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The fossil record of the Peronosporomycetes (Oomycota)

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Abstract: Evidence of fossil Peronosporomycetes has been slow to accumulate. In this review various fossils historically assigned to the Peronosporomycetes are discussed briefly and an explanation is provided as to why the fossil record of this group has remained inconsistent. In recent years there have been several new reports of fossil peronosporomycetes based on structurally preserved oogonium-antheridium complexes from Devonian and Carboniferous rocks that demonstrate the existence of these organisms as fossils and refute the long-standing assumption that they are too delicate to be preserved. Among these are several types characterized by oogonial surface ornamentation patterns not seen in any modern members of the group. To date at least three groups of fossil vascular plants (i.e. lycophytes, ferns and seed ferns) are known to host peronosporomycetes as endophytes; however only one form has been identified as a parasite.

Key words: antheridium, Carboniferous, chert, coal ball, Devonian, fossil water mold, oogonium

INTRODUCTION

The Peronosporomycetes (also called Peronosporomycota, Oomycota or Oomycetes; David 2002) are heterotrophic eukaryotes that at one time were included with the Fungi based on overall morphology and physiology (Dick 2001). Today however they are known to represent close relatives of the chromophyte algae, such as the Bacillariophyta (diatoms) and

Phaeophyceae (brown algae), and other heterokont protists, including the Hyphochytridiomycota among other groups (Gunderson et al. 1987, Porter 2006, Rossman and Palm 2006, Beakes and Sekimoto 2009). Adl et al. (2005) placed the Peronosporomycetes in the Chromalveolata and within this super group the Stramenopiles (alternative names in use are Straminipila and Chromista; Beakes and Sekimoto 2009). Peronosporomycetes are distinguished from true Fungi by the possession of biflagellate zoospores that are anisokont and heterokont, oogamous sexual reproduction with gametangial meiosis, tubular mitochondrial cristae, as well as cell walls containing cellulose and the amino acid hydroxyproline (Dick 2001). The Peronosporomycetes today comprise approximately 500–800 species that thrive in both aquatic and terrestrial environments where they are effective as saprotrophs and disease-causative agents in plants and animals including humans (Margulis and Schwartz 1998). Within the group are economically important phytopathogens, including the root-rotting fungi and downy mildews (Kamoun 2003). One form, *Phytophthora infestans*, has significantly influenced history. As the causative agent of the potato late blight this organism was responsible for the famous potato famine in Ireland (1845–1852), which resulted in a major decline of the population through starvation and emigration (Gregory 1983, Mizubuti and Fry 2006).

Molecular clock estimates have been used to suggest that the first Peronosporomycetes occurred on Earth during the early Neoproterozoic, 1 000 000 000–524 000 000 y ago (Bhattacharya et al. 2009); it also has been speculated that Peronosporomycetes might have been among the first eukaryotes on Earth (Pirozynski 1976a, b). Dick (2001) notes that the environment and substrates in ancient terrestrial ecosystems were certainly suitable and could have supported these organisms by Paleozoic time. If these hypotheses are accurate, one would expect to find direct evidence of the group or at least some indirect indication of their activities in the fossil record. Because Peronosporomycetes today are capable of significantly affecting the performance of other organisms it is reasonable to speculate that they affected ecosystems in the past to a similar extent. Nevertheless efforts in reconstructing the evolutionary history and phylogeny of the Peronosporomycetes or of lineages within this group (e.g. Petersen and Rosendahl 2000, Beakes and Sekimoto 2009, Thines and Kamoun 2010, Uzuhashi et al. 2010) to date are

based exclusively on the analysis of extant members, while fossils have not been incorporated in such considerations for various reasons. In this paper we review the fossil evidence of Peronosporomycetes with a focus on recent discoveries in the group.

