

Origins of the terrestrial flora: A symbiosis with fungi?

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Abstract. Land phototrophs need to exploit both atmosphere (providing gas and light) and substrate (furnishing water and minerals). Yet, their algal ancestors were poorly pre-adapted to such a life at the interface. We review the paleontological evidence that fungal symbioses which can exploit substrate resources, helped adaptation to land constraints. Diverse structures dating back to the Devonian present convincing evidence for lichens, (symbioses between fungi and microscopic algae) but fossils remain scarce, so that early lichen abundance and ecological relevance remain questionable. Several enigmatic but abundant fossils from the Siluro-Devonian, such as *Spongiophyton* or the giant *Prototaxites* (Nematophytes), likely represent fungus-algal symbioses, which shaped early terrestrial ecosystems. Yet, these taxa are fully extinct, and do not have clear affinities with extant groups. Finally, terrestrialization of Embryophyta (land plants), which currently dominate land ecosystems, is linked to a symbiosis with Glomeromycetes. Today, these fungi form arbuscular mycorrhizae, which help most Embryophyta to exploit soil, and molecular data combined with paleontological evidence support the idea that this type of association is ancestral. The role of symbiotic Mucoromycetes during terrestrialization is not fully understood and mycorrhizal association diversified later in the evolution of Embryophyta. Fungal-algal symbioses thus recurrently contributed to terrestrialization of phototrophs.

1. Introduction: Waiting for colonization

Terrestrial ecosystems currently comprise an abundant biomass of phototrophic plants, dominated by Embryophyta which range from liverworts, hornworts and bryophytes to vascular plants, such as lycopods, ferns, gymnosperms and dominant angiosperms (Fig. 1). Beyond these, multicellular complex phototrophs, many morphologically simple, unicellular or filamentous algal lineages also occur in terrestrial ecosystems. Most of these lineages belong to green algae (e.g. Trebouxiophyta or Trentepohliophyta) and cyanobacteria, and are either free-living or forming- lichen symbioses with fungi [1]. But how did such a diverse phototrophic flora arise?

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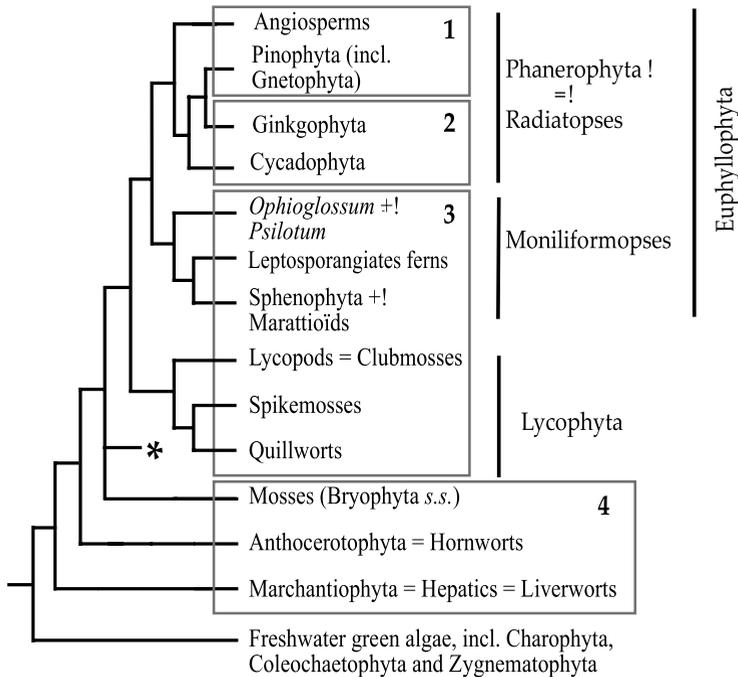


Figure 1. A rooted phylogenetic tree of Embryophyta (numbers indicate paraphyletic groups: 1, Spermatophyta; 2, Presperma(to)phyta; 3, Pteridophyta; 4, Bryophyta *lato sensu*). The asterisk indicates the putative position of two fossil taxa from the Rhyne Chert mentioned in the text, *Aglaophyton* and *Horneophyton*.

1.1 From water to life at the interface between air and substrate

All these phototropic lineages have aquatic algal ancestors (Fig. 1), mostly from freshwater as shown by the current ecology of their closest relatives, with the possible exception of the Trentepohliophyta, filamentous green algae which likely arose from marine ancestors [1]. Obviously, algae are pre-adapted to collect gas and light from the atmospheric environment, exactly as they do in water: in both environments, they are able to exploit the fluids surrounding them. However, phototrophs face two problems on land: the first one is desiccation, since air is often not saturated in water vapour; the second is the location of water and mineral nutrients which are not available in the surrounding fluids, but embedded within the rocky (or soil) substrate (Fig. 2).

