

Systematic Palaeontology (Palaeobotany)

Mycorrhization of fossil and living plants

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Abstract

The widespread mycorrhization together with the fossil record indicate that plants and fungi have evolved in mycorrhizal relationship since the colonization of land by early plants. In living plants most mycorrhizal symbioses are mutualistic associations in which fungus and plant exchange metabolites and nutrients required for their growth and survival. They concern either the gametophyte and/or the sporophyte of most embryophytes. A new nomenclature is suggested to define two types of mycorrhizae: (1) paramycorrhizae for the colonization of thalli and shoot systems; (2) eumycorrhizae for the colonization of root systems. The aim of this paper is to show the mycorrhizal status in relation with the various clades of embryophytes by considering both fossil and living plants and to develop the implications of mycorrhizal symbiosis in the colonization of land by early plants and in the evolution of plants. **To cite this article:** C. Strullu-Derrien, D.-G. Strullu, C. R. Palevol 6 (2007).

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Résumé

La mycorrhization des plantes fossiles et actuelles. Les enregistrements fossiles et la mycorrhization, aujourd'hui largement répandue, montrent que les plantes entretiennent des relations étroites avec les champignons depuis la colonisation de la Terre par les plantes primitives. Chez les plantes actuelles, la majorité des symbioses mycorrhiziennes sont des associations de type mutualiste, à partir desquelles la plante et le champignon échangent les éléments nutritifs nécessaires à leur croissance et à leur développement. La symbiose mycorrhizienne est présente au niveau du gamétophyte et/ou du sporophyte chez la plupart des embryophytes. Une nouvelle nomenclature est proposée pour définir deux types de mycorhizes : (1) paramycorrhizes pour la colonisation des thalles et des systèmes caulinaires ; (2) eumycorrhizes pour la colonisation des systèmes racinaires. Cette note a pour but de montrer le statut mycorrhizien des embryophytes dans les différents clades, en prenant en compte les taxons fossiles et actuels. Les implications de la symbiose mycorrhizienne dans la colonisation du milieu terrestre par les plantes primitives, ainsi que dans l'évolution des plantes, sont ensuite présentées. **Pour citer cet article :** C. Strullu-Derrien, D.-G. Strullu, C. R. Palevol 6 (2007).

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1. Introduction

Mycorrhizae represent symbiotic associations between plants and fungi based on the exchange of metabolites and nutrients. Today the term symbiosis describes a mutualistic association that is beneficial to both partners for a significant period of time [46]. More than 90% of the living embryophytes (land plants) are capable of forming a mycorrhizal symbiosis, and a non-mycorrhizal status is an exception. Mycorrhization occurs in root systems as well as in thalli and shoot systems, depending on the type of plants.

Embryophytes arose from green algae, which became semi-aquatic and then terrestrial. The transition from an aqueous to a gaseous medium exposed plants to new physical conditions. On land, plants encountered a harsh environment; they were subject to desiccation and the soil was poor in nutrients. On the other hand, life on land implied a greater volume of space and little competition to disperse, associated with high levels of CO₂ and light intensity for photosynthesis.

It is considered that fungal symbiosis played a key role in the original colonization of land by early plants [59]. Observing the organisms in the Rhynie Chert (400 million years old), Kindston and Lang [36] found the fungi they described to be most similar to extant mycorrhizal fungi. Later, unequivocal evidence for the occurrence of arbuscular mycorrhizae in early land plants in the Rhynie chert was given by several authors [8,63,85]. More recently, ectomycorrhizae have also been observed from the Eocene of British Columbia and from the Eocene of Belgium [21,41]. In this paper, we present the mycorrhizal status in relation with the various clades of embryophytes, including fossil and living plants; the implications of mycorrhization in colonization of land, soil functioning and plant production are suggested.

2. Mycorrhizal symbiosis

It has been a long time since mycorrhizae interested mycologists and plant scientists. In 1885, Frank [25] developed a new theory of tree nutrition via symbiosis between fungi and tree root and gave the name ‘mycorrhiza’ to the organ he observed. Two years later, he suggested the terms ectotrophic for the mycorrhiza that presented a mantle and endotrophic for those without a mantle. Anatomical descriptions of what are most certainly arbuscular mycorrhizae are given by many researchers; among them, Janse [32] and Gallaud [26] described respectively ‘vésicules’ as the intraradical spores and ‘arbuscules’ as the intracellular structures.

Two basic classes of mycorrhizae were also suggested by Gallaud [26]: the ‘Arum’ and ‘Paris’ types, named after the type of host plant in which they occur. The ‘Arum’ type [11,73] shows an extensive intercellular phase of hyphal growth before penetration into the cortical cells and development of arbuscules. The ‘Paris’ type [73,80] is defined by the absence of the intercellular phase and intracellular growth of the fungus with formation of coils, sometimes without any arbuscules or vesicles.

Weiss [87], observing the remains of plants in coal-balls and starting from the existence of Phycomycetous fungi in Permo-Carboniferous times, considered that the modes of life of the fungi in the Palaeozoic differed very little from those of living fungi. He concluded: “the highly specialized mutual adaptation of fungus and cormophyte did actually exist in the Palaeozoic age”; because of the peculiar character of the fossil he described, he suggested to call it *Mycorhizonium*.