MODES OF PRESERVATION

The success of recognizing and documenting fossil Peronosporomycetes relies heavily on the mode of preservation and technique used to prepare samples. Coal balls and cherts to date represent the only sources of evidence for fossil Peronosporomycetes. While coal balls are concretions of calcium carbonate, chert deposits typically are an extremely dense microcrystalline or cryocrystalline type of sedimentary rock; in both the fossils are embedded by the mineral matrix (Taylor et al. 2009). Coal balls and chert preserve not only three-dimensional and structural features of the organisms (sometimes even in situ) but often also details of individual cells and subcellular structures. As a result of the fidelity of preservation, coal balls and chert provide an optimal matrix from which to extract information about fossil microorganisms in general and their associations and interactions with other components of the ecosystem (e.g. Taylor et al. 2004; Krings et al. 2007a, c). Moreover these modes of preservation provide the only sources of direct evidence of the microbial world within the context of ecosystems. Although various types of body fossils of microorganisms and/or indirect evidence of their activities also have been preserved by other modes, including other types of silicification (e.g. Stubblefield and Taylor 1985, 1986) and amber (e.g. Poinar 1992; Schmidt et al. 2004, 2008), peronosporomycetes have not yet been documented from these types of fossil preservation with a few possible exceptions (Smith 1896, Berry 1916, Ting and Nissenbaum 1986, Nissenbaum and Horowitz 1992, Rikkinen and Poinar 2001).

The high quality of preservation necessary for Peronosporomycetes to be definitively recognizable explains why the record of these organisms to date is largely limited to the Devonian (416 000 000–359 000 000 Ma) and Carboniferous (359 000 000–299 000 000 Ma) where such preservation occurs. Chert deposits and coal balls from these periods have been prepared for more than 100 y and studied more intensively than comparable deposits from the Mesozoic and Cenozoic (e.g. the Eocene [ca. 49 000 000 y ago] Princeton chert from Canada).

The most appropriate technique to study fossil Peronosporomycetes and fossils microorganisms in general that are preserved in chert and coal balls is the standard thin section technique (Hass and Rowe

1999), which involves a piece of the chert or coal ball being cemented to a glass slide, thinly sliced and then ground with an abrasive powder until the section is sufficiently thin to be examined in transmitted light.

HISTORICAL RECORDS

Petsamomyces polymorphus from the Early Proterozoic (ca. 2 000 000 000 y ago) of the Kola Peninsula is perhaps the oldest Precambrian microfossil suggested as being morphologically similar to structures seen in Peronosporomycetes (Belova and Akhmedov 2006); however similarities also exist with Chytridiomycota and other groups of “lower Fungi”. On the other hand Pirozynski (1976a) suggested that, among the abundant microfossils collectively termed acritarchs, which are common as early as the Proterozoic, some might represent either the oogonia or oospores of peronosporomycetes based on similarities in overall morphology. However this hypothesis has been largely overlooked and when addressed has been dismissed for the most part. For example Colbath and Grenfell (1995: p 303) indicated that Pirozynski’s morphological comparisons represented superficial similarities instead of common origins but also note that possible fungal affinities for at least some acritarchs cannot be discounted completely. We generally concur with this estimation but will show in this paper that some Carboniferous microfossils, which readily would be assigned to the acritarchs if found dispersed, are strikingly similar morphologically to certain recently described bona fide peronosporomycete oogonia from the Carboniferous.

There also have been sporadic reports of microborings and (micro)fossil remains interpreted as peronosporomycetous. One of these is *Palaeachlya*, a microboring that occurs in Ordovician (488 000 000–443 000 000 y ago) to Miocene (23 000 000–5 000 000 y ago) corals and other animal hard parts and is believed to have been formed by a peronosporomycete (Duncan 1876, Etheridge 1891). Although the microborings are somehow reminiscent of structures seen in modern peronosporomycetes, diagnostic features that could be used to positively identify their producers are lacking. *Palaeachlya* has been reinterpreted and now is thought to represent activities of endolithic algae (e.g. Elias and Lee 1993). Nevertheless today several endolithic and/or bioeroding marine Peronosporomycetes (e.g. Beuck and Freiwald 2005, Försterra et al. 2005) and also a few ichnotaxa (i.e. taxa based on the fossilized work of organisms) of fossil microborings have been attributed to this group of organisms based on structural similarities of the borings (e.g. Glaub 1994). One of these is *Saccomorpha terminalis* (Late Ordovician [455 000 000–445 000 000 y ago] to recent),