In other words, whereas aquatic algae can live fully in water, terrestrial phototrophs have to live, functionally, **at the interface** between air and substrate (with the exception of the microbial communities, which use dust and aerosols to fulfil their needs, but this remains a marginal niche with low productivity). Terrestrialization is thus the gain of ability to live at the interface, because algae commonly use substrates for fixation and never for nutrition.

There are two main strategies for living at the interface. The first is rather microbial: due to their small size, phototrophic microbes can find a place at the exact interface, on the substrate or within crevasses of limited depth which allow them to access light. The resulting colonization by multiple other microbes, including heterotrophs that feed on phototrophs, creates a complex microbial community called a biofilm. Such biofilms currently exist in land ecosystems, especially in early successional stages, and in any place where slope and erosion prevent the formation of a thicker soil (e.g. on cliffs). Although such biofilms are not easily fossilized, there is some evidence showing that land was once dominated by them [2, 3]. In addition the matrix surrounding microbial cells in such biofilms might have acted as a

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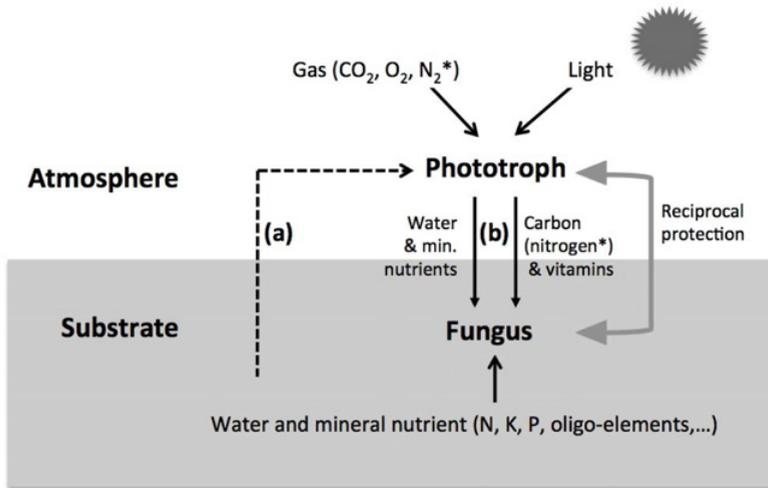


Figure 2. Compartmentalization of resources for phototrophs in land ecosystems. The asterisk (*) indicates resources exploited or provided by N-fixing cyanobacteria only. The non-symbiotic exploitation of substrate resources (a) is used by some phototrophs and entails poikilohydry, while many terrestrial algae and most plants (Embryophyta) currently use the symbiotic association with a fungus (b) which, thanks to lichen or mycorrhizal formation, contributes to homoiohydricity.

protection against UV rays before the rise of a protective ozone layer (see below). Indeed, such biofilms and their productivity may have supported the terrestrialization of myriapods, as early as during the mid-Ordovician [4].

1.2 When symbiotic phototrophs replaced biofilms

Nowadays the land flora is dominated by large multicellular plants, which themselves support a fauna made of much larger animals than during the early colonisation of land. Embryophyta have the ability to harvest water and mineral nutrients from deeper layers of the substrate thanks to the development of underground organs. As a result of better and more continuous access to water and mineral nutrients, they have developed larger gas- and light-harvesting systems in their atmospheric compartments, namely shoots and leaves, since desiccation here can be compensated by increased water flow. While biofilms usually **tolerate** desiccation and consequently the loss of mineral nutrition (poikilohydric strategy), most Embryophyta tend to **avoid** this (homoiohydric strategy). Currently, these are two extremes in a continuum: among Embryophyta, the mosses (Bryophyta) tend to have a low exploitation of the substrate and are rather poikilohydric; the other groups (Tracheophyta), as a result of a more efficient exploitation of the two compartments, are homoiohydric and develop higher biomass and productivity under favourable conditions. An intermediate strategy is displayed by lichen algae: although microbial terrestrial algae are mostly poikilohydric, the association of an algae with a filamentous fungus allows better recruitment of mineral and water resources in the substrate.

