

Review article

Geological History of the Glomaceae With Particular Reference to Mycorrhizal Symbiosis

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Abstract

Fossils resembling hyphae, vesicles, and spores of extant mycorrhizal fungi (Glomaceae *fam. nov.*) from almost all Periods and Epochs of the Phanerozoic are enumerated and their taxonomy and ecology re-appraised. The association of Glomaceae with the Rhynie Chert plants and their successors provides independent dating as well as a basis for comparison with the ubiquitous modern-day vesicular-arbuscular mycorrhizal symbionts. Independently occurring terrestrial and marine fossils are more difficult to classify or date because of simple, generalized morphology and the possibility of active anachronistic intrusion.

Keywords: fossil fungi, Glomaceae, VA mycorrhiza

1. Introduction

Among the multitude of symbioses between fungi and plants, that of vesicular-arbuscular mycorrhiza (VAM) appears to be the most prevalent, important and historically consequential: it is crucial for the functioning of the present-day natural, terrestrial ecosystems (Harley and Smith, 1983), and may have accompanied the rise of vascular plants on land and influenced their succession (Pirozynski, 1981). Yet, the geological history of

VAM fungi, unlike that of vascular plants, is largely unknown. Save for a few sporadic records in the literature of fungi referred or referable to VAM fungi, records which span the Phanerozoic, we do not know when, where and how such fungi came to be associated with plants or their precursors, where they came from and what and where their living relatives are. This uncertainty is reflected in the taxonomic placement of the extant VAM fungi in the Endogonaceae (Mucorales) or in the phylogenetically more distantly isolated Endogonales (Benjamin, 1979) in the zygomycetes. The purported link with zygomycetes is through the type genus *Endogone*, which is in many ways anomalous; *Glomus* and its segregates *Sclerocystis*, *Acaulospora*, *Entrophospora* and *Gigaspora*, all proven or suspected VA mycorrhizal fungi, do not form zygospores (Trappe, 1982; Trappe and Schenck, 1982). The placement of these VAM general alongside *Endogone* in the zygomycetes appears to result from historical precedent, superficial similarity of morphology, occasional involvement of both *Endogone* and *Glomus* in ectomycorrhizal symbiosis (Warcup, 1985), and suggestive use of semantics (Gibson and Kimbrough, 1985; Gibson et al., 1986): terms like "azygospore", "suspensor hypha" appear to make the relationship of VAM fungi with zygomycetes more legitimate than is warranted by the evidence. That evidence was temporarily strengthened by the demonstration of chitin in the cell walls of VAM fungi (Weijman and Meuzelaar, 1979), even though the accompanying presence of beta-glucans is not characteristic of the Mucorales, but rather of the Entomorphthorales which, for this and other reasons, offer a more satisfactory taxonomic repository. However, recent analyses of lipids and sterols tell another story. The high contents of palmitoleic acids (C16:1) and oleic acid (C18:1), the detection of gamma-linoleic acid (C18:3) precursor of very long chain polyunsaturated fatty acids such as C20:4, 20:5 and 22:4 (Beilby, 1980; Jabaji-Hare, 1988), the replacement of ergosterol by derivatives of cholesterol (Beilby and Kidby, 1980), all link VAM fungi with protoctista rather than true fungi. Whatever turn their future taxonomic re-disposition takes, the process must begin with the recognition of at least *Glomus* and its sclerocarpic counterpart *Sclerocystis* as members of a separate family, the Glomaceae (see appendix).

Some of the difficulties in identifying relationships of extant VAM fungi, at all levels of taxonomy, stem from their simplified or generalized morphology. When fossilization and laboratory extraction alter or eliminate characteristic features (e.g. arbuscules), or dissociate the fungus from its typical habitat (e.g. root cortex), there is little to distinguish VAM fungi from similar vesi-

cles with a filamentous attachment occurring in different classes of Fungi, Protoctista, Plantae and Animalia. Nevertheless, in this paper we consider a variety of such simple fossils and express our opinion or the lack of thereof, regarding their affiliation with Glomaceae or relationship to VA mycorrhizal fungi. Furthermore, we are basing some conclusions on published data which are often inadequate or inconclusive. Only a few specimens could be examined as some older preparations have deteriorated or have been lost and others could not be obtained from individuals or institutions.

2. Review of Geological History

Paleozoic

Cambro-Ordovician (590-440 myBP)

Paleobasidiospora taugourdeauii from Cambro-Ordovician of France and the Sahara (Fig. 1), was claimed (Locquin, 1983) to be a "paleobasidiomycete" composed of a filamentous thallus, up to 900 μm long, and a terminal sporangium (110-180 \times 40-90 μm) containing spores. Locquin's illustrations of the French specimen show "sporangia" as opaque, pyriform, somewhat asymmetrical vesicles. The material recovered from the Sahara sub-soils, which Locquin refers to the same genus and probably the same species (Fig. 1), is more translucent and, therefore, more readily identifiable as a *Glomus*, near *G. aggregatum* (known also from sand dunes) (Fig. 2), down to the fine detail of the "spore-in-spore" syndrome (Koske 1984, 1985a). In addition, the peculiar "foot cell" of *P. taugourdeauii* illustrated by Locquin (1983) (Fig. 1) has counterparts in germinating spores of *Glomus* spp. and *Sclerocystis rubiformis* (Fig. 4). Such similarities immediately suggest contamination of sub-soil with extant species associated with surface vegetation, and this we accept, at this stage, as the parsimonious explanation of the Saharan record. Whether the French specimen, which typifies *Paleobasidiospora*, falls into the same category is more open to doubt. The chief reason for this caution is that the fossil illustrated by Locquin is undoubtedly the same as that found by D.R. Kobluk (pers. comm.) in the Lower Cambrian marine sediments of Labrador (Fig. 6). This latter find, while supporting Paleozoic chronology of *Paleobasidiospora*, questions its relationship to *Glomus*, even to fungi generally, despite a close morphological similarity of the vesicle to spores of *Glomus aggregatum* (Fig. 5). In both specimens the filament is relatively long and it ends in another small swelling or vesicle. The determinate length of the filament (Fig. 6) places this organism within morphological range of hystrichospheres especially *Deunffia*



Plate I:

Scale bars = 40 μm

Figure 1. *Paleobasidiospora taugourdeauii* Locquin (1983) Pl. VI Fig. 5. (reproduced from the original).

Figure 2. *Glomus aggregatum* Schenck & Smith emend. Koske. (from National Mycological Herbarium, Ottawa, DAOM 189049).

Figure 3. *Deunffia furcata* Downie (from type, C. Downie collection University of Sheffield).

Figure 4. *Sclerocystis rubiformis* Gerd. & Trappe germinating spore (from DAOM 191549).

Figure 5. *Glomus aggregatum* Schenck & Smith emend. Koske. (from DAOM 189932).

Figure 6. A specimen from Lower Cambrian sediments from Labrador (from D.R. Kobluk, Erindale College, Toronto).

(Fig. 3) and *Domasia* (Downie, 1960), which may also more suitably accommodate another Paleozoic (Silurian) Saharan "fungus" described by Locquin (1981) as *Archechytridium operculatum* (Fig. 7).

