fungal symbiosis occurrence rates in Aneuraceae were based on the assumption that 50% of *Riccardia* species can be colonized by Basidiomycota, i.e. the ratio of symbiotic vs. non-symbiotic *Riccardia* species found by our survey (Table 1) plus our own observations on freshly collected specimens of a range of *Riccardia* species.
2) Plagiochilaceae—This is the most speciose family in the Jungermanniales with 767 species in ten genera; however, fungal symbiosis has only been reported in the four-species genus *Pedinophyllum*. For calculations, we considered *Pedinophyllum* to be the only Plagiochilaceae genus (Feldberg et al. 2010) that can be colonized by symbiotic Basidiomycota and the rest were considered non-symbiotic. Re-enforcing this assumption is that fact that neither Schuster (1980) nor Paton (1999) mention fungi other than in *Pedinophyllum*, and we have never seen them in fresh specimens of over 50 species in the family.
3) Gymnomitriaceae—This relatively speciose family (97 species) of nine genera contains only one genus (*Nardia*) for which fungal symbiosis has been reported, and the rest are non-symbiotic; thus, for calculations, we considered *Nardia* to be the only symbiotic genus in Gymnomitriaceae. As for the Plagiochilaceae, we have never seen fungi in freshly collected specimens other than in *Nardia*. The Gymnomitriaceae predominantly grow on bare rock, a substrate ill-suited to fungal symbioses.
4) Jungermanniaceae—Fungal symbiosis has only been reported in *Eremonotus*, a single species genus (Bidartondo and Duckett 2010). All the other members of this family (37 species) that have been investigated (Paton 1999; Pocock and Duckett 1985; Schuster 1969) do not enter into fungal symbiosis, so only *Eremonotus* was considered to be symbiotic in our calculations.

Numbers of species per genus/family are given in Table S1.

Inferring fungal symbiosis status

Fungal symbiosis status was mapped onto a representative phylogenetic diagram that contained all the plant families included in this survey with the relative positions of the plant families based on previously published phylogenies for the following plant groups: Haplomitriopsida and Marchantiopsida (Flores et al. 2017), Pelliidae and Metzgeriidae (Masuzaki et al. 2010), Jungermanniidae (Forrest et al. 2006; Shaw et al. 2015; Patzak et al. 2016), hornworts (Villarreal and Renner 2013) and lycophytes (PPG1 2016).

Results and discussion

Plant species numbers

The fungal symbiosis status of up to 648 liverwort, hornwort and lycophyte species, belonging to 194 genera, 82 families and 23 orders, was compiled (Table 1) by combining data from 84 publications. The number of species for each of these early-diverging plant groups and the fungal lineages that colonize them are listed in Table 2. The total value, 648 species, includes seven subspecies and 53 samples identified only to the genus level (sp.) that may represent duplicates (except when they are the only entry for that genus, e.g. *Lepidogyna* sp.). Thus, at least 591 species are included in our survey (Table 2). This represents a considerable increase on the number of early-diverging plant species, 180, included in Wang and Qiu's survey (Wang and Qiu 2006). The hornworts and lycophytes are well represented; our survey includes members of every hornwort and lycophyte family and of most genera except for one hornwort and four lycophyte genera (Table 1). The liverworts are less well represented; this is because of their higher diversity, comprising over twenty times the number of genera found in hornworts or lycophytes. While

Table 2 The numbers of early-diverging plant species for which fungal symbiosis status has been reported. M - Mucoromycotina, G - Glomeromycotina, B - Basidiomycota, A - Ascomycota, FA - Fungal association. Where reports were contradictory (symbiotic and non-symbiotic), the symbiotic report is included. The number between parentheses represents the maximum number of different species, reflecting that some species were identified as 'sp.' so could represent duplicates of fully identified species