As stated above, algal ancestors were poorly adapted to exploit the substrate. Moreover, the earliest traces of land plants date back to 470 million of years (Myrs) ago, and are only known from spores and debris [5]. Later only, and caused by falling sea-level on a global scale, major changes occurred in sedimentation and fossilization resulting in the development of more terrestrial deposits which preserved early Embryophyta megafossils [6]. One can be surprised by such a late rise of the terrestrial multicellular flora: indeed, land ecosystems were already open to colonization for a long time, and the

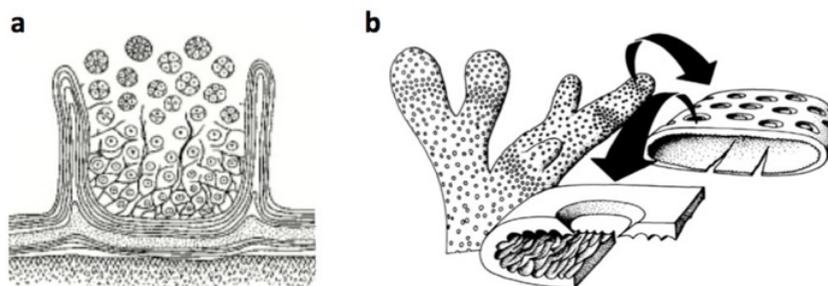


Figure 3. Reconstruction of two Siluro-Devonian lichens. (a) Portion of a *Winfrenatia reticulata* thallus with depression filed with cyanobacterial cells [15]. (b) *Spongiophyton nanum* thallus, a putative lichen [18].

ozone layer was already developed at that time [7], allowing terrestrialization that was previously limited by UV rays.

This text supports the claim that adaptation to terrestrialization of most phototrophs, beyond the ancient biofilms, was enabled by a fungus-algal symbiosis. Our hypothesis is that terrestrialization did not proceed beyond biofilms until a symbiosis was established with fungi, whose mycelium is finely adapted to explore three-dimensional substrates such as the terrestrial substrate (Fig. 2). Moreover, the carbon cost of supporting hyphae is lower than that of building thick roots. Once the association arose, it opened the colonization of many niches. Thus, phototrophs' terrestrialization would essentially be a matter of symbiosis between fungi and phototrophs [8, 9]. Updating previous reviews [10, 11], we successively explore how this hypothesis explains (i) the adaptation of some microalgae to the terrestrial environment, (ii) some enigmatic fossils, and (iii) the late rise of Embryophyta and their further evolution.

2. Were lichen the first players of terrestrialization?

Nowadays, beyond the biofilm stage during substrate colonization, lichens are very efficient colonizers. The exploitation of the substrate and anchoring ability of the fungus adds up to the photosynthetic ability of the algae to develop a certain level of homoiohydricity; moreover, the structure of the thallus and the secondary metabolites (the so-called lichen substances [12]) formed by the association protect the partners from grazing as well as excessive light and UV. Thus, one can imagine that lichens were pioneering phototrophic forms in land ecosystems: but what is the paleontological evidence for this?

2.1 Fossil lichens

There are very few fossil lichens described so far. Some Ediacaran organisms described as lichens, by G. Retallack [13] are highly controversial, mainly due to the palaeo-environment where such fossils were supposed to live and the absence of structural evidence. Other possible Precambrian lichens encompass a South China fossil dated <551 Ma, which mixes filaments and cyanobacterial- or algal-like cells and is considered to have colonized a subtidal environment [14]. The occurrence of lichens reported from Siluro-Devonian terrestrial environments is far more convincing. First, *Winfrenatia reticulata* [15, 16] is an unusual algal-fungal structure with a thallus made of aseptate hyphae (= coenocytic), which forms depressions harbouring coccoid cyanobacteria (Fig. 3a), whereas in modern lichens, phototrophic algal cells are surrounded by a thick sheath of hyphae, and the fungi are septate (Table 1; the only exception is the likely recent *Geosiphon pyriforme*, in which a non-septate fungus harbours intracellular *Nostoc* [17]). *Winfrenatia reticulata* is reported from the Devonian Rhynie Chert (Scotland, ca. 407 Ma), a

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Table 1. Main fungal groups (Eumycetes) that display extant mutualistic associations with plants (septate hyphae are made of a succession of cells separated by septa, while non-septate hyphae are coenocytic). For a definition of paramycorrhizae, see Sect. 4.1; for main mycorrhizal types, see Fig. 5.