The name used to define the mycorrhizal symbiosis has changed through the years. Wilde and Lafond [88] replaced the adjectives ‘ectotrophic’ and ‘endotrophic’ with ‘ectocellular’ and ‘endocellular’, and Peyronel et al. [57] suggested the terms ‘ectomycorrhizas’ and ‘endomycorrhizas’. The endomycorrhizal association has been frequently called ‘phycomycetous mycorrhiza’; because of the absence of systematic significance, ‘phycomycetous mycorrhiza’ have been replaced with ‘vesicular-arbuscular mycorrhiza’ and with ‘arbuscular mycorrhiza’ after the recognition that not all fungi formed vesicles.

The naming of the fungus has also been of great discussion. Before Peyronel’s works [56], fungi involved in arbuscular mycorrhiza were considered to belong to the genus *Pythium*. Peyronel suggested placing them in the genus *Endogone*. Then Nicolson and Gerdemann [52] and Mosse and Bowen [48] added new species to this list and each of them divided the fungi into two groups of *Endogone*. Later Gerdemann and Trappe [28] split the genus *Endogone* into seven genera and retained four mycorrhizal genera including *Glomus*, *Sclerocystis*, *Gigaspora*, and *Acaulospora* that were placed in the Endogonaceae, Zygomycetes. Several arbuscular mycorrhizal fungal genera were then added, the order of the Glomales was suggested by Morton and Benny [47], and a new phylum the Glomeromycota was established by Schüßler et al. [71] using molecular data.

In the earliest land plants such as in extant bryophytes and pteridophytes, structures analogous to mycorrhizae of spermatophytes are observed. As it has been clarified by several authors, the underground axes of these plants are not roots and the infested organs may be rhizomes

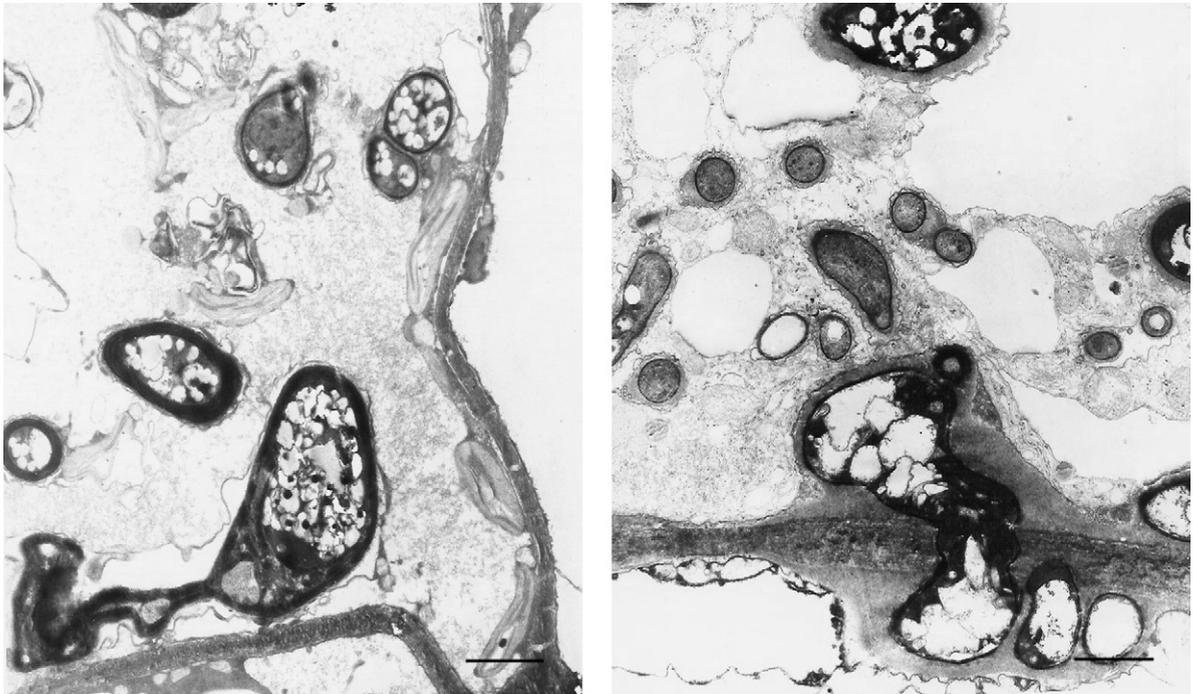


Fig. 1. Paramycorrhizae and eumycorrhizae in living plants. Left: paramycorrhizae represented by endomycorrhalli in *Pellia epiphylla* showing the colonization by a glomeromycotan fungus. Ultrastructural aspects of the arbuscules in a cortical cell containing plastids with grana (detail of Fig. 35 [77]). Scale bar = 3 μm . Right: eumycorrhizae showing the penetration of a symbiotic fungus into a cortical root cell of *Taxus baccata*. Ultrastructural aspects of the arbuscules surrounded by a dual apoplast and the host plasmalemma (detail of Fig. 51 [77]). Scale bar = 1 μm .