	Total	M	G	B	A	FA
Liverworts	491 (538)					
Haplomitriopsida	12	9	1	0	0	2
Haplomitriidae	8	6	1	0	0	1
Treubiidae	4	3	0	0	0	1
Marchantiopsida	88 (98)	14 (16)	33 (36)	0	0	4 (7)
Blasiidae	2	0	0	0	0	0
Marchantiidae	86 (96)	14 (16)	33 (36)	0	0	4 (7)
Jungermanniopsida	391 (428)	19 (20)	40 (41)	65 (70)	59 (64)	56 (58)
Pelliidae	48 (52)	19 (20)	40 (41)	0	0	0 (2)
Metzgeriidae	52 (56)	0	0	16 (20)	0	12
Jungermanniidae	291 (320)	0	0	49 (50)	59 (64)	44
Hornworts	27 (33)					
Anthocerotopsida	26 (32)	15 (21)	14 (19)	0	0	0
Anthocerotidae	7 (9)	6 (8)	5 (7)	0	0	0
Dendrocerotidae	12 (14)	5 (7)	4 (6)	0	0	1
Notothylatidae	7 (9)	4 (6)	5 (6)	0	0	0
Leiosporocerotopsida	1	0	0	0	0	0
Lycophytes	73 (77)					
Lycopodiopsida	73 (77)	6	53 (55)	1	0	0
Lycopodiales	35 (37)	6	22	1	0	0
Isoëtales	4	0	3	0	0	0
Selaginellales	34 (36)	0	28 (30)	0	0	0

coverage for liverworts is robust at the family level and includes 72 of the 87 families (Söderström et al. 2016), this is less so at the genus level where the fungal status of 217 of the 386 genera is currently unknown. However, early-diverging lineages are well represented at the genus level with only one Haplomitriopsida, one Marchantiopsida and five Pelliidae genera not included in Table 1. The remaining 210 genera with unknown fungal symbiosis status are members of the Metzgeriidae and Jungermanniidae. This reflects a research bias, as most studies have focused on species from known symbiotic clades (e.g. 24% of Pelliidae species and 17% of Marchantiopsida species have been investigated) while neglecting those from clades considered to be largely asymbiotic. Indeed, only 5% of Jungermanniidae species have been investigated to date, reflecting that the Lejeuneaceae, the most speciose Jungermanniidae family with ca. 2000 species, is asymbiotic (Kowal et al. 2018).

Since the survey by Wang and Qiu was published in 2006, the use of DNA sequencing to identify plant fungal symbionts has increased dramatically. To date, the fungal status of 259 fully named early-diverging plant species has been analysed by molecular methods versus only six reported in Wang and Qiu (2006).

Our survey unveiled contradictory reports on the fungal symbiotic status (symbiotic vs. non-symbiotic) of 51 species (42 liverworts, one hornwort and eight lycophytes) probably reflecting low fungal colonization levels (Rimington et al. 2015), habitat type and/or seasonal variation in colonization (personal observations) in these species. Colonization by two fungal lineages has been reported in 51 species (35 liverworts, 11 hornworts and 5 lycophytes). We found no report of more than two fungal lineages colonizing the same plant species. All dual colonisations involve either members of Mucoromycotina and Glomeromycotina (Mucoromycota) or Ascomycota and Basidiomycota (Dikarya), with the former (45 species) being more common than the latter (5 species).

Estimating symbiosis occurrence rates

Our estimates of fungal symbiosis occurrence rates for the different fungal lineages in liverworts, hornworts and lycophytes show that fungal symbiosis appears to be the norm in hornworts and lycophytes, but not in liverworts (Table 3). Occurrence rates were easier to estimate for hornworts and lycophytes than for liverworts, as these two groups contain less species and engage in less diverse symbioses than liverworts. We estimated that 69% of hornwort species can be colonized by Mucoromycotina fungi and 78% by Glomeromycotina (Table 3). In lycophytes, colonization by Glomeromycotina is higher than by Mucoromycotina; 99% of lycophyte species can potentially form AM while only 4% are estimated to be symbiotic with Mucoromycotina

Table 3 Fungal symbiosis occurrence rate estimates

	Mucoromycotina	Glomeromycotina	Basidiomycota	Ascomycota
Liverworts	4%	5%	7%	17%
Haplomitriopsida	100%	0	0	0
Marchantiopsida	22%	38%	0	0
Jungermanniopsida				
Pelliidae	97%	99%	0	0
Metzgeriidae	0	0	44%	0
Jungermanniidae	0	0	5%	20%
Hornworts	69%	78%	0	0
Lycophytes	4%	99%	0	0

(Table 3). The fungal status of each hornwort and lycophyte genus is found in Table S1.