Name	Features	Main associations with phototrophs
Mucoromycetes	non-septate hyphae	Associate with liverworts, hornworts thalli, Lycophyta, and Filicophyta rhizomes and roots
Glomeromycetes	non-septate hyphae, obligatory biotrophic	Associate with roots (arbuscular mycorrhizae), or thalli and rhizome (paramycorrhizae) of most Embryophyta (except mosses), and rarely with intracellular cyanobacteria (<i>Geosiphon pyriforme</i>)
Ascomycetes	septate, ancestrally free-living (or perhaps lichenized, but this remains debated)	Some clades respectively associate with roots of several shrubs and trees (ectomycorrhizae), with Ericaceae and some Orchids (endomycorrhizae); some of the previous mycorrhizal fungi form paramycorrhizae in some liverworts; several clades form lichens (<i>ca.</i> 98% of lichens); many clades are also symptomless plant endophytes
Hymenomycetes (Basidiomycetes)	septate, ancestrally free-living (probably saprophytic)	Some clades respectively associate with roots of several shrubs and trees (ectomycorrhizae), some Ericaceae and Orchids (endomycorrhizae); some of the previous mycorrhizal fungi form paramycorrhizae in some liverworts; some clades form lichens (<i>ca.</i> 2% of lichens); many clades are also symptomless plant endophytes

well-known Lagerstätten (i.e., deposit with exceptional fossil preservation, whose strata have not been compressed or deformed later through geological time). In this chert, several early Embryophyta have also been described (see below); they evolved in the context of hot springs, which have allowed fast silicification and exquisite preservation.

Second, lichens displaying a more modern ultrastructure were recently described from the Late Silurian (415 Ma). In these organisms, outer fungal layers protect an internal layer of algae. *Cyanolichenomycites devonicus* and *Chlorolichenomycites salopensis* are lichens, nicely preserved in charcoal caused by fire, and they are considered to be associated respectively with cyanobacteria and green algae. These few fossils prove that phototrophic organisms forming lichens were already diverse by the Siluro-Devonian, but because their remains have been transported and preserved in fluvial deposits their precise environmental associations and ecology remain unknown.

2.2 Were true lichens important players?

The rather scarce evidence for fossil lichens can be explained in two non-exclusive ways. On the one hand, this may reflect the scarcity of lichenologists investigating the fossil record, and the low lichen biomass, which further limits the opportunity to find them. More study may unravel their diversity and ecological relevance in early land ecosystems. However, the analysis of fossils will never prove mutualism, and the differences among biotrophic algal parasites will always be difficult to assess. On the other hand, it may be that lichens were not at all major players during the early stages of terrestrialization, and indeed the Palaeozoic lichens are not older than the most ancient Embryophyta. It has also been suggested that lichenization may have been secondarily evolved in algal and cyanobacterial lineages [9, 10] after the Embryophyta colonized most terrestrial areas and partly

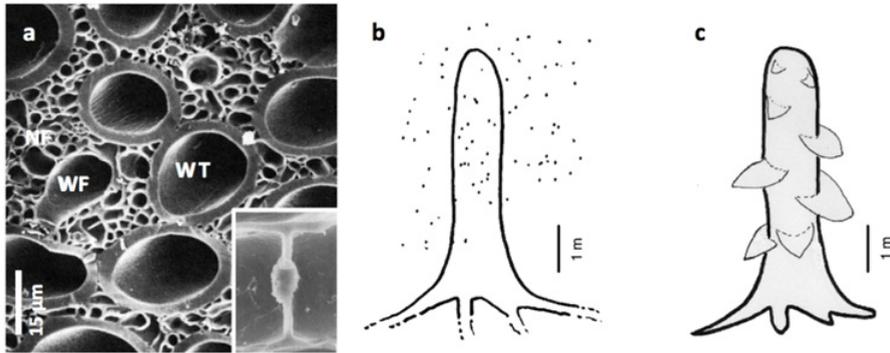


Figure 4. Nematophytes. (a) Scanning electron microscopy of *Nematosketum diversiforme* from the Lower Devonian, displaying interwoven filamentous structures, including wide tubes (WT) with thick walls, contrasting with filaments with thinner walls, either wide (WF) or narrow (NF; from [22]). Inset: a septum in a longitudinal section of WF. (b) Reconstitution of *Prototaxites* as a columnar fruitbody supposed to produce spores. (c) Reconstitution as a lichen with leaf-like appendages often lost during fossilization (see also similar reconstitution in [23]).

outcompeted free-living unicellular and filamentous algae. By enlarging the ecological niche of algae and cyanobacteria, lichen associations may have allowed them to stay and diversify on land after the rise of Embryophyta. Rejecting or supporting this speculative view will anyway require more lichenologists and mycologists to look at the fossil record...