Brunel et al. (1984) discovered more or less obovoid, sometimes stalked, bodies in Nepalese carbonates, and recorded them under the name *Paleobasidiospora cambronepalensis*. The dating of the matrix to Cambrian was influenced by two assumptions: that the largely non-descript fossils are congeneric with *Paleobasidiospora*, and that *Paleobasidiospora* is a narrowly specific, stratigraphic "index" or "marker" fossil. Neither assumption is warranted at present. We do not know what *Paleobasidiospora* is, or if any relationship exists between it and the hystrichospheres (whose biological affiliation is also uncertain) on one hand, and between it and *Glomus* as a mutualistic endophyte on the other. If the simplified morphology of VAM fungi is the product of evolution in an intracellular microhabitat (Law and Lewis, 1983; Law, 1985), their more free-living ancestors may be sufficiently different to be unrecognizable to us either as fossils or as living descendants.

Silurian (440-410 myBP)

A stronger contender for the earliest *Glomus* is Locquin's (1981) *Palaeomyces* from the Silurian of Estonia (Fig. 8). But, if there are no grounds for questioning its relationship to *Glomus*, there must be much less certainty about its age: in records based on dissociated *Glomus*-like fungi the probability of contamination is very real.

However, there are no good reasons for denying the existence of *Glomus* in the second half of the Silurian, when the first vascular plants or their imme-

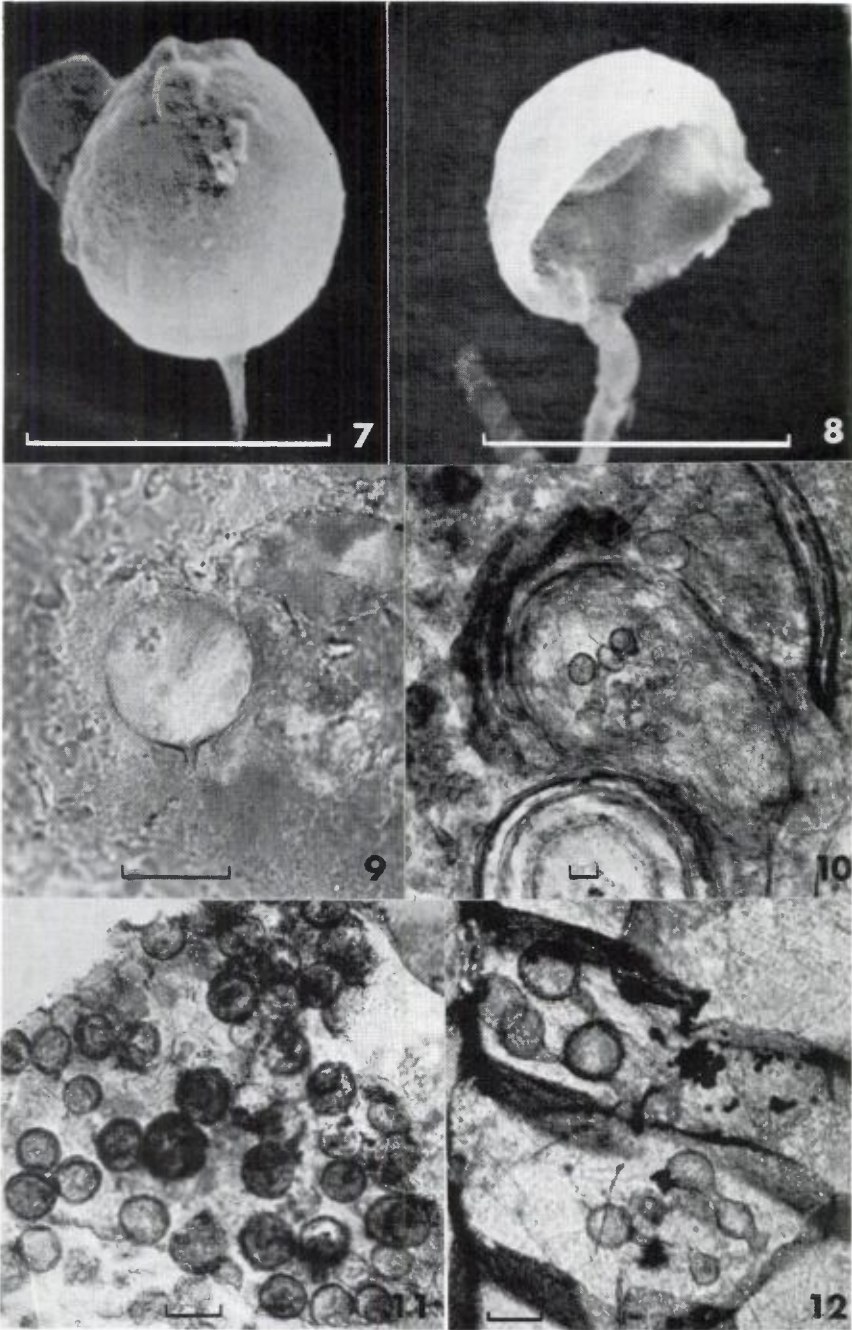


Plate II:

Scale bars = 40 μm

Figure 7. *Archechytridium operculatum* Locquin (1981) Pl. 9 Fig. 2 (reproduced from the original).

Figure 8. *Palaeomyces* sp. (Locquin, 1981) Pl. 9 Fig. 1 (reproduced from the original).

Figure 9. Single spore in the inner cortex of *Aglaophyton* (*Rhynia*) *major* stem (from W.C. Darah slide collection, National Museum of Natural Sciences, Ottawa).

Figure 10. *Palaeomyces simpsonii* Kidston & Lang, clusters of spores enclosed in a resting spore in the cortex of *Aglaophyton* (*Rhynia*) *major* stem (from W.C. Darah slide collection, National Museum of Natural Sciences, Ottawa).

Figure 11. Globose spores in the cortex of *Aglaophyton* (*Rhynia*) *major* stem (from W.C. Darah slide collection, National Museum of Natural Sciences, Ottawa).

Figure 12. *Peronosporites antiquarius* W. Smith (from type in Williamson collection #1923, British Museum, Natural History).

diate precursors appeared on land. The occurrence of endophytic Glomaceae in all three major lineages of Devonian tracheophytes, and what has been interpreted (Edwards, 1986) as their extinct protovascular relative, suggests an earlier, pre-Devonian origin of the association. Unfortunately a less equivocal fossil example of *Glomus*, as an "inhabitant" of a Silurian plant is yet to be collected.

Devonian (410-360 myBP)

In the now classical series of papers by Kidston and Lang, describing Rhynie Chert plants, one part (Kidston and Lang, 1921) was largely devoted to fungi. There they described fifteen types of fungi, of which seven were formally assigned binomials in *Palaeomyces*, a genus established earlier (Renault, 1896) for Carboniferous endophytes. Fourteen consist of non-septate hyphae bearing globose, ovoid or pyriform vesicles and thick-walled "resting spores" singly, (Fig. 9), or in clusters e.g. *P. simpsonii* (Fig. 10), within plant tissues or in the adjoining peaty matrix (Fig. 11). They compared *P. asteroxyli* and *P. gordonii* with Carboniferous *Peronosporites antiquarius* (Fig. 12) and *Protomycites protogenes* (Fig. 15). "Fungus No. 14" was compared to *Oochytrium lepidodendri* (*vide infra*), and all were compared with *Stigeosporium* (= *Glomus*) in roots of extant Marattiaceae (West, 1917). Vesicle-bearing hyphae which had intruded into spores of larger endophytes were compared with another Carboniferous fungus discovered by Williamson

(1888) in a *Lepidodendron* megaspore. Although Kidston and Lang regarded the endophytes to have been chiefly saprotrophic, they considered the possibility that the Rhynie plants, especially *Asteroxylon*, were mycotrophic when alive, or that some saprotrophs may have originated from mycotrophic organs. Butler (1939) and Stubblefield and Banks (1983) concurred. During a study of new material from Rhynie Chert, Boullard and Lemoigne (1971) found more evidence for a parasitic, rather than saprotrophic, relationship of the endophytic fungi. Furthermore, they considered an endophyte of *Rhynia gwynne-vaughanii* and *R. major* to be the same mutualistic, possibly even VA symbiont, and used this observation to support a claim that *R. gwynne-vaughanii* and *R. major* were respectively the gametophytes (mycothalli) and the sporophytes (mycorrhizomes) of the same plant. This view of relationship has been challenged on botanical evidence by Edwards (1986) who considered *Aglaophyton (Rhynia) major* to be a non-vascular intermediate between bryophytes and tracheophytes.