Fig. 1. Paramycorrhizes et eumycorrhizes chez les plantes actuelles. À gauche : paramycorrhizes représentées par des endomycorhales chez *Pellia epiphylla*, montrant la colonisation par un glomérormycète. Ultrastructure des arbuscules visibles dans une cellule corticale montrant des plastides à grana (détail de la Fig. 35 [77]). Barre d'échelle = 3 μm . À droite : eumycorrhizes montrant la pénétration du champignon symbiotique dans les cellules racinaires de *Taxus baccata*. Ultrastructure des arbuscules entourés par un apoplaste mixte et le plasmalemma de la cellule-hôte (détail de la Fig. 51 [77]). Barre d'échelle = 1,5 μm .

or thalli. The associations are called mycorrhizomes and mycorrhalli [6], endomycorrhalli [79], or mycorrhiza-like associations [9,38,66]. Considering this, a new nomenclature is suggested in this paper to define two types of mycorrhizae (Fig. 1):

- paramycorrhizae for the colonization of the thallus and shoot system. This case is represented in the gametophyte or/and the sporophyte. The fungal associations are mycorrhalli or mycorrhizomes;
- eumycorrhizae for the colonization of the root system. In this case, only the sporophyte is concerned.

The term 'mycorrhiza' embraces three basic types of dual organs involving plants of most clades of embryophytes and the three fungal phyla : Glomeromycota, Ascomycota and Basidiomycota types (Fig. 2). Arbuscular mycorrhiza and ectomycorrhiza are the most widely distributed and one other form exists, concerning two groups of plants: the orchid/ericoid type restricted

respectively to the Orchidaceae and to the order Ericales [78].

In arbuscular mycorrhizae, fungal hyphae penetrate inside the cortical tissues of roots or shoot systems or also inside thallus cells; they display intracellular coils, vesicles and arbuscules as well as lysis of the fungus in the host cells. Fungi of the glomeromycetous type form endomycorrhizal associations with a wide range of clades among the embryophytes [74,77].

Ectomycorrhizae develop a fungal network closed to the roots; they show a mantle that surrounds bifurcate or monopodial short roots and a Hartig net that penetrate between the cortical cells. Ascomycetous and basidiomycetous fungi form ectomycorrhizae with Gymnosperms [*Pinaceae* (all genus), *Cupressaceae*, *Gnetaceae*] and a few family of Angiosperms (*Fagaceae*, *Betulaceae*, *Salicaceae*, *Juglandaceae*, *Ulmaceae*, *Dipterocarpaceae*, *Sarcocaulaceae*, *Rosaceae*, *Caesalpinioidea*, *Tiliaceae*, and *Myrtaceae*).

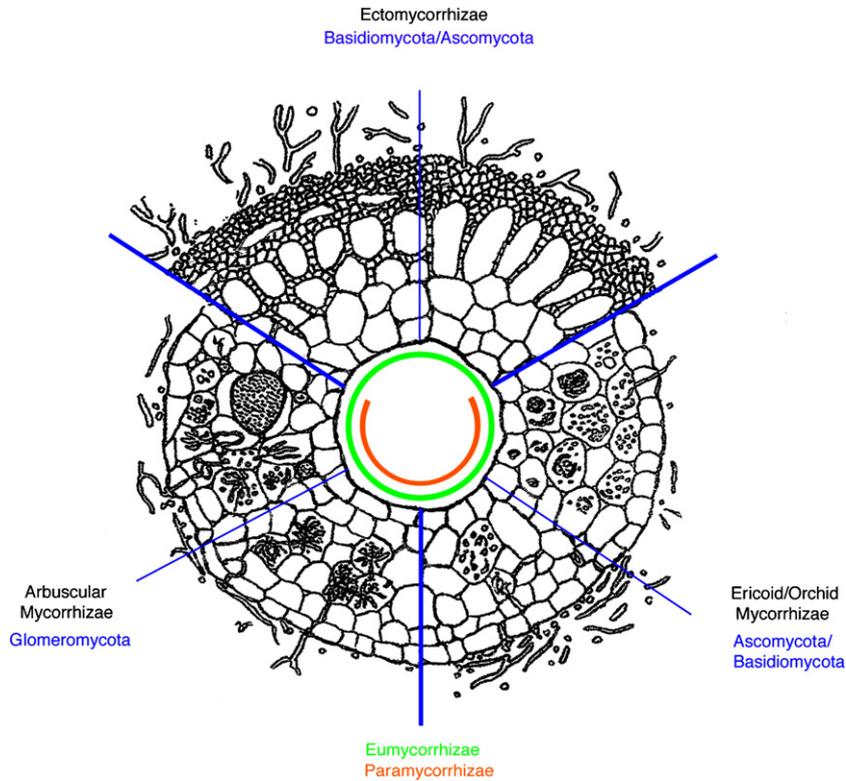


Fig. 2. The three basic types of mycorrhizae.
Fig. 2. Les trois principaux types de mycorrhizes.

Ericoid and orchid mycorrhizae also show intracellular colonization. Fungal hyphae penetrate inside the tissues of the host; intracellular coils and vesicles are present. Ascomycetous fungi are associated with members of the order Ericales and a few liverworts, while Basidiomycetous associations are found in Orchidaceae and also a few liverworts [61].

3. The embryophytes

The origin and early evolution of embryophytes occurred in the mid-Palaeozoic era (480–360 Myr). Land plants evolved from simple structures consisting of only a few cells to complex organisms with specialized organs and tissue systems. Land plants are recognized in the fossil records in the mid-Silurian, 50 Myr after land plant spores, which appeared as spore tetrads (mid-Ordovician).

Phylogenetic studies favour a single origin of land plants from charophycean green algae: either Coleochaetales, or Charales, or a group containing both is sister group to land plants. However, the exact relationships between bryophytes (i.e. liverworts, hornworts, and mosses) and tracheophytes remain controversial.