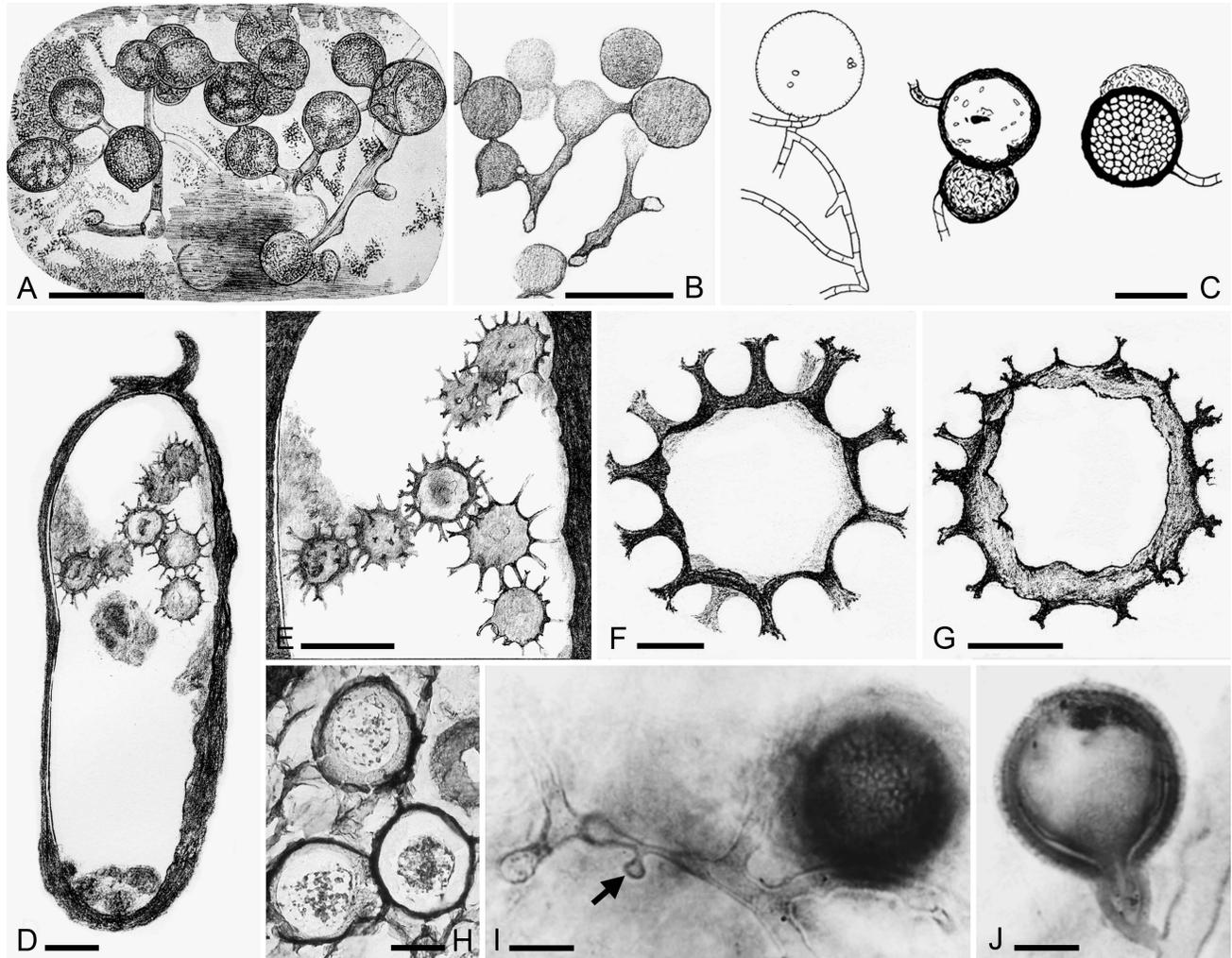


FIG. 1. A–H. Fossils historically assigned to the Peronosporomycetes. A. *Peronosporites antiquarius* (from Smith 1877: FIG. 1); bar = 50 μ m. B. *Peronosporites antiquarius* (from Williamson 1881: pl. 48, FIG. 36); bar = 50 μ m. C. *Peronosporoides palmi* (from Berry 1916: pl. 181, FIGS. 9–11); bar = 50 μ m. D and E. Cluster of *Zygospores* sp. in a sporangium (from Williamson 1883: pl. 31, FIG. 17 and pl. 32, FIG. 18); bars = 100 μ m. F and G. *Zygospores brevipes* (from Williamson 1880: pl. 19, FIGS. 51 and 53); bars = 20 μ m. H. *Albugo*-like oogonia from the Pennsylvanian of North America; bar = 50 μ m. I and J. *Hassiella monospora* (from Taylor et al. 2006: FIG. 1B, C). I. Arrow indicates an early developmental stage in oogonium formation. J. Note mature oogonium with what is interpreted as an amphigynous antheridium; bars = 10 μ m.

an ichnotaxon composed of narrow tunnels from which arise spherical structures on short pedicels that has been ascribed to a *Phytophthora*-like endolithic peronosporomycete (Radtke 1991, Vogel and Brett 2009). Wisshak et al. (2008: p 39) however state that the identity of the producer of *S. terminalis* remains problematic and requires reevaluation. A structurally preserved fossil organism interpreted as a peronosporomycete is *Peronosporites antiquarius* from the Carboniferous of Great Britain (Smith 1877, 1878). It consists of terminal and intercalary swellings produced on septate hyphae (FIG. 1A); smaller spherules within the swellings have been interpreted as oospores. After reviewing Smith's type material and analyzing additional specimens (FIG. 1B), Williamson (1881) con-

cluded that affinities with the Peronosporomycetes were questionable. Another fossil interpreted as a peronosporomycete is *Palaeophthora mohgaonensis* from the uppermost Maastrichtian (ca. 65 000 000 y ago, Cretaceous) Deccan Intertrappean beds of India (Singhai 1975, 1978). This fungus consists of a coenocytic mycelium endophytic in plant tissue. Some hyphal tips produce spherical structures (up to 12 μ m diam) referred to as oogonia; tubular hyphal tips occurring in the same host cells as the oogonia have been interpreted as antheridia. We hold the opinion that neither *P. antiquarius* nor *P. mohgaonensis* display features of sufficient clarity to allow assignment to any group of fungi or fungus-like organisms with confidence.