Our estimates of fungal symbiosis occurrence rates in liverworts had to be calculated at the family, rather than genus, level (except for four families, as explained previously) because this group contains many more genera (ca. 386) than hornworts and lycophytes (12 and 18 genera, respectively) and the fungal symbiosis status of less than half (169) of these genera is currently known. However, the fungal symbiotic status of most liverwort families has been reported, with that of only 15 out of 87 families remaining unassigned. These 15 families all have low species numbers: less than ten species except for one family. Thus, the fungal symbiosis status of liverworts is well represented at the family level (Table S1).

We estimated that only 4% and 5% of liverwort species are colonized by Mucoromycotina and Glomeromycotina, respectively (Table 3). Symbioses involving Basidiomycota (7%) and Ascomycota (17%) appear to be more common in liverworts but an absence of fungal symbiosis is by far the prevalent state (71%). The sum of these estimates is greater than 100% due to several liverwort species forming dual colonization with both Mucoromycotina and Glomeromycotina. Below we consider the major liverwort groups individually:

Haplomitriopsida—Up to 100% of these earliest-diverging liverworts can be colonized by Mucoromycotina fungi. There has been a single molecular report of Glomeromycotina symbiosis in *Haplomitrium chilensis* (Ligrone et al. 2007); however this report was published prior to the discovery of Mucoromycotina colonization in liverworts and has since been questioned by several molecular investigations (Bidartondo et al. 2011; Field et al. 2015; Rimington et al. 2018). Presence of Mucoromycotina and not Glomeromycotina in Haplomitriopsida liverworts also agrees with the cytology of the fungus colonizing *H. chilensis* (Ligrone et al. 2007), which we now know to be typical of Mucoromycotina and not Glomeromycotina symbioses (e.g. Field et al. 2015). We have not included in our analyses a recent study by Yamamoto et al. (2019) reporting rare Glomeromycotina associations in *Haplomitrium mnioides* from Japan, with Mucoromycotina being dominant, because the lack of anatomical details (i.e. sections of colonized axes and electron microscopy) and the limited molecular analyses presented indicate that further, more rigorous studies of this species may be required.

Marchantiopsida—These are the earliest-diverging liverworts to form Glomeromycotina symbioses; however, fungal colonization is relatively low and 22% and 38% of Marchantiopsida liverworts are estimated to be colonized by Mucoromycotina and Glomeromycotina, respectively. These results are skewed by the absence of symbionts from the most speciose Marchantiopsida family, Ricciaceae (Table S1), where both terrestrial and aquatic taxa lack symbionts. When Ricciaceae is excluded from calculations, the colonization estimates increase to 43% for Mucoromycotina and 74% for Glomeromycotina.

Pelliidae—This is the latest-diverging liverwort group to form Mucoromycotina and Glomeromycotina symbioses, and colonization is common at 97% and 99%, respectively.

Metzgeriidae—Basidiomycota colonization is estimated to occur in 44% of Metzgeriidae liverworts. If no assumption of 50% colonization in *Riccardia* species was applied to our calculations (see exception 1 in 'Methods'), then this estimate would increase to 75%.

Jungermanniidae—Ascomycota and Basidiomycota have only been reported in the Jungermanniales and are not present in the Porellales or Ptilidiales. Our calculations suggest that 5% of Jungermanniidae species can be colonized by Basidiomycota while 20% can be colonized by Ascomycota.