3. Enigmatic fossils in early terrestrial ecosystems: Overlooked lichens?

Several other early terrestrial fossils may have a lichen-like nature, which is obscured by an unusual shape, and likely represent extinct types of organisation. In a recent book, Taylor et al. [18] reviewed the diverse claims for early lichens – here, we only analyse two fossils that, in our opinion, have the most convincing lichen affinities.

3.1 Spongiophyton

A lichen affinity was suggested for the enigmatic early Devonian *Spongiophyton*, a species which developed a dichotomous branching thallus with a perforated surface (Fig. 3b), and likely grew on riverbanks or wet places [19]. Although no alga was clearly observed, a lichen nature was first supported by a ^{13}C isotopic value close to that found in extant lichens [20], but later it was demonstrated on a larger dataset of extant tissues that this value does not differ from those found in lower Embryophyta [21]. Moreover, the use of such isotopic arguments, especially compared to extant values, assumes that burial and fossilization did not distort isotopic content and makes strong assumption of uniformitarianism. *Spongiophyton* is still waiting for finer structural analysis to confirm its lichen affinity.

3.2 Prototaxites and other Nematophytes

The Nematophytes are striking and enigmatic organisms which might have lichen affinities; they occurred in Silurian to Mid-Devonian (400–350 Myr ago) appear to be cosmopolitan, including in the Rhynie Chert (Scotland), and they span a broad size range from millimetres to meters. *Prototaxites* is the largest terrestrial organism from these times, reaching up to 9 m long and more than 1 m in diameter [24, 25]. *Prototaxites* looked like a tree trunk (Fig. 4b), which had been transported to deltaic

sites before fossilization [25, 26]. Its enlarged base was likely connected to root- or rhizomorph-like structures penetrating the substrate. These might have formed casts commonly found in early Devonian strata [26]. The ultrastructure of *Prototaxites* (Fig. 4a) is more unexpected: the trunk-like structure was made of concentric rings, possibly reflecting rhythmic growth; at higher magnifications, *Prototaxites* and other Nematophytes, such as *Nematosketum* spp. (Fig. 4a), display interwoven filaments of various sizes [22], some of which are septate [25].

The affinities of *Protoaxites* and other Nematophytes remain highly debated: they were tentatively affiliated to Embryophyta, green or red or brown algae [25], or viewed as rolled liverwort mats (but this view was challenged; [27]). Hueber [25] proposed that *Prototaxites* was the gigantic fruitbody (= macroscopic spore bearing structure) of a saprotrophic Basidiomycete (Fig. 4b), similar to extant *Clavaria*. While Basidiomycetes may have existed by that time, Hueber failed to convincingly show basidia and spores. Saprotrophism was supported by some isotopic data [24], but (see concerns above) the sharing of similar isotopic content with extant taxa is not necessarily evidence of functional or metabolic identity. To support a saprotrophic hypothesis one needs to take into account (i) the enormous biomass of the fossil, that might not have been supported by the limited primary production of the small surrounding Embryophyta, (ii) the extinction of *Prototaxites* at a time were the first trees arose (even though they could have provided more carbon resources for heterotrophs) and (iii) the detection of biochemical signatures of Embryophyta affinities [28]. It was thus proposed that *Prototaxites* was a phototroph, and taking account of the fungal affinity of its constitutive filaments (Fig. 4a), probably a lichen [23, 28, 29]. *Prototaxites* might even have displayed ramifications or leaf-like appendages [30] (Fig. 4c), which were lost during transport, fitting the view of a light-harvesting organism analogous to extant squamule-bearing *Stereocaulon* and *Cladonia* lichens. Even if it has often been claimed that no algae were observed (e.g. [29]), the occurrence of two symbiotic organisms might explain the diversity of the filaments (Fig. 4a).

Despite some debatable attempts to classify the fungus as a basidiomycete [25] or a Glomeromycete [23], it maybe heuristic to consider that it belongs to a lineage either fully extinct, or without extant members. Indeed, the idea that decimation occurred, leading to the extinction of whole taxa or organisation types [31], is familiar to plant and animal palaeontologists, but may be overlooked by palaeomycologists. Although their lichen nature remains speculative, Nematophytes are the most intriguing fossils linked to terrestrialization, and given their abundance and impact on the substrate [24–26], they likely played major roles in biogeochemical cycles and ecosystem structure in the Siluro-Devonian. Further study of their nature and causes of their extinction may help clarifying these roles.

4. The rise of Embryophyta

Currently, Embryophyta largely display a symbiotic phenotype for substrate exploitation, since more than 85% of living species possess mycorrhizae [9, 11, 32]. This raises questions as to why mycorrhizal associations are such a widespread feature, as well as its exact origin and link with early terrestrialization.