Peronosporites antiquarius is an excellent example of the type of fossil that historically have been referred to the Peronosporomycetes. The fact that the fossils described in these accounts (e.g. in Cash and Hick 1879, Williamson 1881, Loomis 1900, Pampaloni 1902, Elias 1966, Agashe and Tilak 1970 among others) cannot be assigned with confidence because diagnostic features are absent probably is the major reason that there has been no systematic study or comprehensive treatment of the fossil history of the group. This suggestion also was articulated by Johnson et al. (2002) in their comprehensive treatment of the Saprolegniales. In fact these authors regarded as inconclusive the fossil record published to date (i.e. 2002). This assumption is further supported by Dick (1988, 2001, 2002), who indicated that no indubitable fossil Peronosporomycetes had been reported to date and that fossil genera, such as *Achlyites*, *Ordovicimycetes*, *Palaeoperone*, *Peronosporoides*, *Palaeachlya*, *Propythium* and *Pythites* (TABLE I), can be discounted. However a slightly different opinion is offered by Blackwell and Powell (2000) who considered at least some of the old(er) records of fossils interpreted as Peronosporomycetes as persuasive. For example *Peronosporoides palmi* (later renamed *Peronosporites palmae* [Kalgutkar and Jansonius 2000]) (FIG. 1C) reported from structurally preserved wood of *Palmoxylon* from the lower Oligocene (ca. 30 000 000 y ago) of North America (Berry 1916) consists of spherical structures interpreted as oogonia, each approximately 135 µm diam, that are borne on narrow, septate hyphae. Some oogonia contain what appear to be oospores. What is interesting about these fossils are the collapsed sacs attached to the oogonia that are interpreted as antheridia. It is equally possible however that the sacs represent immature spherical structures of *P. palmi* or propagules of a second organism that incidentally became associated with the alleged oogonia. It also has been suggested that genus *Albugo* was present at least by the Carboniferous (Stidd and Cosentino 1975). An *Albugo*-like organism, which occurs in a Middle Pennsylvanian (ca. 310 000 000 y ago) seed specimen of *Nucellangium glabrum*, consists of irregular masses of tissue that extend into the region of the megagametophyte. Oogonia, each about 100 µm diam, are reported just beneath the integument (FIG. 1H). They possess a thick wall and may have an opaque central inclusion, which may represent the oosphere or developing oospore. The fossil oogonia are in various stages of development with some associated with structures suggestive of antheridia.