Our occurrence rate estimations for Glomeromycotina colonization in early-diverging land plants disagree with those published previously by Brundrett (2009), except for lycophytes. For the latter, our results agree with 100% colonization (Brundrett 2009) (Table 3). For hornworts, our estimate of 78% is lower than the previous one of 100% (Brundrett 2009), although it confirms that colonization by Glomeromycotina in hornworts in common. The most striking discrepancy is between our finding that only 5% of liverworts likely form arbuscular mycorrhizal-like associations and the

60% estimate by Brundrett (2009). Furthermore, our results indicate that previous estimates for the formation of any type of fungal symbiosis in bryophytes have also been excessive. Wang and Qiu (2006) estimated that 46% of bryophytes enter into symbiosis with fungi, whereas Brundrett and Tedersoo (2018) put this value at 25%, while also stating that in bryophytes the majority of these relationships involve Glomeromycotina fungi. In our study, after accounting for the ca. 13,000 non-symbiotic moss species, we estimate that only 11% of bryophytes enter into a symbiosis with fungi and that the most widespread symbiosis is with Ascomycota (53%) rather than Glomeromycotina (33%). The large number of species in Lepidoziaceae, within Jungermanniidae (751 species), is principally responsible for the Ascomycota occurrence rate estimate being higher than that of the other fungal lineages combined. Even though our fungal symbiosis occurrence rates are considerably lower than previously published ones, they too may represent overestimates since our calculations are based on the assumption that all members of a plant genus (or family for liverworts) can be colonized by a fungal lineage if at least one member of the genus (or family) is colonized by that lineage. While efforts were made to prevent overestimation in four liverwort families where an absence of symbiosis is common (Aneuraceae, Gymnomitriaceae, Jungermanniaceae and Plagiochilaceae), more data are needed to determine which families are fully symbiotic and for which symbiosis is more variable.

Another important consideration in these estimations is the symbiotic status of the fungi colonizing plants. All lineages of Mucoromycotina related to the Endogonales and Glomeromycotina are considered to be mycorrhizal-like when in association with early-diverging plants (Rimington et al. 2015; Field et al. 2016a, b). This is however not the case for Ascomycota and Basidiomycota, which are far more diverse than Mucoromycotina and Glomeromycotina and regularly colonize these plants as commensals or parasites (Davis and Shaw 2008). The structures formed by Ascomycota and Basidiomycota while colonizing early-diverging plants are not necessarily diagnostic of mutualisms, and thus, it is difficult to infer mutualistic, commensal or parasitic relationships based on morphology alone (Pressel et al. 2010). Therefore, morphological observations of Basidiomycota in Metzgeriidae and Ascomycota and Basidiomycota in Jungermanniidae may not necessarily reflect mycorrhizal-like relationships. An additional complication is that, at present, *Hyaloscypha* (*Pezoloma, Rhizoscyphus*) *ericae* is the only Ascomycota species for which mutualistic nutrient exchange with liverworts has been confirmed (Kowal et al. 2018); thus, reports of colonization by Ascomycota that have not been identified as *H. ericae* using DNA sequencing may not represent mutualisms. For Basidiomycota, so far only *Tulasnella* and *Serendipita* (*Sebacina*) have been reported as genera symbiotic with liverworts (Bidartondo and Duckett 2010); however, both associations await physiological tests for exchange between partners. It follows that colonization of liverworts by mycorrhizal-like Ascomycota and Basidiomycota may have been overestimated and efforts are now required to identify molecularly the fungal symbionts of these plants as well as testing for nutrient exchange.

In contrast, Mucoromycotina occurrence rates are likely underestimates, especially for lycophytes. Traditionally, the unique structures of Glomeromycotina, in particular the arbuscules, made them easily and accurately identifiable through microscopy (Smith and Read 2008). However, the recent discovery of endosymbiotic Mucoromycotina, which cannot be distinguished from Glomeromycotina cytologically (Desirò et al. 2013; Field et al. 2016a, b) together with a report that arbuscule-forming fine root endophytes may be members of the Mucoromycotina (Orchard et al. 2017), indicates that Mucoromycotina symbionts have likely been misidentified as Glomeromycotina on a number of occasions (Field et al. 2019). It is possible, therefore, that some of the reports of Glomeromycotina symbioses in Table 1 are actually incorrect, although, at present, it is not possible to determine if and how these potential misidentifications might have influenced our occurrence rate estimations.

These caveats aside, our estimates can still be considered the best fungal symbiosis occurrence rates to date for early-diverging plants. While those for early-diverging liverworts are based on fairly comprehensive information and are unlikely to change with additional data, those for later-diverging groups are likely to improve as more data become available for these plants.