Among vascular plants, lycophytes are the sister group to euphyllophytes that contains all other living vascular plants. The split between lycophytes and euphyllophytes occurred in the Silurian. Most extant lycophytes are relatively small plants that possess microphylls; they comprise three main clades: Lycopodiales (clubmosses), Isoetales (quillworts) and Selaginellales (spikemosses). However, in the Carboniferous period, many lycophytes, as *Lepidodendron*, were large arborescent forms.

Living euphyllophytes belong to two major clades: monilophytes and spermatophytes (seed plants). Euphyllophytes exhibit a great diversity; they possess megaphylls, pseudomonopodial or monopodial branching, a basically helical arrangement of branches, sporangia in pairs grouped into terminal trusses and a lobed primary xylem strand [35]. The monilophytes (= Moniliformopses, sensu Kenrick & Crane [35]) have protoxylem confined to lobes of the xylem strand. Extant members belong to two clades: Equisetopsids (horsetails), and Filicopsids (ferns). The fossil cladoxylopsids belong almost certainly to the monilophytes. Like lycophytes, monilophytes are plants that produced spores and not seeds; these clades were traditionally called ‘pteri-

dophytes' [60]. Spermatophytes are characterized by the presence of seeds, secondary xylem, and phloem produced by a bifacial cambium and axillary branching. Cycads, Ginkgo, conifers, gnetophytes, and angiosperms are the five major clades of extant seed plants. Several extinct fossil clades or grades of pteridosperms also belong to this group [33].

4. Origin and evolution of mycorrhizal symbiosis

It is likely that the colonization of land by terrestrial eukaryotes has been possible only through associations between a photosynthetic organism and a fungus. The two organisms formed a mutualistic symbiosis that allowed them both to exploit the new environments. Today these symbioses are mainly represented by lichens and mycorrhizae. By reporting that glomeromycotan symbioses show a broad spectrum of phototrophs, Schüßler and Wolf [70] expand Pirozynsky and Malloch's hypothesis [59] about the relationship between an aquatic alga and a 'phycomycetous' fungus suggested as the initial step in land plant colonization.

The AM fungi, which are now the most widely distributed mycorrhizal symbiosis, represent one of the few plant-fungus relationships that have a fossil record. Glomeromycota has a record beginning with Ordovician spores (460 Myr) [62] and evidence for the occurrence of arbuscular mycorrhizae dated from 400 Myr ago [63].

Taking account both the basal designation of live-works in land plant evolution and the basal position assigned to the genus *Haplomitrium* and *Treubia* in phylogenetic reconstructions, Duckett et al. [20] suggest that the glomeromycotean associations in these plants could be even more ancient than those in rootless vascular plants and even could be establish before the evolution of rhizoids. Otherwise, Schüßler and Wolf [70] consider the *Geosiphon* symbiosis as the only known fungal endosymbiosis between cyanobacteria and glomeromycotan fungus. For these authors, the *Geosiphon* symbiosis appears to mirror a possible ancestor to arbuscular mycorrhiza that could have occurred in terrestrial ecosystems before land plants evolved.

Other mycorrhizal forms evolved later. The evolution of ectomycorrhizae is relatively recent; the first fossil ectomycorrhizae described by LePage et al. [41] are dated from 50 Myr ago, and more recently Fairon Demaret et al. [21] observed this type of association also from the Eocene (55 Myr). Ectomycorrhizae are the most frequent type in the forests and woodlands of cool-temperate and boreal latitudes and they also occur in tropical forests. Alexander [1] reported that the ECM habit has arisen independently of the course of evolution

in Pinaceae; he also reported several disparate lineages of angiosperms. It has been suggested that the evolution of ectomycorrhizae can be pushed to before 135 Myr [49]. Orchid and ericoid mycorrhizae are more difficult to date; the only information is given by the evolution of their host taxon. Fossil records of the Ericaceae date back only to the Early Tertiary [42], and several putative proto-orchids have been identified from the Eocene [69].

Except the earliest arbuscular mycorrhizae, which are quite different from the other forms, and according to Marks [46], ectomycorrhizae seem to be of the earliest type from which ericoid and orchid types developed. However, Brundrett [9] suggested that all types of mycorrhizae are derived from arbuscular mycorrhizae, with possible intermediate stages.

5. Mycorrhizal status related to the different clades of Embryophytes

Mycorrhization that occurs in most embryophytes is shown following the various clades presented in Fig. 3. For each clade, fossil occurrences are reported and then mycorrhizal status in living plants is developed.

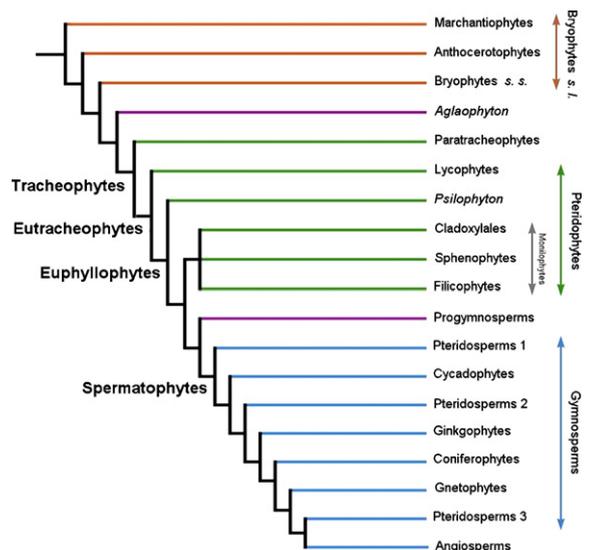


Fig. 3. Phylogenetic tree of the Embryophytes. Progymnosperms: Aneurophytales and Archaeopteridales; Pteridosperms 1: Hydrasperman Pteridosperms, Medullosales and Callistophytales; Pteridosperms 2: Peltaspermales; Pteridosperms 3: Glossopteridales, Benettitales and Caytoniales.