More recently Stubblefield and Banks (1983) demonstrated the presence of a vesicular fungus in the cortex of the aerial axes of *Psilophyton*. This endophyte was compared with *Palaeomyces gordonii* and, in turn, with *Glomus*. They did, however, reserve judgment regarding the plant's mycotrophic status. One of the reasons behind this caution (which has also been often expressed in the past) is the widespread misconception that the fungal symbiont is necessarily restricted to the subterranean parts, and that the endophyte's presence in decayed tissues negates its mycorrhizal habit. In answer to the first of these queries we refer the reader to Boullard's (1979) survey of mycotrophism in Pteridophytes. From this work it appears that the more nearly systemic presence of the fungus in both the sporophyte and the gametophyte might have been the rule rather than exception in Devonian tracheophytes. The association of VAM fungi with decaying tissues can derive not only from persistence of spores or vesicles in decomposing mycorrhizomes, mycothalli or mycorrhizae, but also from colonization of dead organic substrates by VAM fungi (Warner and Mosse, 1980; Warner, 1984). VA mycorrhizal fungi appear to have strong affinity for such substrates, and in some cases, grow saprophytically in soil (Hepper and Warner, 1983). Not only will they grow and sporulate inside spores of other species of VAM fungi (Koske, 1984, 1985b) but also in senescent or decaying leaves and leaf scales (Taber and Trappe, 1982; Parke and Linderman, 1980; Stasz and Sakai, 1984; Bagyaraj et al., 1979) seeds (Taber, 1982; Arvanetes and Taber, 1985) and mites (Rabatin and Rhodes, 1982). Several sporocarpic VAM fungi, epigeous (e.g. *Glomus*

macrocarpum, *G. radiatum*) or hypogeous (e.g. *Sclerocystis rubiformis*), are regularly associated with dead roots, wood debris and other decaying plant components in the soil.

Boullard and Lemoigne's (1971) re-examination of Rhynia Chert plants clearly demonstrated the presence, in addition to endophytic vesicles, of "sporocysts" containing an assortment of "spores" varying in number and size. They considered the fungus producing them to be parasitic rather than mutualistic. The somewhat enigmatic bodies contained within "sporocysts" are themselves morphologically similar to "sporocysts" suggesting a sporangium-spore relationship, though the possibility of the "spore" representing an intrusive fungus was already considered by Kidston and Lang (1921) and Gerdemann and Nicolson (1963). We can now state with more confidence that both interpretations are well founded: as Koske (1984, 1985b) demonstrated, VAM fungi frequently intrude their own spores, or spores of related species, and they also may play host to endoparasites, including chytrids. This last aspect of VAM fungi was reviewed by Paulitz and Menge (1984). The presence of parasitic chytrids inside Devonian Glomaceae is supported by Boullard and Lemoigne's demonstration of what can be interpreted as "exit pores". Nicolson (1981) remarked on the close morphological similarity of Devonian "sporocysts" to parasitized living examples, which claim is supported by recent demonstration of essentially modern-looking chytrids inside *Horneophyton* spores (Illman, 1984).

From Devonian (and Carboniferous) shales of North America Wood and Basson (1972) recovered an organism which they identified as *Microcodium elegans* (Fig. 13), a species originally described from Germany (Glück, 1912) as a calcified, Miocene green alga having discoid thalli made up of cuneiform cells. They assayed their specimens for chitin with positive results and concluded that *M. elegans* was a fungus. In fact, we interpret the "Devonian" specimen as a sporocarp and spores of *Sclerocystis clavisporea* (Fig. 14). Wood and Basson correctly regarded the fungus to be a contaminant which has actively intruded older laminar rocks and does not represent the Paleozoic biota. Whether the type and other specimens of *M. elegans* are of the same affiliation and origin is doubtful. The interpretations of calcite crystals recorded under this binomial from the Permian of Russia and from the Cretaceous, Eocene, Miocene, Pleistocene and Recent of Europe, Bikini, Saipan and Yucatan include physiochemical precipitates, anachronic organic intrusions and calcified mycorrhizae (Klappa, 1978).

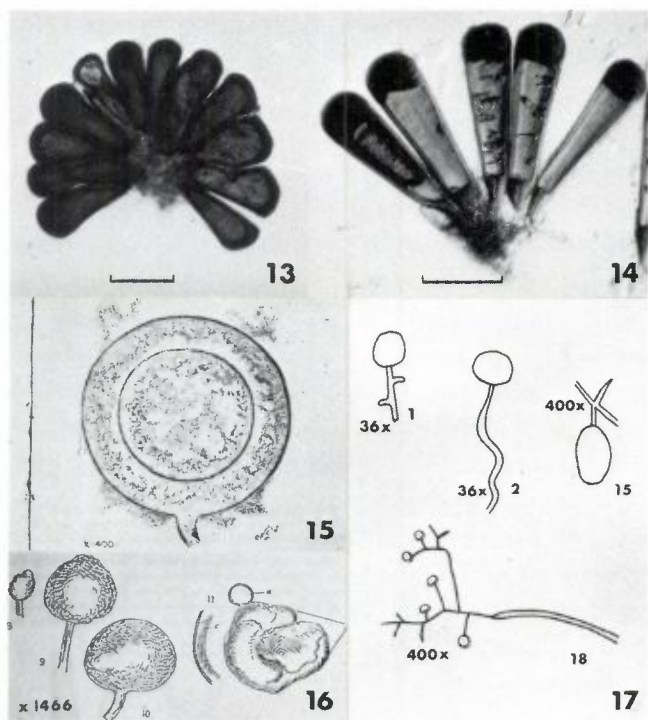


Plate III: Scale bars = 40 μ m

Figure 13. *Microcodium elegans* Glück cross section of sporocarp (from J.M. Wood M 1086, University of Missouri-Columbia).

Figure 14. *Sclerocystis clavispora* Trappe section of sporocarp (from J.M. Trappe 3568, Oregon State University Collection).

Figure 15. *Protomyces protogenes* W. Smith (1884) Fig. 140 (from the original).

Figure 16. *Phycomycites frodinghamii* Ellis (1915) Fig. 8-11 (reproduced from the original).

Figure 17. *Sphairanema*, *Nemaclada* and *Peronosporoides* species J. Smith (1896) Plate VII Figs. 1, *S. curta*; Fig. 2, *S. plana*; Fig. 15, *N. beveridgei*; Fig. 18, *P. carbonifera* (reproduced from the original).

Carboniferous (360-280 myBP)

The Carboniferous Period, which attracted so much palaeobotanical attention and yielded such wealth of data, has also provided references to endophytic fungi, either explicitly identified as mycorrhizal or assignable to VAM fungi in the light of present-day knowledge.

The story of these early discoveries was briefly recounted by Stubblefield et al. (1985) who have also documented with original data the incidence

of *Glomus*-like endophytes in several Carboniferous (and a Late Devonian) locations in North America.