Inferring gains and losses of symbiosis

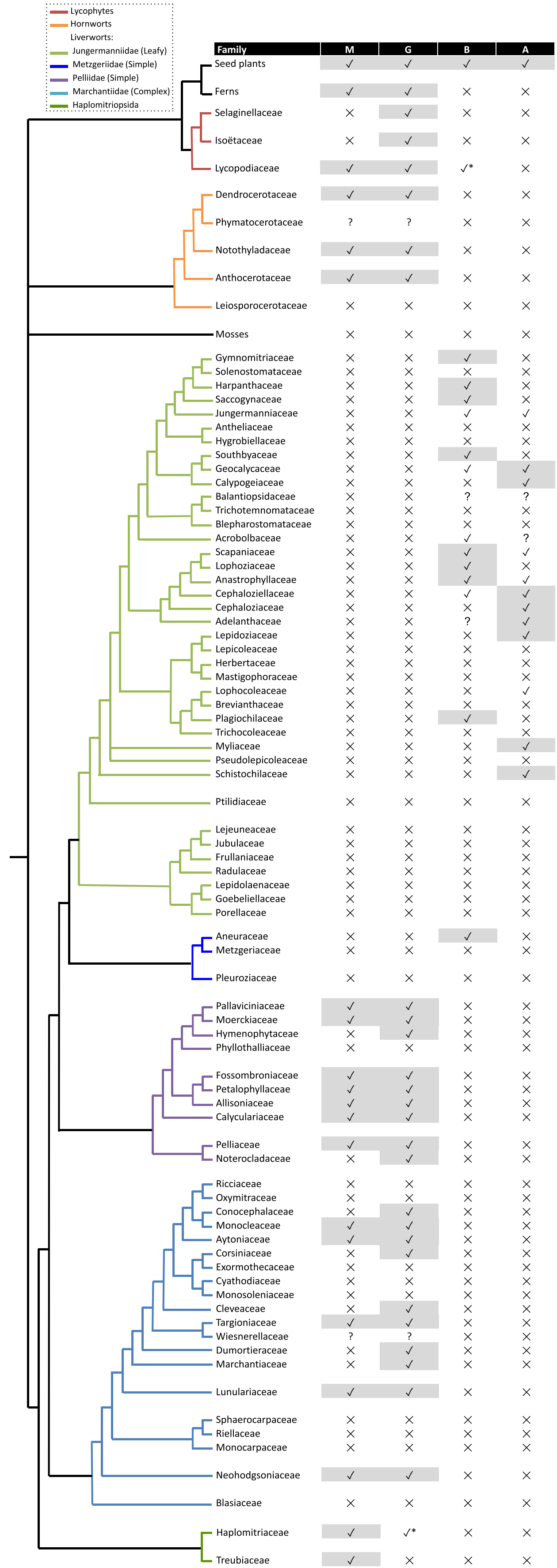
The gains and losses of fungal symbiosis during the evolutionary history of the early-diverging plant families included in Table 1 have been inferred (Fig. 1). These are discussed below:

Liverworts—The liverworts have had a more diverse history of losses and gains of symbiosis than the hornworts and lycophytes. Mucoromycotina likely formed the ancestral symbiosis with liverworts and appear to have been maintained as the sole symbionts in the Haplomitriopsida (Rimington et al. 2019). There have been losses of Mucoromycotina symbiosis in Marchantiopsida liverworts during the divergence of the Blasiales, Sphaerocarpales and Marchantiales. In the Marchantiales, symbiosis has been regained in three families, Monocleaceae, Aytoniaceae and Targioniaceae. In Pelliidae, Mucoromycotina symbiosis has been maintained in all families except four (Hymenophytaceae, Phyllothalliaceae, Petallophyllaceaeand Noterocladaceae). Conversely, Glomeromycotina symbiosis likely had a single origin in liverworts after the divergence of the Haplomitriopsida, followed by several losses in the Marchantiopsida, from