4.1 The extant mycorrhizal diversity

The roots of most plants associate with soil fungi, forming a dual organ called mycorrhiza [32]. Here, the fungus exploits plant photosynthates and receives carbon from its host; as a reward, it provides to the plant mineral nutrients and water collected from the soil, in an association considered to be mutualistic. Moreover the two partners reciprocally protect each other against soil biotic (parasites) and abiotic (drought, toxic compounds, etc.) adversities (Fig. 2). Different fungal groups form different morphological types of mycorrhizae on various host plants, and sometimes in different ecosystems (Fig. 5, Table 1, [32, 33]). Glomeromycetes form the arbuscular mycorrhizae on most land plants

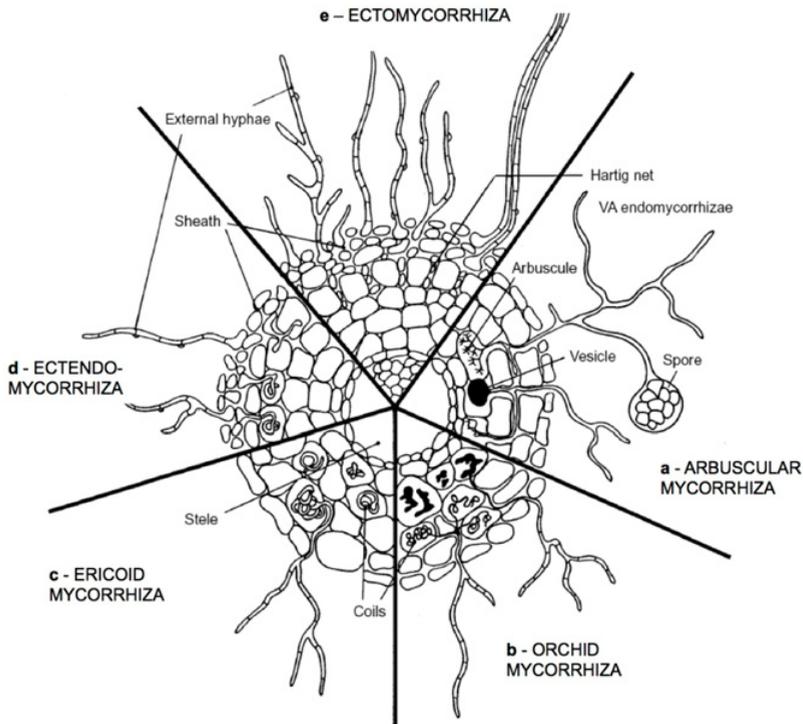


Figure 5. The main mycorrhizal associations in the extant land flora. (a), associations with Glomeromycetes; (b–e) associations with Basidio- and Ascomycetes.

worldwide: the cortex of the root is colonized by the fungus and specialized hyphae form arbuscules penetrating the host cell wall; the fungus sometimes stores reserves in vesicles within or between the root cells (Fig. 5a). Several Basidiomycetes and Ascomycetes form ectomycorrhizae, mostly on shrubs and trees from temperate and Mediterranean regions, and in some restricted parts of tropical forests: here, the root colonization remains strictly intercellular and a hyphal sheath is formed surrounding the plant root (Fig. 5e). The same fungus sometimes forms ectendomycorrhizae, where some hyphae penetrate within the host cells (Fig. 5d): ectendomycorrhizae are a subtype of ectomycorrhizae, since both involve the same fungal species. Finally, in two plant families, namely orchids (Fig. 5b) and Ericaceae (Fig. 5c), mycorrhizae involve intracellular colonization by hyphal coils; here again, Basidiomycetes and Ascomycetes are involved. Finally, some liverworts and hornworts also interact with fungi that are otherwise mycorrhizal on root-bearing plants (Glomeromycetes, Basidiomycetes or Ascomycetes, Table 1, [34]): here, in the absence of roots, thallus cells are colonized. Such interactions, together with those in some vascular plants in which the fungus colonised the rhizome, have been called “paramycorrhizae” since no root is involved [11].

Within this diversity, two strikingly different patterns exist. On the one hand, the arbuscular associations are present in all clades of Embryophyta, excepted mosses, forming mycorrhizae or paramycorrhizae, and involving the single group Glomeromycetes, which is strictly biotrophic (Table 1). On the other hand, all associations involving Basidiomycetes or Ascomycetes are secondarily and more recently derived on both the host plant side [32, 34] and the fungal side [32]. For example, the ectomycorrhizal association arose more than 80 times among Basidiomycetes [35]. Thus, while associations involving Basidiomycetes or Ascomycetes are derived, the arbuscular association is a good candidate to have arisen early in the ancestor of Embryophyta.