An early find of what has been indirectly or directly compared with a VAM fungus (Seward, 1898; Butler, 1939; Wolf, 1969; Pirozynski, 1976) was described as *Peronosporites antiquarius* Smith (1877). It was found associated with a vascular axis of *Lepidodendron* in England. The fungus was in the form of globose "bladders" containing smaller bodies, and was interpreted as oogonia or zoosporangia containing zoospores. The specimen was subsequently redescribed (Smith, 1884), and the presence of discrete "zoospores" and the septate nature of hyphae de-emphasized, following criticism of the earlier interpretation. The fungus was re-illustrated by Seward (1898) from the original preparations (Fig. 12) and although in his version the endophyte looks much more like a VAM fungus, we interpret the fungi in the original slide as non-glomaceous endophytes. The same applies to Smith's other find, *Protomyces protogenes*, inside a rootlet of a *Lepidodendron* (Fig. 15): the original specimen does not represent Glomaceae. However, an unnamed fungus described by Cash and Hick (1879) from a rootlet of an English Carboniferous plant and identified with oospores of an oomycete, according to the illustrations and interpretation of Seward (1898), is more like a glomaceous endophyte.

J. Smith (1896) investigated plant and fungal microfossils in Carboniferous amber from Scotland. From the original descriptions and illustrations it is not possible to identify the organisms with any certainty (Fig. 17), but the "plants" described as *Sphairanema* ("a thread with globe") *curta* and especially *S. plana* and *Namaclada beveridgei*, and the fungus *Peronosporoides carbonifera* are potential synonyms of *Glomus*.

In France, Renault and Bertrand (1885) described *Grilletia sphaerospermii* which they claimed was a chytrid inhabiting the nucellus of a Carboniferous gymnosperm *Sphaerospermum*. The fungus consisted of hyphae about 5 μm in diameter, here and there bearing "sporangia" measuring 40–45 \times 20–25 μm . No illustrations were provided and, although one could argue that *Grilletia*'s modern representatives are semicolourous forms of *Glomus* (Taber, 1982; Arvanetes and Taber, 1985), the decision must be deferred until the original specimens have been re-examined. Oliver (1903) discussed *Grilletia sphaerospermii*-like organisms found in seeds of *Polylophospermum* and *Conostoma* from the Lower Carboniferous of France and Scotland respectively. Their identity remains obscure. The other chytrid identified by Renault (1895a, b) and in 1896 described as *Oochytrium lepidodendri* is

a stronger contender for redispotion into Glomaceae: although found in wood of a *Lepidodendron*, Renault himself suggested the endophyte's relationship to the "Endogènes". Even less doubt surrounds the glomaceous affinity of *Palaeomyces* established by Renault (1896) for *P. gracilis* and *P. majus* discovered in fragments of *Lepidodendron*. Seward (1898) compared *Palaeomyces* with the English Carboniferous endophytes referred to above. It will be remembered that Kidston and Lang (1921) adopted *Palaeomyces* for the Rhyne endophytes. Although Renault's material has not been available for study it is reasonable to interpret the original members of *Palaeomyces* as glomaceous endophytes referable to *Glomus*. One other taxon established by Renault (1896) may be of relevance and needs taxonomic re-appraisal: *Arthroon rochei* which was found in the cortex of a *Lepidodendron* root and identified as eggs of an arthropod.

More recent finds of spores in several coal swamp plants (Wagner and Taylor, 1981, 1982) were referred to *Glomus* and linked with mycotrophism. Stubblefield et al. (1985) reviewed earlier records of purported mycorrhizae of Palaeozoic plants with the following conclusions: the vesicles reported by Osborn (1909) and Halket (1930) from *Amyleon radicans* appear to be homologous with the vesicles of VAM fungi (Wolf, 1969), despite Cridland's (1962) reservations. The mycorrhizal nature of Weiss' (1904) "*Mycorrhizonium*" was questioned by Stubblefield et al. (1985), but this may be debated. Boullard (1973) not only considered this fossil to be a VAM fungus but also claimed a symbiotic (mutualistic) relationship of the association. On the other hand, Lignier's (1906) and Zimmerman's (1933) evidence for VAM fungi in a sequoioid root is not conclusive, and Cridland (1962) thought them more likely to be saprotrophic or parasitic. Similarly, what Andrews and Lenz (1943) claimed to be mycorrhizae or mycorrhizomes of a Carboniferous fern is not convincing. However, we have more confidence in identifying the "aquatic phycomycetes" of Agashe and Tilak (1970) from arborescent roots of an American calamite as Glomaceae.

A further source of Carboniferous Glomaceae may be sclerotinites associated with coals and considered by some authorities to be of fungal origin. The various globose and pyriform bodies discovered in thin polished sections and described by Stach and Pickhardt (1957) in *Globosasclerotes* and by Havlena (1956), Beneš (1978) and Beneš and Kraussová (1964, 1965) as *Crenasclerotes durus*, show some similarity to sections of VAM spores. However, this is as far as we are prepared to pursue this matter.

*Mesozoic**Triassic (250-210 myBP)*

Silicified roots, apparently of *Antarcticycas*, from Antarctica contain cortical endophytes which "compare closely to extant vesicular-arbuscular endomycorrhizae" (Stubblefield et al., 1987b). The similarities involve hyphae, *Glomus*-like vesicles and spores and, what is particularly significant as indicative of mycorrhizal mutualism, the arbuscules (Stubblefield et al., 1987c; Taylor and Stubblefield, 1987). In addition, a discrete sporocarp of a fungus referable to *Sclerocystis*, possibly even *S. rubiformis*, was found in the adjoining matrix (Stubblefield et al., 1987a).

Jurassic (210-140 myBP)

Ellis (1915) described and illustrated *Phycomycites frodinghamii*, a Jurassic mould from England (Fig. 16), which was not associated with any plant material, but rather with fragments of marine animals. Although compared by its author with Weiss' (1904) *Mycorrhizonium* and with *Peronosporites antiquarius* Smith (1877), *P. frodinghamii* must, at this stage, be interpreted as a marine microboring organism having its fossil counterpart in *Mycellites* recorded by Schmidt (1962) from a tooth of a Cretaceous shark from Belgium, and in modern fungal borings in pteropod shells (Zeff and Perkins, 1979). The second fungus recorded by Ellis (1915) from oolitic sandstone of Scotland and provisionally named *Palaeomyces* sp., also qualifies for classification among boring organisms of calcareous animal remains. In the same category belong the following:

1. *Phycomycites organisatus* and *P. rectus* described by Bender (1951) from Lias oolitic sediments in Germany
2. Globose bodies depicted in SEM photographs from late Jurassic foliated limestones of France (Debrand-Passard et al., 1975)
3. The specimens of Kar and Sah (1970) from Jurassic shales of India.