Sphaerocarpales and six families of the Marchantiales, but only one loss in the Pelliidae, from the Phyllothalliaceae. After the divergence of the Pelliidae, there was a complete loss of both Mucoromycotina and Glomeromycotina symbioses in liverworts. Basidiomycota and Ascomycota symbioses appear to have been gained and lost multiple times during the evolution of the Metzgeriidae and Jungermanniidae. In the Metzgeriidae, there was a single gain of Basidiomycota symbiosis within the Aneuraceae and a subsequent loss from a large number of the later-diverging *Riccardia* species (Rabeau et al. 2017). Because the fungal symbiosis status of many Jungermanniidae families remains unresolved, it is not yet possible to accurately estimate gains and losses of Ascomycota and Basidiomycota symbioses in this subclass. Based on the better-studied families (highlighted in grey in Fig. 1), Ascomycota symbiosis appears to have evolved at least six times, with two major losses, while Basidiomycota symbiosis appears to have been gained on at least four occasions, with at least one loss. Alternatively, it is possible that Ascomycota and Basidiomycota symbioses had a single origin in the Jungermanniales followed by a large number of losses. Although this seems less likely, multiple losses of AM and rhizobia have been inferred in angiosperms, so until the fungal symbiosis status of these liverworts is fully resolved for all families, ancestral reconstruction will be of limited value to further our understanding of fungal associations in these plants.

Hornworts—Apart from some individual losses and apparent regains in certain hornwort species (Desirò et al. 2013), both Mucoromycotina and Glomeromycotina symbioses have been maintained throughout the Anthocerotopsida. Fungal symbiosis has never been recorded in the single species class Leiosporocerotopsida that contains the earliest-diverging extant hornwort *Leiosporoceros dussii*. *Leiosporoceros dussii* is notable not only for its lack of fungal symbiosis but also for its unique cyanobacterial symbiosis (Villarreal and Renzaglia 2006). With the order of divergence of the bryophytes under debate (Puttick et al. 2018), it is unknown whether Mucoromycotina and Glomeromycotina are both ancestral symbionts of all hornworts and were lost from Leiosporocerotopsida or whether these symbioses were gained in the hornworts only after Leiosporocerotopsida branched off. It also remains to be determined whether members of the Phymatocerotaceae are colonized by Mucoromycotina, Glomeromycotina or both fungi since the only record for this family is a report of 'a fungal association' (Stahl 1949); however, the regular colonization of the other Anthocerotopsida families by Mucoromycotina and Glomeromycotina suggests this family is also colonized by both fungal lineages.

Lycophytes—Phylogenetic inference (Fig. 1) and fossil evidence (Strullu-Derrien et al. 2014) both support that the ancestor of all vascular plants entered into symbiosis with



◀ **Fig. 1** The phylogenetic position and fungal symbiosis status of early-diverging plant families. Branch lengths have no value and only show how the families are currently considered to be related. Initials in the table denote: M Mucoromycotina, G Glomeromycotina, A Ascomycota, B Basidiomycota. A check indicates presence, a cross absence, and a question mark indicates an unknown identity reported only as 'fungal association'. Checks highlighted in grey are likely accurate reports and were used for occurrence rate estimations, whereas the mutualistic status of un-highlighted checks remains unknown (only relevant for Ascomycota and Basidiomycota symbioses in liverworts). An asterisk indicates a likely incorrect report of symbiosis

Mucoromycotina and Glomeromycotina. Within the lycophytes, there have only been losses of symbiosis and no subsequent gains. The loss of Mucoromycotina symbiosis appears to have occurred on a larger scale than that of Glomeromycotina symbiosis, with a major loss after the divergence of the Lycopodiaceae which resulted in Isoëtaceae and Selaginellaceae apparently being colonized only by Glomeromycotina. It should be noted however that no fungal molecular data have been generated from Isoëtaceae and all microscopy reports predate the discovery of Mucoromycotina in lycophytes; therefore a symbiosis with Mucoromycotina cannot be ruled out. Additionally, only three of the 688 Selaginellaceae species have been analysed molecularly (Rimington et al. 2015); therefore, this family may also enter into symbiosis with Mucoromycotina as well as Glomeromycotina. There have also been losses of Mucoromycotina symbiosis within the Lycopodiaceae and the subfamily Huperzoideae is only colonized by Glomeromycotina. Within the subfamily Lycopodioideae there appears to have been a complete loss of symbiosis in the *Lycopodiastrum-Pseudolycopodium-Austrolycopodium-Dendrolycopodium-Diphasium* clade (Field et al. 2016a). The low levels of colonization of lycophytes by symbiotic fungi and the evolution of non-symbiotic species suggest that these plants may have a low dependence on their mycorrhizal partners when mature (Rimington et al. 2015). On the other hand, the gametophytes of lycophytes are often subterranean and achlorophyllous and therefore fully dependent on their symbiotic fungi for nutrition (Schmid and Oberwinkler 1993).