Fig. 3. Arbre phylogénétique des embryophytes. Progymnospermes : Aneurophytales et Archaeoptéridales; Ptéridospermes 1 : Ptéridospermes hydraspermiennes, Médullosales et Callistophytales; Ptéridospermes 2 : Peltaspermales; Ptéridospermes 3 : Glossoptéridales, Benettitales et Caytoniales.

5.1. *Marchantiophytes*

Although fossil liverworts have been described from the Aptian of Spain and that of Antarctica, no fossil record exists for mycorrhizae. Marchantiophytes (liverworts) belong to the paraphyletic Bryophyta. They are divided into Marchantiopsida and Jungermanniopsida [72]. In the living clade, the colonization by the mycorrhizal fungus is restricted to the gametophyte. The occurrence of symbiosis between hepatics and fungi has been known for over a century; these early works have been reviewed by Boullard [7] and have been confirmed for the last 30 years [61]. Two types of associations are recognized according to whether the fungus possesses septate or no septate hyphae:

- glomeromycetous infections of the arbuscular mycorrhizal type occur in many liverworts: this is reported for thalloid [20,65,79] as well as leafy species [12];
- ascomycetous/basidiomycetous infections occur in Jungermanniopsida: the rhizoid infections observed in some leafy Jungermanniopsida are caused by ascomycetous fungi [19], the intercellular growth resembling pelotons developed in ericoid mycorrhizae. In leafy and thalloid Jungermanniopsida, basidiomycetes form intracellular hyphal pelotons with lysis in the host cells similar to the infection in orchid mycorrhizae [45,61]

5.2. *Anthocerotophytes*

Frahm [24] reported the first record of a fossil hornwort from Dominican amber, but to date no fossil record is available for mycorrhizae. The mycotrophic status of living anthocerotophytes is also uncertain. Inter- and intracellular fungal endophytes were found in several anthocerotophytes species [64], but this clade has been considered as devoid of fungal infection until the observation of fungal infection in *Phaeoceros laevis* (L.) Prosk. [44]. The gametophyte of *P. laevis* is associated with an aseptate fungus that forms extracellular thick-walled hyphae, intercellular thin-walled hyphae and intracellular arbuscules; vesicles are also present.

5.3. *Bryophytes s.s.*

There are very few descriptions of fossil bryophytes and no data concerning mycorrhization. For extant mosses, the largest group of bryophytes are considered as being non mycorrhizal, but often contain endophytic hyphae. Read et al. [61] stated that it is certainly of phys-

iological interest that the mosses resist colonization by mycorrhizal fungi.

5.4. *Aglaophyton/Lyonophyton*

The fossil relationships between fungi and plants suggested by Kidston and Lang [36] in the Rhynie chert have now been documented [8,63,85]. Arbuscular mycorrhizal symbioses may be deduced based on the presence of hyphae, vesicles, intracellular arbuscules and spores. The fungus *Glomites rhyniensis* is known from *Aglaophyton* sporophyte, and from the young gametophyte *Lyonophyton rhyniensis*. A continuous dark band in the cortex of *Aglaophyton* contains the arbuscules; the first recognisable arbuscules occur in young aerial axes in the gametophyte.

5.5. *Paratracheophytes: Rhynia*

As for *Aglaophyton*, Boullard and Lemoigne [8] reconsidered the possible fossil relationship suggested by Kindston and Lang [36] about *Rhynia*. They proved that *Rhynia* elaborated mycothallus by pointing typical arbuscular mycorrhizal structures.

5.6. *Lycophytes*

The presence of endomycorrhizal fungi has been reported from fossil lycophytes. Krings et al. [39,40] describe rhizomatous axes of *Nothia aphylla*, an early plant from the Rhynie chert with possible affinities in the zosterophyllophytes (the sister group to lycophytes), that host a fungus reminiscent of *Glomites rhyniensis* (Glomeromycota), the endomycorrhizal fungus of *Aglaophyton major*. The infection pathway in *N. aphylla* is distinctly different from that seen in *A. major*. The fungus enters the plant as an intracellular endophyte and then becomes intercellular in the cortex. The authors hypothesized that *N. aphylla* displays an alternative mode of colonisation by endomycorrhizal fungi, perhaps related to the peculiar anatomy of the lower portion of the rhizomatous axis (i.e. the rhizoidal ridge).

Palaeomyces asteroxylii has been observed in the inner cortex of rhizomes and basal parts of stems of *Asteroxylon*. It formed aseptate hyphae, which gave rise to fine branches and terminal vesicles. The similarity of this fungus and mycorrhizal fungi has been reported by several authors [8,30,36,51,52,59].