THE PROBLEM OF IDENTIFICATION

Several inherent problems have limited our understanding of the fossil record of the Peronosporomy-

cetes. Historically it has been assumed that Peronosporomycetes are extremely delicate organisms with poor preservation potential and thus probably not well represented in the fossil record (Taylor et al. 2006). Another problem relates to the usual incompleteness of the fossil record that results in the preservation of incomplete individuals and/or isolated stages of a life cycle. The life cycle of Peronosporomycetes includes both an asexual and a sexual reproduction phase (Dick 2001). Most of the structures formed during the life cycle are non-diagnostic (at least at the level of resolution available with light microscopy) if preserved isolated, thus making it difficult if not impossible to identify a fossil peronosporomycete based on these structures alone. One of the features that could be used to positively identify a fossil peronosporomycete is the biflagellate zoospores. However these structures are far too small to be observed in sufficient detail in transmitted light microscopy and the flagella normally would not be preserved (Taylor et al. 1992). As a result the only life cycle stage that lends itself to preservation and that can be used to positively identify fossil Peronosporomycetes is the characteristic oogonium-antheridium complex, a structure that forms during sexual reproduction (Dick 2001, Judelson 2009). While it is possible to identify fossil Peronosporomycetes based on the oogonium-antheridium complexes, determining their exact systematic position remains very difficult, if not impossible, because essential features used today in peronosporomycete taxonomy, especially molecular data, cannot be obtained from the fossils.

FOSSIL OOGONIUM-ANTHERIDIUM COMPLEXES

The oldest fossil evidence of a peronosporomycete that has been identified based on oogonium-antheridium complexes is *Hassiella monospora* from the Lower Devonian Rhynie chert (Taylor et al. 2006). The famous Rhynie chert, which has provided some of the most exquisitely preserved examples of late Paleozoic non-marine microbial life, represents a silicified hot-spring ecosystem approximately 400 Ma old (e.g. Kidston and Lang 1921, Taylor et al. 2004, Kerp and Hass 2004). *Hassiella monospora* occurs within the degrading plant material matrix and consists of a small mycelium of branched, aseptate (coenocytic) hyphae of varying diameter. Arising from several hyphae are ornamented (verrucate) oogonia, some showing evidence of amphigynous antheridia encircling the neck of the oogonium (FIG. 1J). What is perhaps most interesting is that, in addition to mature oogonia, several stages also show oogonium development (e.g. arrow in FIG. 1I). Also

TABLE I. Synopsis of fossil taxa (historically) assigned or related to the Peronosporomycetes, arranged according to their appearance in the text (in part based on Tiffney and Barghoorn 1974). The summary opinion of the taxonomic assignment (right column), is dealt with in three categories: (1) accepted, indicating that the fossils have been identified as peronosporomycetes based on oogonium-antheridium complexes or other persuasive structural correspondences to living forms; (2) inconclusive, indicating that the fossils are (somewhat) reminiscent of structures seen in modern peronosporomycetes, but lack features of sufficient clarity to assign them to that group with confidence; and (3) dubious, indicating that the fossils in all probability do not belong to the Peronosporomycetes