The rich biota of marine calcareous substrates is a "grey" area of biology, a twilight world in which boundaries between fungi and algae become very diffuse. It is neither our purpose, nor do we feel competent to discuss the subject in relation to fungi generally and the Glomaceae in particular. Since, however, some marine microborings resemble or were identified as Endogonaceae (Cavaliere and Alberte, 1970; Kohlmeyer, 1969), a few pertinent references need to be included. There can be little doubt that the fungus discovered inside cast-off shells of Atlantic jingle (*Anomia simplex*) by Johnson and Anderson, (1962 as "*Endogone*") is a *Glomus* referable to

G. aggregatum (Koske, 1985a). What is open to question is how the fungus got there? Did it invade living or cast off shells in the sea, or penetrate washed out, discarded shells from roots of coastal plants? Little information is available regarding the exact circumstances of the *Glomus-Anomia* association: the original specimens have been lost (T. Johnson, pers. comm.) and our examination of hundreds of *Anomia simplex* shells from intertidal and beach zones of the original site yielded no additional evidence. The only purportedly fungal microborings found by us were those resembling a form of *Protomyces protogenes* (Duncan, 1876 pl. XVI Fig. 14) inside the skeleton of a Silurian coral *Coniophyllum*, and assignable to *Arborella kohli* (Zebrowski, 1936; Porter and Zebrowski, 1937). Although it is tempting to comment on their resemblance to "small vegetative spores" described in *Glomus* by Warner and Mosse (1980), there are too many similar looking borings attributed to both fungi (Perkins and Tsentas, 1976) and algae (Golubic et al., 1975) in the sea.

Two other boring organisms, *Lithopythium gangliiforme* (Bornet and Flahault, 1889) from a mollusc shell and *Propyrium carbonarium* (Elias, 1966) from a Carboniferous bryozoan, closely resemble *Glomus*.

Cretaceous (140-65 myBP)

Srivastava (1968) described from the Maestrichtian of Alberta, *Rhizophaqites acinus* (Fig. 18), a species which he compared with *Endogone* (*Glomus fasciculatum*), and which Berch and Warner, (1985) and Berch (1985) identified as *Glomus deserticola*. The specific matching of the fossil with an extant VAM species, the state of preservation of the individual spores as well as "articulated" thalli, and the characteristics of the site, cumulatively call for caution in accepting the Cretaceous origin of this fossil. Even allowing for the usual sampling precautions, and the chronological congruence of the associated assemblage of pollen and spores (Srivastava, pers. comm.), intrusive contamination from roots cannot be wholly dismissed. However, the presence in the Late Cretaceous of essentially modern-looking VAM fungi is not unexpected. Also from Alberta, and preceding Srivastava's specimen by some 20 m.y., is Singh's (1983) *Peronosporites* (Fig. 19) which may be assigned both to the Cretaceous Period and to *Glomus aggregatum*. Also, what appears to be a poorly preserved spore of *Glomus* was recorded by Jen (1958) from China as *Sporites* sp.

An altogether different aspect of Late Cretaceous vesicles with filamentous attachments is *Ariadnaesporites* (Fig. 20) discussed by Hills (1967),

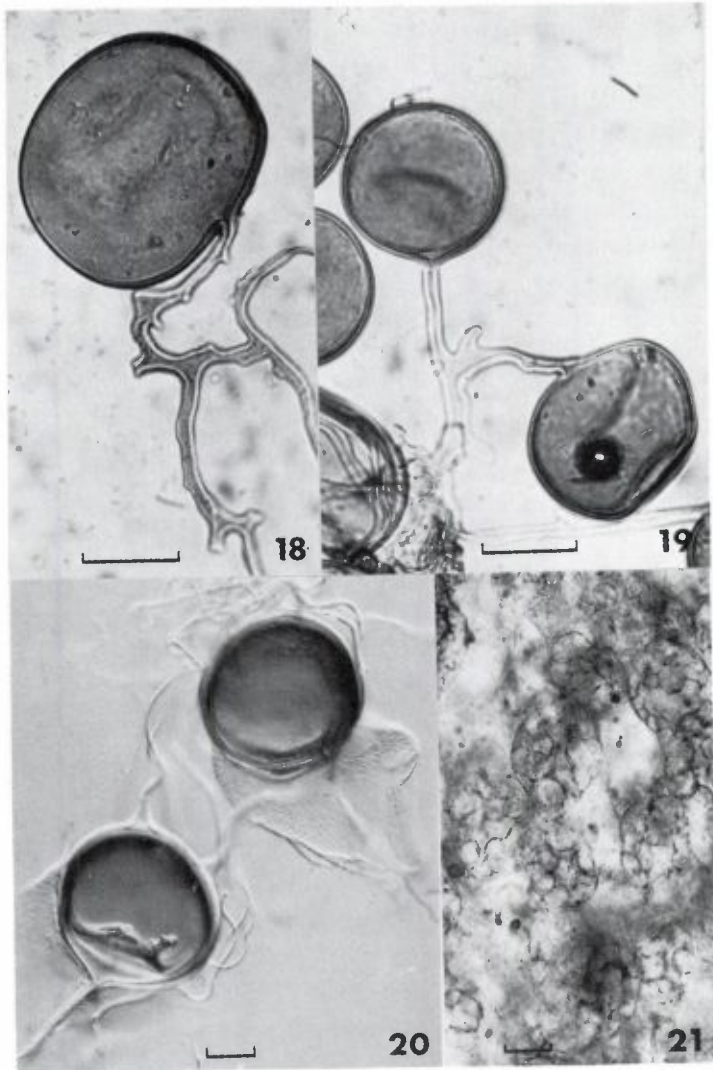


Plate IV: Scale bars = 40 μm

Figure 18. *Rhizophagites acinus* Srivastava (from type slide CH-14/1, Chevron Oil palynological collection).

Figure 19. *Peronosporites* sp. (from C. Singh slide C-25 #2, Research Council of Alberta).

Figure 20. *Ariadnaesporites intermedius* Hall (from the type slide M-70, J.W. Hall collection).

Figure 21. Endophytes in the type-specimen of *Osmundites dawkeri* (from W.G. Smith slide V6126, British Museum, Natural History).

Gunther and Hills (1970), Paden-Phillips and Felix (1971), Saad and Ghazaly (1976), Saad (1978) and Odéboode and Sharby (1980). Although on casual encounter, some of these fossils can be confused with intrusive *Glomus* species having more than one subtending hypha (e.g. *G. multisubstensum* Mukerji et al. (1983), *G. multicaulis* Gerdemann and Bakshi (1976) and *G. glomeratum* Sieverding (1987)), they represent an extinct group of apparently heterosporous aquatic ferns. Whether all tailed vesicles referred to *Ariadnaesporites* can be so disposed remains to be seen. We have not succeeded in obtaining loans of several requested specimens.

Tertiary

Paleocene (65-55 myBP)

In the Paleocene sediments of Yenisey Ridge, Western Siberia, Popov (1962) identified both *Rhizophagites butleri* and *R. minnesotensis* (vide infra) but his drawings, even though apparently of Glomaceae, are not sufficiently detailed to be more critically appraised.

Eocene (55-38 myBP)

A fungus discovered in the roots of *Osmundites dawkeri* (Smith, 1877, 1884) has been implicated with vesicular mycorrhizae (Seward, 1898; Boullard, 1973). The relevant specimen (at British Museum, Natural History) is inconclusive but not likely to represent Glomaceae (Fig. 21).

Oligocene (38-25 myBP)

Peronosporites palmi Berry (1916) was found in what was claimed to be a small stem of *Palmoxydon celluloseum* in the Lower Oligocene of Mississippi. Although described as having closely septate hyphae it was, nevertheless, confidently assigned to the Oomycota and compared with both *Peronosporites* and *Palacomycetes*. Until the specimen is located its identity will remain obscure.

Kar (1979) established *Aplanosporites* for *A. robustus*, a single spore with "tail-like appendage" or "flagellum". He pointed out its resemblance to Elsik's *Thecaspora* except for the absence of trilete mark and spinose perispore. He compared his find to a planktonic form recorded by Kar and Bose (1976) and Kar and Sah (1970) from the Carboniferous and Jurassic respectively, and considered fungal affinity suggested for a similar palynomorph from the Cretaceous of China by Jen (1958). The specimens, which we have not been able to examine are, most probably, *Glomus* spp.