A few works on Carboniferous floras described endomycorrhizae in rhizomes or roots of different plants. Weiss [87] observed this type of association showing digestion phases on root or rhizome of a plant having

affinity to the Lycopodiales, and several authors noted the occurrence of mycorrhizal fungi (Endogonaceae) in Carboniferous coal balls from Europe and America (see [86]).

Lycophytes were the first plants with roots [36]. They have a separate gametophyte phase without roots and a sporophyte with roots and microphylls. The living lycophytes comprise Lycopodiales, Selaginellales, and Isoetales. The gametophytes of *Lycopodium* can be either subterranean and achlorophyllous, or surface living and chlorophyllous, depending on the species, and both are invaded by fungi. Boullard [6] considered that these gametophytes generally formed mycothalli. An association showing some characteristics of AM without arbuscules and with very fine coiled hyphae has been observed in the subterranean gametophyte of *Lycopodium clavatum* [66]. Arbuscule-like structures have also been described in chlorophyllous gametophytes of *Lycopodium cernuum* [17]. *Lycopodium* and *Selaginella* sporophytes develop AM associations, whereas *Isoetes* until now appear to lack this type of association.

5.7. *Psilophyton*

Fungal reproductive structures have been found within aerial axes of *Psilophyton dawsonii* restricted to the inner cortical regions [82]. These fungal structures are compared to other fossil and extant spores and a possible mycorrhizal status is discussed.

5.8. *Cladoxylales*

Several occurrences of mycorrhizal associations have been reported from the axis of a putatively primitive member of the Cladoxylales (W. Stein, pers. commun.). Fungal hyphae and vesicles occur in the cortex, and extraradical spores arise from intraradical hyphae, or are disarticulated in the matrix.

5.9. *Sphenophytes*

Equisetum is the surviving genus of the well-represented arborescent sphenophytes from Carboniferous period. Fossil mycorrhizae have not yet been discovered in this clade. Mycorrhizae are unknown in the photosynthetic gametophytes of *Equisetum* and the mycorrhizal status of the sporophyte is still controversial. First, the genus was classified as non-mycotrophic, but Koske et al. [37] showed that the infection depends upon associated plants and/or soil moisture conditions. However, their conclusions are based on a small sample.

According to Dhillon [16], typical vesicular-arbuscular mycorrhizal structures occurred in the roots of the sporophytes of *Equisetum* and it is reported that plants growing in wet (hydic) habitats had lower levels of colonization by AM mycorrhizal fungi than plants growing in mesic/dry-mesic habitats. The habitat is considered to play putatively an important role in determining the degree of mycotrophy in these plants.

5.10. *Filicophytes*

Andrews and Lenz [2] observed symbiotic fungus in the cortical cells of a fern stem, possibly a rhizome of *Scleropteris illinoiensis* from the Middle Pennsylvanian of Illinois. They called this association mycorrhizome, based on the comparison between dense tangles of mycelium or ovoid bodies and living mycorrhizae. Colonization by fungal hyphae have been observed in the inner cortex of *Botryopteris antiqua* (Strullu-Derrien, personal observation); the occurrence of coils and vesicles is consistent with the notion of ‘Paris’-type mycorrhiza.

Mycorrhizal symbiosis is of general occurrence in living filicophytes, except Marsilaceae and Salviniaceae [6,30]. By studying the arbuscular mycorrhizae of pteridophytes in New Zealand, Cooper [14] reached practically the same conclusion. Berch and Kendrick [4] in southern Ontario and Zhao [89] in Yunnan (southwestern China) observed that the arbuscular mycorrhizal colonization was low in sporophytes of leptosporangiate ferns, whereas it was relatively high in the eurosporangiate ferns. According to Brundrett [9], ferns like *Ophioglossum* and *Botrychium* have sporophytes with relatively thick roots, which are consistently mycorrhizal, while Filicales that have more fine roots with long roots hairs, show limited or inconsistent mycorrhization. On the other hand, Gemma et al. [27] observed that the highest proportion of arbuscular mycorrhizae among the 89 species studied in Hawai concerned Dicksoniaceae, Dryopteridaceae, and Lindsaeaceae. The occurrence in the eurosporangiate ferns was low.

Two different growth forms exist among gametophytes of ferns: green epiterrestrial forms and achlorophyllous subterranean forms [61,67]. Boullard [6] suggested that the dependence of fern gametophytes on mycotrophism decreased with increasing the photosynthetic ability.

Arbuscular mycorrhizal associations have been reported for the gametophytes of *Psilotum* and *Tmesipteris* [6,55]; cortical cells are occupied by dense coils of aseptate hyphae with some of which bearing terminal vesicles. Rhizomes and roots of the sporo-

phytes are generally colonized. More recently, Duckett and Ligrone [18] observed glomeromycotean fungi in sporophytes and gametophytes of *Psilotum* and *Tmesipteris* that are entirely intracellular, and colonization closely resembles the ‘Paris’-type mycorrhiza; large-trunk hyphae, arbuscules and degeneration in the host cells are described.

Other patterns have been presented for mycorrhization in ferns. Schmid and Oberwinkler [68] observed associations with coils in the roots of *Gleichmniaceae*, which are formed by an unidentified ascomycete. Cooper [14] reported the occurrence of ectomycorrhizae in a fern, but as it is shown by the illustrated root, it is probably the root of a *Nothofagus* that is concerned [9].

5.11. *Progymnosperms and Pteridosperms*

To date no data are available for mycorrhization of Progymnosperms and Pteridosperms.