Taxon ¹	References ¹	Geologic age	Occurrence	Our opinion
<i>Petsamomyces polymorphus</i>	Belova and Akhmedov (2006)	Early Proterozoic	isolated in black shale	dubious
<i>Palaeachlya</i>	Duncan (1876); Etheridge (1891); Chapman (1911); Elias and Lee (1993)	four species; Ordovician to Miocene	endozoic in corals and other animal hard parts	inconclusive
<i>Saccomorpha terminalis</i>	Radtke (1991); Wisshak et al. (2008); Vogel and Brett (2009)	Ordovician to Recent	endolithic in rocks and animal hard parts	inconclusive
<i>Peronosporites</i>	Smith (1877, 1878); Loomis (1900); Ellis (1918); Pampaloni (1902); Ting and Nissenbaum (1986)	several species; Silurian, Pennsylvanian, Cretaceous, and Miocene	endozoic in animal hard parts (Silurian); in coal ball matrix and endophytic in lycophyte tissue (Pennsylvanian); in amber from Israel (Cretaceous); isolated in sediment (Miocene)	inconclusive
<i>Palaeophthora mohgaonensis</i>	Singhai (1975, 1978)	Cretaceous	endophytic in plant tissue preserved in chert	inconclusive
<i>Achlyites penetrans</i>	Duncan (1876); James (1893a, b); Meschinelli (1898)	Silurian and Tertiary	endozoic in corals and foraminifers	inconclusive
<i>Ordovicimycetes</i>	Elias (1966)	two species; Ordovician	endozoic in bryozoans	inconclusive
<i>Palaeoperone endophytica</i>	Etheridge (1891); Meschinelli (1898)	Pennsylvanian	endozoic in corals	inconclusive
<i>Peronosporoides</i>	Smith (1896); Berry (1916)	two species ² ; Pennsylvanian and Oligocene	in amber [Middletonite] from Great Britain (Pennsylvanian); in silicified palm stem (Oligocene)	inconclusive
<i>Propythium carbonarium</i>	Elias (1966)	Pennsylvanian	endozoic in bryozoans	inconclusive
<i>Pythites disodilis</i>	Pampaloni (1902)	Miocene	isolated in sediment	inconclusive
Albugo-like organism	Stidd and Cosentino (1975)	Pennsylvanian	endophytic in seed preserved in coal ball	inconclusive
<i>Hassiella monospora</i>	Taylor et al. (2006)	Devonian	in chert matrix	accepted
Unnamed 1 (FIG. 2A–C)	Krings et al. (2007b)	Devonian	in plant debris and microbial mats preserved in chert	accepted
Unnamed 2 (FIG. 2D and E)	Krings et al. (2010c)	Mississippian	in chert matrix	accepted
<i>Galtierella biscalithecae</i>	Krings et al. (2010b)	Pennsylvanian	endophytic in sporangia preserved in chert	accepted
Unnamed 3 (FIG. 2K)	Krings et al. (2010d)	Pennsylvanian	endophytic in lycophyte periderm preserved in coal ball	accepted
<i>Combresomyces</i>	Dotzler et al. (2008); Schwendemann et al. (2009); Strullu-Derrien et al. (2010)	two species; Mississippian, Pennsylvanian, and Triassic	endophytic in plant tissue preserved in chert and coal balls (Carboniferous); isolated in chert matrix (Triassic)	accepted
<i>Zygosporites</i>	Williamson (1878, 1880, 1883)	several species; Pennsylvanian	in coal ball matrix and endophytic in fern sporangia	inconclusive

¹ For additional fossils variously referred to the Peronosporomycetes and for further references, see Chapter 26 *The Fossil Record* of Johnson et al. (2002).

² The Oligocene species (*P. palmi* Berry 1916) has later been renamed *Peronosporites palmae* by Kalgutkar and Jansonius (2000).