Miocene (25-5 myBP)

Pythites disodilis was described by Baccarini (in Pampaloni, 1902) from Sicily and compared with *Endogone*. In fact what he illustrated in Fig. 6 could well be a zygosporangium of *Endogone* sensu stricto, or — perhaps — chlamydospore of *Scutellospora calospora* (cf. Trappe, 1982).

Macko (1957) illustrated a selection of globose fossils from the Lower Miocene of Poland which he interpreted as perithecia of a foliicolous ascomycete *Balladyna gardeniae* in different stages of development. They are clearly spores of *Glomus*.

Singh and Saxena (1981) recorded Kar's *Aplanosporites robustus* and another species, *A. bharwainensis*, from the Upper Siwalik Beds (mid — to late Miocene), claiming for both an uncertain affinity. Saxena et al. (1984) re-collected *A. robustus* from similarly dated strata, and although they did not explicitly identify it as *Glomus*, they correctly listed it among fossil fungi.

Pliocene (5-2 myBP)

Rhizophagites cerasiformis (Norris, 1986), sporadically found in the Nutwak formation, Mackenzie delta region, can be confidently assigned to *Glomus*.

*Quaternary**Pleistocene (2-0.1 myBP)*

The earlier record of Pleistocene Glomaceae, albeit not very conclusive, appears to be a vesicle inside wood of a Silesian *Cupressoxylon* included by Conwentz in the description of *Agaricites melleus* (Conw.) Meshinelli (1902).

Wolf (1969) correctly identified *Glomus* (as *Endogone*) in the late Pleistocene of North Carolina. Terasmae (1958) noted but failed to identify glomaceous spores from the Quaternary of Prince Edward Is., Canada, and Rao and Menon (1969) from South India.

Rhizophagus, which Butler (1939) recorded from Pleistocene clays of Alberta, was later formally described as *Rhizophagites butleri* by Rosendahl (1943) who typified it with a specimen from Minnesota, and who added another species *R. minnesotensis*. According to a later report (Rosendahl, 1948), both these fungi were common in Minnesota throughout the Pleistocene. Miller (1973) reported *Rhizophagites* from a glacial deposit of Lake Iroquois in New York State. Wilson (1965) repeatedly collected *Rhizophagites* in Pleistocene deposits of Oklahoma and, contradicting Rosendahl's (1943) interpretation, considered *R. butleri* to be extant.

Koske (1985a) reviewed the history of *R. butleri* which he considered to be *Glomus aggregatum*. According to Koske, *G. aggregatum* is particularly common in sand dunes where it sporulates between layers of mica, roots, decaying organic matter and, frequently, in dead spores of VAM fungi. The habitat conforms to that described by Butler (1939) for the Albertan specimen of *R. butleri*. *Rhizophagites butleri* and an unidentified, apparently glomaceous spore, were found in the Quaternary of Argentina (Schillizzi and Quattrocchio, 1982). Anderson et al. (1984) recorded a number of *G. fasciculatum* complex (apparently *G. aggregatum*) from postglacial lake sediments in Maine. Pirozynski et al. (1988) found what appear to be spores of *Glomus* and *Sclerocystis rubiformis* in clay balls associated with skeleton of an American mastodon in New Brunswick, Canada. A *Glomus* sp. was identified in clayey matrix containing a skeleton of a Giant Ground Sloth in Texas (Elsik, 1986 as "*Rhizophagites*"), but it is probably a contaminant from intruding roots.

3. Conclusion

Our conclusion, summarized in Table 1, is that fungi referable on the basis of simple morphology to the extant ubiquitous *Glomus* (and its close relatives) have a history that spans the Phanerozoic. Like the modern vesicular-arbuscular mycorrhizal *Glomus*, the fossils appear to have been characteristically associated with plants as biotrophic, symbiotic endophytes or intruders of plant remains. That the colonization of land by plants could have been facilitated by a mutualistic association with these fungi is, from circumstantial evidence, a reasonable and long-standing assumption (Nicolson, 1967, 1975; Boullard and Lemoigne, 1971; Lewis, 1987; Stubblefield and Taylor, 1988). That vascular plants are a product of that symbiosis (Pirozynski and Malloch, 1975; Pirozynski, 1981; Atsatt, 1988) is more speculative, but may yet prove testable at the molecular level.

Whether biotrophic fungi evolved early from similarly specialized progenitors and are at the base of phylogenetic radiation of fungi generally, or whether biotrophic fungi are polyphyletic end products of progressively specialized lineages is the subject of perennial debate (Heath, 1987). Each point of view calls for a different interpretation of the origin of mutualistic mycotrophic symbiosis and even of mutualism generally which is often argued as deriving from parasitism via coevolution. In the case of a mutualistic symbiosis of a plant with a basically soil-borne VAM fungus there are few compelling reasons to insist that, in the initial association the fungus par-

asitized the plant. Indeed, it may be more enlightening to consider the opposite, i.e. the plant parasitizing the fungus (Lewis, 1987; Malloch, 1988). In the early plants, and the surviving exponents of more ancient lineages, the presence of achlorophyllous mycotrophic gametophytes appears to be the rule rather than the exception (Boullard, 1979). Therefore the initial vesicular endophyte may not have been a biotrophic symbiont of algal progenitors of plants as suggested by Pirozynski and Malloch (1975) but a saprotroph. Perhaps one of the endolithic *Glomus*-like heterotrophs whose geological history in the sea parallels that of terrestrial vesicular or vesicular-arbuscular endophytes.

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4. Appendix

GLOMACEAE Piroz. et Dalpé *fam. nov.*

Typice symbiontes endophyticae radicum. Hyphae coenocyticae vesiculis intercellularibus, arbusculis intracellularibus. Status sexualis sporarum ignotus. Sporae singulares, fasciculatae vel in sporocarpis, extra et intraradicales, unicellulares, hyalinae ad pigmentiferam, plusminusve globosae, pariete crasso laeve vel scabrum.. Sporae affixae per unam ad aliquot hypham subtendam.

Genus typicus: *Glomus* Tulasne et Tulasne, *Giorn. Bot. Ital.* **2(1)**: 63. 1845.

(necnon *Sclerocystis* Berk. et Broome, *J. Linn. Soc. London* **14**: 137. 1875).

Typically endophytic root symbionts. Hyphae coenocytic, vesicles intercellular, arbuscules intracellular. Sexuality of spores not known. Spores occurring individually, in small clusters, or in sporocarps, extra and intraradical, hyaline to pigmented, more or less globose, thick-walled smooth or ornamented. Spores attached to one or several subtending hyphae.

Type genus: *Glomus* Tulasne and Tulasne

Other accepted genus: *Sclerocystis* Berk. and Broome.