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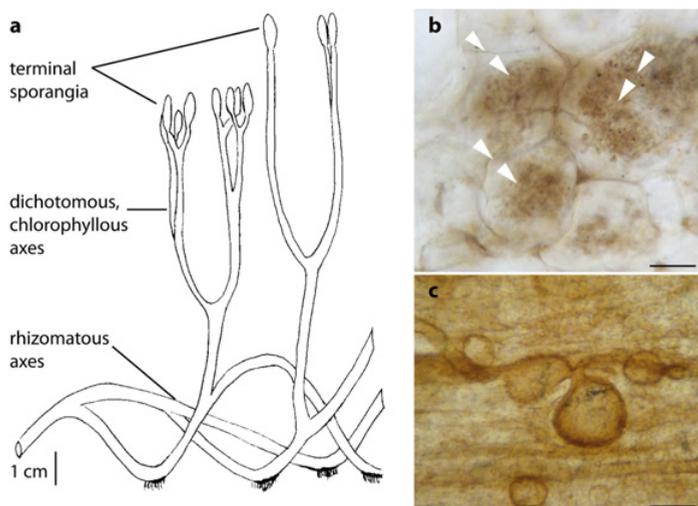


Figure 6. Arbuscular mycorrhizal colonization by Glomeromycetes (paramycorrhizae) in aerial and rhizomatous axes of the Rhynie chert plant *Aglaophyton major*. (a) General shape of the plant. (b) Colonized cortical cells of *A. major* showing intracellular arbuscules (white arrows) in turgid cells (photo courtesy of H. Kerp). (c) Hyphae and vesicles in the cortex of an aerial axis of *A. major* (photo C. Strullu-Derrien). Scale bars: (b) = 20 μm; (c) = 40 μm.

4.2 The arbuscular (para)mycorrhizal symbiosis at the origin of Embryophyta?

Over the past twenty years, both palaeontology and molecular biology nicely converged in supporting the idea that Glomeromycetes were associated with the ancestors of land plants. It has been long recognized that molecular clock approach placed the origin of Glomeromycetes in a time range overlapping the rise of land plants [36]. Indeed, the oldest Glomeromycete known, *Palaeoglosum grayi*, is from the Ordovician of Wisconsin and it falls within the age of the origin of the group based on molecular clock assumptions [37]. However, this early fossil record is problematic, because it has been suggested that *P. grayi* is a contaminant from later sediments (see discussion in [18]). Yet, although the rise of Embryophyta started 470 Myrs ago [5], it is not until the Rhynie Chert flora (ca. 407 Myrs ago) that fossils allow investigations of tissues at the cellular level. The presence of Glomeromycetes is well established in the Rhynie Chert [18, 38, 39]. Moreover, Glomeromycetes colonization, with intercellular hyphae, arbuscules and vesicles has been reported from some plant aerial axes [40–42] (Fig. 6), closely resembling the colonisation occurring in living liverworts, hornworts and lycophytes. This supports the idea that arbuscular paramycorrhizae represent the ancestral type [8, 9, 11]. These fossil plants (e.g. *Aglaophyton*, *Horneophyton*) occupy a quite basal place within the Embryophyta (see asterisk on Fig. 1), at the base of vascular plants (Tracheophyta). In these fossils, the cells colonized by arbuscules have thin cell walls, but they look turgid (Fig. 6b), so that it can be inferred that the colonization was biotrophic.

Beyond the presence of Glomeromycetes in the oldest observed plant tissues, some results from evo-devo also support the hypothesis that all Glomeromycete associations are homologous. In extant plants, the *sym* genes are involved in transduction of signals emitted by Glomeromycetes, upon which they launch the expression of the genetic program allowing fungal colonization of the root. Not only are these genes present in all Embryophyta, including basal lineages such hornworts and liverworts (Fig. 1), but also gene copies from these lineages can rescue alfalfa (*Medicago*) mutants deficient for *sym* [43, 44]. These genes also exist in mosses, which do not associate with Glomeromycetes, but interestingly show evidence of relaxation of selective constraints [43] suggesting (i) that they fulfil non-symbiotic roles in this and possibly other lineage and (ii) that *sym* genes are indeed ancestral.