5.12. *Cycadophytes*

Fossil arbuscular mycorrhizae occurred in silicified roots from the Triassic of Antarctica; Stubblefield et al. [83,84] observed nonseptate fungal hyphae within and between cells of the central cortex and swellings comparable to chlamydospores and vesicles. Arbuscules are also present nearly filling the host cell. Example of a mixed colony comprised of fungi with affinities to the *Glomineae* and the *Gigasporineae* are given by Phipps and Taylor [58] also from the Triassic of Antarctica. The fossil gigasporinean mycorrhiza shows irregular intercellular and intracellular hyphae coiled within the cells and arbuscules with thick trunks and narrow branches. In the glominean form, hyphal diameter is more uniform, with coiling rarely present and arbuscules showing thin trunks. Vesicles may be lateral or terminal and spores are not found.

Like fossil members, living cycads show arbuscular mycorrhizae in their roots. Muthukumar and Udaiyan [50] reported that root colonization is a typical ‘Arum’ mycorrhizal type; however various levels of colonization exist among the species. It has been suggested that the endomycorrhizal fungi in cycads have a special function, i.e. to promote the fixing of nitrogen by the endosymbiotic cyanobacteria [23].

5.13. *Ginkgophytes*

Fossil mutualistic associations have not yet been shown in Ginkgophytes. In living *Ginkgo biloba* Bonfante-Fasolo and Fontana [5] described arbuscular

mycorrhizal symbioses; intercellular hyphae and vesicles are rare while intracellular coils and intercalary arbuscules are abundant in the inner cortex. According to Smith and Smith, *Ginkgo* should be included in a ‘near-Paris’ or ‘intermediate’ type.

5.14. *Coniferophytes*

Fossil mycorrhizae have been reported in cordaitan rootlets by several authors [29,43,54,90]. In *Amyelon radicans*, Osborn observed aseptate hyphae that have given rise to clumps in the inner cortical region; vesicles were also found. Halket confirmed these observations, but found more frequent septa in the hyphae. Later Harley [30] and Boullard and Lemoigne [8] corroborated Osborn’s observations. Cridland [15] re-examined most specimens of cordaitan rootlets supposed to contain mycorrhizae and found that fungi are sometimes present, but not constant in occurrence, and seem to be parasites or saprophytes and not symbionts. Baxter [3] considered that the mycorrhizal nature of the fungi is open to question, because he never found any hyphae in the tissues of well-preserved specimens.

Cordaites are the sister group to Coniferophytes. Fossil mycorrhizae have been observed in a few members of the latter clade. Stockey et al. [76] described arbuscular mycorrhizae from anatomically preserved roots of the Middle Eocene taxodiaceous conifer *Metasequoia milleri*. Mycorrhizal structures occur in the root cortex. Coiled hyphae are most common within cells of the inner cortical region, and these produce numerous, highly branched arbuscules. Another example of mycorrhizal association has been given by Cantrill and Douglas [10] on fossil roots with nodular and abbreviated lateral roots from the Lower Cretaceous of the Otway Basin, Victoria (Australia). Roots are placed together with foliage of *Geinitzia tetragona sp. nov.*, which is possibly taxodiaceous.

The occurrence of fossil ectomycorrhizae in Coniferophytes has been first demonstrated by LePage et al. [41]. Ectomycorrhizae have been found among permineralized plant remains in the Middle Eocene Princeton chert of British Columbia. They are associated with roots of *Pinus* and show a Hartig net that extends into the endodermis, a pseudoparenchymatous mantle, and contiguous extramatrical hyphae. The mycorrhizal rootlets lack root hairs and dichotomize repeatedly to form large, coralloid clusters. Reproductive structures are absent. For the fungus, the authors suggested the comparison with the extant basidiomycete genera *Rhizopogon* and *Suillus*. Ectomycorrhizal associations have also been described by Fairon-Demaret et al. [21] on small roots

that may belong to the taxodiaceous *Glyptostroboxylon* from the Eocene of Belgium (55 Myr). A mantle of hyphae surrounds each root frequently branched and a tiny Hartig net has been observed.

Except for all the Pinaceae and some genus in the Cupressaceae that form ectomycorrhizae, all living Coniferophytes in the northern hemisphere as well as in the southern hemisphere show arbuscular mycorrhizal associations [74,77].

5.15. *Gnetophytes*

No fossil mycorrhizae are known in Gnetophytes. Living Gnetophytes comprise the three genus *Gnetum*, *Ephedra*, and *Welwitschia*. Ectomycorrhizae have been observed in *Gnetum* by several authors [22,53,75]. Collier et al. [13] described the tendency to be mycorrhizal

for desert annual and perennial plants, and reported the occurrence of arbuscular mycorrhizae in *Ephedra trifurca*. *Welwitschia mirabilis* is also associated with arbuscular mycorrhizal fungi, but Jacobson et al. [31] noted that *W. mirabilis* is not mycorrhizal at sites of the Namib Desert where grasses are absent.

5.16. *Angiosperms*

To date no fossil mycorrhizal record is available for angiosperms. However, the three basic types of mycorrhizae occur in extant angiosperms. Only a few orders (Ceratophyllales, Caryophyllales, Brassicales) are usually considered as non-mycorrhizal [74,77]. A review of mycorrhizae in living angiosperms with information on the mycorrhizal status of the various families is given by Brundrett [9].