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Table 1. Fossil record of Glomaceae and similar organisms

Paleozoic

Organisms	Fig.	Period/Epoch	Source	Description	Affiliation	References
<i>Paleobasidiospora taugourdeausii</i>		Cambro-Ordovician	Soil, France	Pyriform vesicles filaments ca. 20 μm wide	Hystrichospheres 50–60 \times 150 μm	Locquin, 1983
<i>Paleobasidiospora taugourdeausii</i>	1	Cambro-Ordovician	Sub-soil, Sahara		<i>Glomus aggregatum</i>	Locquin, 1983 contaminant
<i>Paleobasidiospora cambronepalensis</i>		Cambrian	Carbonates, Nepal	Obovoid stalked vesicles 170–700 \times 100–400 μm ; wall single, double or multilayered	? Glomaceae	Brunel et al., 1984
<i>Archechytridium operculatum</i>	7	Silurian	Sahara	Globose vesicles 300–370 μm diam., filaments 20 μm wide	Hystrichospheres or contaminant	Locquin, 1981
<i>Palaeomyces</i> sp.	8	Silurian	Soil, Estonia	Vesicle ca. 300 μm diam.	<i>Glomus</i> ? contaminant	Locquin, 1981
Fungus #1		Devonian	<i>Asterozylon mackiei</i> . Decayed phloem, Scotland	Septate hyphae	? <i>Rhizoctonia</i>	Boullard & Lemoigne, 1971 Kidston & Lang, 1921
Fungus #2 <i>Palaeomyces gordonii</i>		Devonian	<i>Aglaophyton (Rhynia)</i> <i>major</i> resting spores <i>R. gwynne-vaughanii</i> , <i>Horneophyton lignieri</i> , <i>Asterozylon mackiei</i> . Decayed stems, Scotland	Vesicles & multilayered	<i>Glomus</i>	Kidston & Lang, 1921 ca. 240 μm diam.
Fungus #3 <i>P. gordonii</i> var. <i>major</i>		Devonian	<i>Rhynia gwynne-vaughanii</i> . Decayed stems or peaty matrix, Scotland	Resting spore ca. 500 μm diam. wall stratified	<i>Glomus</i>	Kidston & Lang, 1921 Boullard & Lemoigne, 1971
Fungus #4		Devonian	<i>Asterozylon mackiei</i> . Decayed stem, Scotland	Thick-walled resting spores 120–150 μm diam.	?	Kidston & Lang, 1921
Fungus #5	9	Devonian	<i>Aglaophyton (Rhynia)</i> <i>major</i> Decayed stem, Scotland	Oval resting spores ca. 60 μm diam.	?	Kidston & Lang, 1921

Paleozoic

Organisms	Fig.	Period/Epoch	Source	Description	Affiliation	References
Fungus # 6		Devonian	<i>Aglaophyton (Rhynia) major</i> Decayed stem, Scotland	Vesicle-bearing mycelium (cf. <i>P. gordonii</i>)	<i>Glomus</i>	Kidston & Lang, 1921
Fungus # 7 <i>Palaeomyces asterozyki</i>		Devonian	<i>Asterozylon mackiei</i> . Inner cortex, Scotland	Vesicles ca. 80 μ m diam.	<i>Glomus</i>	Kidston & Lang, 1921
Fungus #8 <i>Palaeomyces horneae</i>		Devonian	<i>Horneophyton lignieri</i> . Protocorm-like rhizome, Scotland	Oval, dark, thick-walled vesicles or resting spores ca. 100 μ m diam.	<i>Glomus</i>	Kidston & Lang, 1921
Fungus #9 <i>Palaeomyces vestita</i>		Devonian	<i>Asterozylon mackiei</i> . Decayed stem, Scotland	Spherical resting spores ca. 45 μ m often in clusters	? Glomaceae	Kidston & Lang, 1921
Fungus # 10		Devonian	<i>Aglaophyton (Rhynia) major</i> , <i>R. gwynne-vaughanii</i> , <i>Asterozylon mackiei</i> , Decayed stem, Scotland	Clusters of vesicles ca. 40 μ m in decaying stems and adjoining matrix	? Glomaceae	Kidston & Lang, 1921
Fungus #11 <i>Palaeomyces agglomerata</i>		Devonian	As # 10	As # 10, smaller	? Glomaceae	Kidston & Lang, 1921
Fungus #12		Devonian	<i>Rhynia gwynne-vaughanii</i> . Decayed stem, Scotland	Piriform vesicles ca. 60 μ m diam.	<i>Glomus aggregatum</i> aff.	Kidston & Lang, 1921
Fungus #13 <i>Palaeomyces simpsonii</i>	10	Devonian	As #12	Erumpent clusters of vesicles up to 100 μ m diam.	<i>Glomus</i> immature	Kidston & Lang, 1921
Fungus #14	11	Devonian	Peaty matrix, Scotland	Vesiculate mycelium & resting spores in most cells & resting spores of other fungi	cf. <i>Oochytrium</i>	Kidston & Lang, 1921
Fungus # 15		Devonian	<i>Aglaophyton (Rhynia) major</i> . Decayed stem, Scotland	Spherical spores in vesicles of <i>Palaeomyces gordonii</i>	?	Kidston & Lang, 1921

Paleozoic

Organisms	Fig.	Period/Epoch	Source	Description	Affiliation	References
Unnamed		Devonian	<i>Aglaothyton (Rhynia) major</i> , <i>R. gwynne-vaughanii</i> . Cortical parenchyma, Scotland	Sporocysts with spores 185–230 μm , wall single or double, "spore in spore"	<i>Glomus aggregatum</i> aff.	Boullard & Lemoigne, 1971
<i>Palaeomyces gordonii</i>		Devonian	<i>Psilophyton dawsonii</i> .	Vesicles 175 μm diam. Aerial axes, Canada	<i>Glomus</i> sp. diam. wall double	Stubblefield & Banks, 1983
<i>Microcodium elegans</i>	13	? Devonian	Shales, USA	Discs 302–364 \times 354–426 μm made of cuneiform cells 82–152 \times 30–75.	<i>Sclerocystis rubiformis</i> contaminant	Wood & Basson, 1972
<i>Peronosporites antiquarius</i>	12	Carboniferous	<i>Lepidodendron</i> . Rootlets, England	Oogonia-zoosporangia 32.5 μm diam. hyphae 2–2.5 μm	? non glomaceous symbiont	Smith, W.G., 1877; Seward, 1898
<i>Protomyces protogenes</i>	15	Carboniferous	<i>Lepidodendron</i> . Rootlets, England	Oomycetes 160 μm diam. hyphae 10–15 μm	? non glomaceous symbiont	Smith, W.G., 1884
Unnamed		Carboniferous	Rootlets, England	Parasitic Oomycetes, 15 μm diam. Hyphae 1–2 μm	Glomaceae	Cash & Hick, 1879; Seward, 1898; Ellis, 1915 Weiss, 1904
<i>Nemaclada beveridgei</i> <i>Sphairanema curta</i> , <i>S. plana</i> <i>Peronosporoides carbonifera</i>	17	Carboniferous	Amber in coal,	Filaments with terminal Scotland	? vesicles	Smith, J., 1896
<i>Grilletia sphaerospermaii</i>		Carboniferous	<i>Sphaerospermum</i> . Nucellus, France	Chytrid 40–45 \times 20–25 μm hyphae 5 μm	? Glomaceae	Renault & Bertrand, 1885
<i>Oochytrium lepidodendri</i>		Carboniferous	<i>Lepidodendron</i> . Wood, megaspores, France	"Endogènes"	? Glomaceae	Renault, 1895–1896 Williamson, 1888
<i>Palaeomyces gracilis</i>		Carboniferous	<i>Lepidodendron</i> . Debris, including roots, France	Globose, ovoid of pyriform vesicles 25–40 μm diam. (spores)	<i>Glomus</i>	Renault, 1896
<i>Palaeomyces majus</i>		Carboniferous	<i>Lepidodendron</i> . Debris, France	Globose spores 96 μm diam.	<i>Glomus</i>	Renault, 1896
<i>Arthroon rochei</i>		Carboniferous	<i>Lepidodendron</i> . Root cortex	Egg of an arthropod	? Glomaceae	Renault, 1896

