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# Mycorrhization of fossil and living plants

Christine Strullu-Derrien [a,b,*], Désiré-Georges Strullu [a]

[a] *Laboratoire Mycorhizes, UFR Sciences, université d'Angers, 2, boulevard Lavoisier, 49045 Angers cedex, France*
[b] *'Paléobotanique, paléopalynologie et micropaléontologie', département de géologie, université de Liège, 4000 Liège 1, Belgium*

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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).***


**Résumé**

**La mycorrhization des plantes fossiles et actuelles.** Les enregistrements fossiles et la mycorhization, 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 mycorhiziennes 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 mycorhizienne 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) paramycorhizes pour la colonisation des thalles et des systèmes caulinaires ; (2) eumycorhizes pour la colonisation des systèmes racinaires. Cette note a pour but de montrer le statut mycorhizien des embryophytes dans les différents clades, en prenant en compte les taxons fossiles et actuels. Les implications de la symbiose mycorhizienne 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).***


*Keywords:* Mycorrhizae; Nomenclature; Embryophytes; Colonization of land

*Mots clés :* Mycorhizes ; Nomenclature ; Embryophytes ; Colonisation du milieu terrestre

* Corresponding author.
*E-mail address:* christine.strullu-derrien@univ-angers.fr (C. Strullu-Derrien).

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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 $CO_2$ 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 coalballs 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