This is consistent with the hypothesis that Glomeromycetes have accompanied Embryophyta since their first appearance [45] and that algal ancestors were helped to exploit the substrate by fungi. Plants from the Rhynie Chert are devoid of roots, so that exploration of soil was unlikely to be autonomous. The discoveries of *sym* genes and strigolactone, a molecule important for the plant-Glomeromycetes molecular dialog, in Charophyta (fresh algae closely related to Embryophyta, Fig. 1) [45, 46] now raise the question whether such interactions started to evolve in the water, and thus before terrestrialization. More studies on green algae closely related to Embryophyta may help clarifying this intriguing question.

4.3 A role for Mucoromycetes during terrestrialization?

The consensus on an exclusive role for Glomeromycetes was recently challenged by two discoveries. First, it has recently been shown that extant basal land plants such as liverworts, hornworts and lycophytes, associate with Mucoromycetes [47] (Table 1), and this symbiosis looks mutualistic, providing soil resources, in some hornworts at least [48]. The presence of Mucoromycetes was overlooked because they form hyphal coils in host cells and hyphal swellings that are not very different from those of some Glomeromycetes [47]. Second, a similar symbiosis was demonstrated in the corm (basal part) of the Rhynie chert plant *Horneophyton* [41] (Fig. 1) and possibly in another species from the same site, *Nothia* [49].

These are limited data on the precise role of Mucoromycetes in plants, and they have not been reported from Euphyllophyta. It can be speculated that they were present from very early on. Given that Glomeromycetes and Mucoromycetes are two sister lineages [50], it might also be possible that their common ancestor interacted with early Embryophyta, or even with their algal ancestors. This emerging possibility deserves further analyses, especially to distinguish the colonization by Mucoromycetes from that by endophytic fungi, which grow in host tissue, sometimes with positive outcome on the physiology, but without allowing exploitation of the substrate.

5. Conclusion: Phototrophy in land ecosystems, a matter of fungal symbiosis?

Living land phototrophs display two strategies for exploiting the soil substrate (Fig. 2). Some are non-symbiotic: this encompasses some algae and cyanobacteria, for which this strategy is plesiomorphic (= ancestral), and some non-mycorrhizal Embryophyta, for which this strategy is derived (= secondary in evolution). Several non-mycorrhizal Embryophyta reverted to a poikilohydric strategy that existed before the invention of mycorrhizal association, such as mosses, which thus depends, as biofilms, on superficial water to live. Other non-mycorrhizal Embryophyta from highly derived vascular lineages (e.g. Brassicaceae, Proteaceae, Polygonaceae) tend to live in sites that are either rich in nutrients, or they are pioneers (and thus without fungal partners), or they live in extremely nutrient poor environments where they develop alternative strategies [51]. These plants use their roots to autonomously support their needs: this also happens in seedlings of Embryophyta, transiently after germination, before the first mycorrhizal colonization occurs. Thus, non-mycorrhizal plants evolved a secondary (and convergent) neotenic strategy. Moreover, roots, which primarily evolved in the framework of the mycorrhizal symbiosis, were secondarily recruited to escape it. In fact, this might even be a true turnaround, since the root likely evolved in the Tracheophyta as a symbiotic organ allowing the plant to meet with and harbour the fungus in the soil [33].

The fact that most phototrophs nowadays use fungi to exploit soil resources exemplifies adaptation by symbiosis. Such adaptation also arose again later in Embryophyta evolution, when some plants shifted to other mycorrhizal types. The ectomycorrhizal symbiosis adapted several lineages to the poorly mineralized and poorly weathered soils from temperate regions [1, 52]; Ericaceae adapted a form of mycorrhizal symbioses to exploit even more poorly mineralized soils from high latitudes and altitudes

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[52]. In both ectomycorrhizal and ericoid mycorrhizal symbioses, the fungus extracts N and P directly from soil organic matter, bypassing the need to extract these elements from minerals directly [32, 45].

The current diversity of plant-fungal interaction may be only a subset of the diversity that existed, especially early in the history of terrestrialization. From the diverse fossils suspected to have lichen affinities, many do not fit the current concept of lichens. At least, whatever their exact nature might be, they suggest that some of the first lineages/body plans (= organismal organisations) experimented during land colonisation, later disappeared. Similarly, the 505 Myrs old Burgess Shale Fauna shows many more body plans and lineages than we can recognize nowadays: a “decimation” likely occurred, either by drift or by competition, as suggested by S.J. Gould [31]. The same principal likely applied following the evolution of the first terrestrial flora, and the extent to which algal-fungal symbioses played a role in terrestrialization remains to be fully assessed by analysing in more details early land phototrophs. Without doubt, the discovery of new Lagerstätten would help, together with the use of emerging tools in palaeontology (such as X-ray synchrotron microtomography or confocal laser scanning microscopy [53]).

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