PLANTS	MYCORRHIZAL TYPES	PARAMYCORRHIZAE	EUMYCORRHIZAE
Marchantiophytes	AM Orchid/Ericoid M		
Anthocerotophytes	AM ?		
Bryophytes	NM		
<u>Aglaoophyton/Lyonophyton</u>	AM		
Paratracheophytes : <u>Rhynia</u>	AM		
<u>Zosterophyllophytes : Nothia ?</u>	AM ?		
<u>Asteroxylon</u>	AM		
<u>Lepidodendron</u>	AM ?		
Lycophytes	AM		
<u>Psilophyton</u>	?		
<u>Cladoxylales</u>	AM ?		
Sphenophytes	AM		
<u>Scleropteris</u>	?		
Filicophytes	AM		
Progymnosperms	?		
Pteridosperms	?		
<u>Cordaites : Amyelon</u>	AM ?		
<u>Geinitzia - Metasequoia</u>	AM		
<u>Pinus - Glyptostroboxylon</u>	ECM		
Coniférophytes	AM ECM		
<u>Antarticycas</u>	AM		
Cycadophytes	AM		
Gnetophytes	AM ECM		
Gingkophytes	AM		
Angiosperms	AM Orchid/Ericoid NM ECM		

Fig. 4. Mycorrhizal status of the embryophytes (including fossil and living clades). Orange: paramycorrhizae; green: eumycorrhizae; purple: awaiting further investigation; underlined: fossil members; AM = arbuscular mycorrhizae; NN = non-mycorrhizal; ECM = ectomycorrhizae; Orchid/Ericoid M = Orchid/Ericoid mycorrhizae.

Fig. 4 Statut mycorrhizien des embryophytes (regroupant les clades fossiles et actuels). En orange : paramycorhizes ; en vert : eumycorhizes ; en violet : cas demandant à être réétudiés ; les clades, genres et espèces fossiles sont soulignés ; AM = mycorhizes à arbuscules ; NN = non mycorrhizien ; ECM = ectomycorhizes ; Orchid/ericoid M = mycorhizes de type Orchidaceae/Ericales.

The above analyses of the mycorrhizal status of embryophytes are summarized in Fig. 4. The mycorrhizal status is presented in relation with the different clades of embryophytes, including fossil and living plants, and it shows the distinction between paramycorrhizae and eumycorrhizae. While mycorrhization is documented very well for living plants, there are only a few studies for fossil plants and the examples reported are often controversial. Some examples awaiting further analyses are shown in Fig. 4 and some others are being studied (*Nothia*, *Botryopteris*, *Amyelon*, *Glyptostroboxylon*...).

Plants belonging to the lycophytes and monilophytes clades represent the group in which fossil and living members develop both paramycorrhizae and eumycorrhizae. It seems very important to study the fungal symbiosis on this turning point group. This may contribute to understand why lycophytes and monilophytes have now so few surviving arborescent genus and why the angiosperms are dominant in modern environments.

An important point to be taken into consideration is the wet habitats of the earliest plants and of plants growing in cold environments [81]. It has been generally accepted that AM associations exist in living plants growing in wet habitats. Additionally, dark pigmented septate endophytes are frequent colonisers of plant roots under these extreme environmental conditions, capable of forming mutualistic associations functionally similar to mycorrhiza [34], together with an important role of melanin synthesis for protection. AM associations in wet habitats as well as dark pigmented septate endophytes reported by only a few authors have to be taken into account for an overall study of the mycorrhization.

6. Conclusion

Once on land, early plants had to build most of their organs and tissue systems. To do this, they had two alternatives: obtaining their own means of taking nutrients and water from the environment or developing associations with fungi that could provide these nutritional elements. The key role of the fungal symbiosis in the colonization of land has been recognized. The existence of mycorrhizae in fossil groups indicates that compatibility and ability to bypass the host defences were already developed in paramycorrhizae before the acquisition of root system and the evolution of eumycorrhizae. Further molecular studies are needed to detail this idea.

In both paramycorrhizae and eumycorrhizae types, plant cells are invaded by the fungus; the fungus is surrounded by the host plasmalemma and a dual apoplast; in living plants, the reduction of amyloplasts

is visible. Paramycorrhizae and eumycorrhizae are distinguished by many characteristics. Paramycorrhizae colonize thalli and shoot systems, show presence of chloroplasts in infected cells and limited photosynthetate transport. Thalli and shoot systems grow above ground and are highly dominant compared to underground structures. They display functions such as photosynthesis, transpiration, reproduction, transport and hormone production; they are also storage organs. These associations represent a primitive photosynthesis-powered plant–fungi–soil system; they are a key element of plant colonization, and they can be spread by vegetative reproduction. Eumycorrhizae, on the other hand, colonize root systems. Chloroplasts are absent in infected cells and a significant photosynthetate transport can be noted. Roots develop various functions such as carbon pumps, hydraulic conduits, or chemical factories; they represent storage organs, mechanical structures and develop an important absorptive network. In the course of plant evolution, roots have become more and more sophisticated. In spermatophytes, the root system is of equal importance to that of the shoot system, and eumycorrhizae occur as a highly evolved photosynthesis-powered plant–fungi–soil system. They are a key element of soil functioning and plant production. Associated with structures such as seeds and flowers, the existence of eumycorrhizae could explain the success of angiosperms in aerial environments.

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