Paleozoic

Organisms	Fig.	Period/Epoch	Source	Description	Affiliation	References
Unnamed		Carboniferous	<i>Amyleon radicans</i> . Cordaitean root, England	Mycorrhiza	Glomaceae	Osborn, 1909; Halket, 1930 Wolf, 1969
<i>Mycorrhizonium</i> sp.		Carboniferous	Rootlet or rhizome, England	Mycorrhizome	<i>Glomaceae</i>	Weiss, 1904
Unnamed		Carboniferous	Sequoiod roots, France	Saprophyte / parasite	? <i>Glomaceae</i>	Lignier, 1906 Zimmerman, 1933 Cridland, 1962
Unnamed		Carboniferous	Fern, USA	Mycorrhizome	? <i>Glomaceae</i>	Andrews & Lenz, 1943
Unnamed		Carboniferous	<i>Astromyleon</i> <i>cauloides</i> . Arborescent roots, USA	Parasitic aquatic oomycetes or chytrids	<i>Glomaceae</i>	Agashe & Tilak, 1970
<i>Crenasclerotes durus</i> <i>Globosascletores</i>		Carboniferous Czechoslovakia	Sclerotinites, (thin sections)	Pyriform fungal spores	? Havlena, 1956;	Stach & Pickhardt, 1957 Beneš & Kraussová, 1964

Mesozoic

<i>Glomus</i>		Triassic	? <i>Antarcticyces</i> . Root cortex, Antarctica	VAM hyphae, pelotons, vesicles & arbuscles	<i>Glomus</i>	Stubblefield et al., 1987a, b
<i>Sclerocystia</i>		Triassic	Silicified peat, Antarctica	Cluster of vesicles (sporocarps)	<i>Sclerocystia</i> <i>S. rubiformis</i> aff.	Stubblefield et al. 1987c
<i>Phycomycites</i> <i>frodshamii</i>	16	Jurassic	Calcareous remains of marine animal, England	Sporangia 15–23 μ m diam. hyphae 2 μ m diam.	Marine boring microorganism	Ellis, 1915
<i>Phycomycites organisatus</i> <i>P. rectus</i>		Jurassic	Oolitic sediments, Germany	Fungal hyphae & globose or ellipsoid vesicles ca. 20 μ m diam.	Marine boring microorganism	Bender, 1951

Mesozoic

Organisms	Fig.	Period/Epoch	Source	Description	Affiliation	References
Unnamed		Jurassic	Foliated limestone, France	Filaments & vesicles microorganism 4-10 μm diam.	Marine boring microorganisms	Debrand Passard et al., 1975
Unnamed		Jurassic	Shale, India	Stalked vesicle ca. 40 μm diam.	? <i>Glomaceae</i>	Kar & Sah, 1970
<i>Mycellites</i> sp.		Cretaceous	Shark tooth, Belgium		Marine boring	Schmidt, 1962
<i>Rhizophagites acinus</i>	18	Cretaceous	Coal seam, Alberta, Canada	<i>Glomus fasciculatum</i> spores, 50-55 μm diam. hyphae 4-5 μm , wall 2-3 μm	<i>Glomus deserticola</i> , ? contaminant	Srivastava, 1968
<i>Peronosporites</i> sp.	19	Cretaceous	Deltaic, carbonaceous shale, Alberta	Vesicle 28-72 μm diam. hyphae 4-7 μm wide	<i>Glomus aggregatum</i>	Singh, 1983; Jen, 1958
<i>Sporites</i> sp.		Cretaceous	Gray clayey shale, Hunan, China	Ovoid stalked fungal spore ca. 80x40 μm	<i>Glomus</i> sp.	Jen, 1958

Tertiary

<i>Rhizophagites butleri</i> <i>R. minnesotensis</i>		Paleocene	Sediments, western Siberia	VAM fungi	<i>Glomus</i> aff.	Popov, 1962
Unnamed	21	Eocene	<i>Osmundites dawkeri</i> . Roots, England	Endophyte	? non glomaceous symbionts	Smith, 1877, 1884 Seward, 1898; Boullard, 1973
<i>Peronosporites palmae</i>		Oligocene	<i>Palmoxyton</i> <i>cellulosum</i> . Stem, USA	Oomycetes, 357 μm diam. hyphae septate	?	Berry, 1916
<i>Aplanosporites robustus</i>		Oligocene	Carbonaceous shale,	Planktonic vesicles with tail-like appendage 70-140 μm diam.	? <i>Glomus</i>	Kar, 1979 Singh & Saxena, 1981
<i>A. bharwainensis</i>		Miocene	Greenish/gray sandstone, India	Appendaged vesicles 62 x 49 μm	? <i>Glomus</i>	Singh & Saxena, 1981 Saxena et al., 1984
<i>Pythites disodilus</i>		Miocene	Bituminous shale Sicily	<i>Endogone</i> . Oospore 70-100 μm diam.	? <i>Endogone</i> or <i>Scutellospora</i>	Pampaloni, 1902
<i>Balladyna gardemiacae</i>		Miocene	Loam, Poland	Perithecia of follicolous ascmycetes up to 85 μm diam.	Glomaceae	Macko, 1957
<i>Rhizophagites</i> <i>cerasiformis</i>		Pliocene	Shallow marine shale NWT, Canada	spores (30-60 μm) with aseptate filaments	<i>Glomus</i> sp.	Norris, 1986

Quaternary

Organisms	Fig.	Period/Epoch	Source	Description	Affiliation	References
<i>Aqaricites melleus</i>		Pleistocene	<i>Cupressozylon</i> . Wood, Silesia	Vesicles 125 μm diam.	? <i>Glomus</i> aff.	Meshinelli, 1902
<i>Endogone</i> sp.		Pleistocene	Black lacustrine sediment, N.C., USA	VAM	<i>Glomus</i> sp.	Wolf, 1969
Unnamed		Pleistocene	Shallow marine silty clay, P.E.I., Canada	fungi	<i>Glomus</i> aff.	Terasmae, 1958
Unnamed		Pleistocene	Sediments, India	non septate hyphae bearing "swollen bodies" ca. 50 μm diam.	<i>Glomus</i> aff.	Rao & Menon, 1969
<i>Rhizophagites butleri</i> <i>R. minnesotensis</i>		Pleistocene	Lacustrine silts, Alberta, Minnesota, Oklahoma, Canada & USA	VAM fungi, 72-104 μm diam. wall, 4.8-7.9 μm hyphae 6-11.2 μm	<i>Glomus aggregatum</i>	Butler, 1939 Rosendahl, 1943; Wilson, 1965
<i>Rhizophagites</i> sp.		Pleistocene	Lacustrine sediments,	Chlamydo spores	<i>Glomus aggregatum</i>	Miller, 1973
Chlamydo spore I		Pleistocene	Clays, Argentina	Chlamydo spores 119-154 μm diam. walls 7 μm wide, 3 layers	<i>Glomus</i> sp.	Schillizzi & Quattrocchio, 1982
<i>Glomus fasciculatum</i>		Pleistocene	Lacustrine sediments Maine, USA		<i>Glomus aggregatum</i>	Anderson et al., 1984
<i>Glomus</i> & <i>Sclerocystis</i>		Pleistocene	Organic clay balls N.B., Canada	Spores	<i>Glomus</i> sp. <i>Sclerocystis rubiformis</i>	Pirozynski et al., 1988
<i>Rhizophagites</i> sp.		Pleistocene	Clay, Texas, USA	Spores	<i>Glomus</i> sp. ? contaminant.	Elsik, 1986