Identifying lycophyte fungal symbionts

The identity of the fungi that enter into symbiosis with lycophytes and the extent of these symbioses remain poorly resolved. While the available evidence indicates that only Mucoromycotina and Glomeromycotina colonize members of this lineage (Pressel et al. 2016), more work is needed to confirm this and to determine which symbionts dominate in nature (Lehnert et al. 2017). Symbiosis with Glomeromycotina has been reported more frequently than with Mucoromycotina (53 species vs. 6); however, most of these reports precede the discovery of Mucoromycotina-plant symbiosis and also lack molecular identification. Indeed, a recent molecular survey found a smaller difference in incidence of colonization between the two fungal lineages, albeit with Glomeromycotina also being the dominant type (Rimington et al. 2015). There has only been one report of colonization by Basidiomycota in lycophytes (Horn et al. 2013). However, because of a lack of electron microscopy evidence and of molecular methods suitable for detecting Mucoromycotina in this report, and as it contradicts all previous and subsequent reports (Table 1), its conclusion has been called into doubt. Reassessing the published images in Horn et al. (2013), Strullu-Derrien et al. (2014) proposed that the colonizing fungus more likely belongs to Mucoromycotina than Basidiomycota. Dark-septate endophytes (DSE) are Ascomycota fungi (Pressel et al. 2016) and so far have been recorded in ten lycophyte species from all three lycophyte families. However, there is no evidence that DSE may form mutualistic associations with lycophytes (Pressel et al. 2016). Thus, at present, only Glomeromycotina and Mucoromycotina can be considered mycorrhizal partners of this early-divergent vascular plant lineage.

Conclusions

In concluding their seminal work, Wang and Qiu (2006) highlighted that 'more basal land plants should be investigated, as they occupy an especially important position in our understanding of the origin of mycorrhizal symbiosis'. In the subsequent 13 years considerable effort has gone into addressing some of these gaps in knowledge so that the fungal symbiosis status of more than three times the number of early-diverging species reported in Wang and Qiu is now known. Nevertheless, further research is still required as to date only 6% of liverwort, 13% of hornwort and 5% of lycophyte species have been examined. Within liverworts, our survey highlights Jungermanniidae as the group in most need of further investigation. Lycophytes also require further investigation; it is likely that estimates of the occurrence of Mucoromycotina symbiosis in this lineage will increase with additional use of molecular methods.

Compiling this survey of fungal symbioses in early-diverging plants has highlighted the importance of both DNA sequencing and microscopy for determining the identity of plant fungal symbionts. Microscopy alone is not enough to identify fungi unless they display truly diagnostic characteristics; DNA sequencing allows us to determine fungal presence, but not whether this represents a symbiosis. Combining these two complementary methods is essential to fully understand the distribution and diversity of fungal symbiosis in plants, while physiological studies of resource exchange between partners are needed to assess whether the plant-fungus association is functionally mycorrhizal or mycorrhizal-like.

Acknowledgments WRR was supported by the NERC Doctoral Training Programme (Science and Solutions for a Changing Planet).

Author contributions WRR, JGD, MIB and SP conceived the study; WRR, JGD and SP compiled and examined data; WRR carried out analysis and wrote the first draft, and all authors contributed to the manuscript. We thank the editor and two reviewers for their comments.

Funding information We received support from NERC to KJF, SP (NE/N00941X/1) and MIB (NE/N009665/1). KJF is funded by a BBSRC Translational Fellowship (BB/M026825/1).

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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