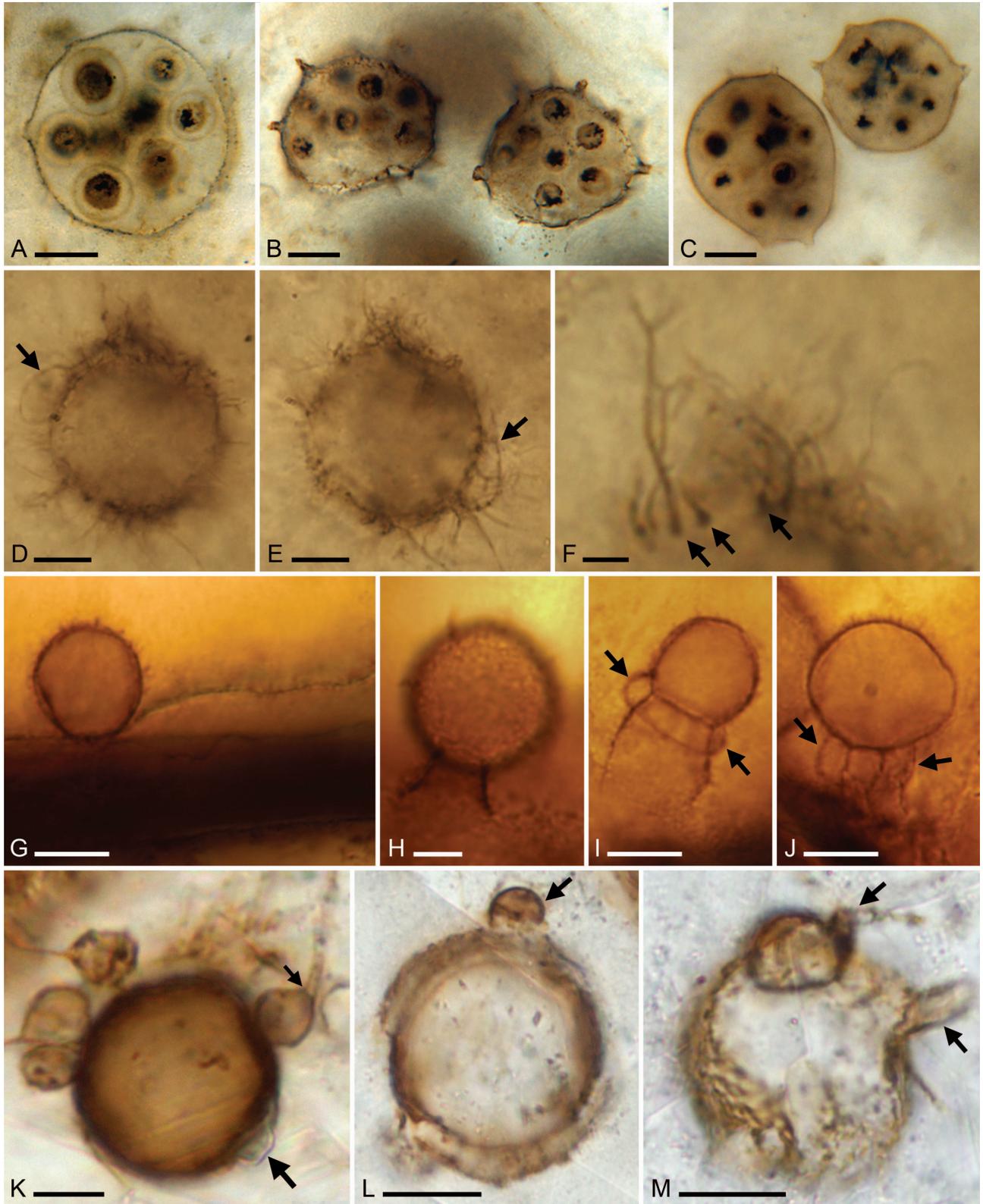


FIG. 2. A–C. Spherical putative oogonia containing several oospores from the Lower Devonian Rhynie chert (unpubl material, paleobotanical collection, Westfälische Wilhelms-Universität, Münster, Germany); bars = 10 μ m. D and E. Unnamed oogonium with two attached paragynous antheridia (arrows) from the Mississippian of France (from Krings et al. 2010c: FIGS. 2D, E); bars = 10 μ m. F. Surface ornament of oogonium (2D, E); arrows indicate bulb-like swellings at base of two surface

occurring in the Rhynie chert are various types of smooth-walled or spiny spherical or ovoid structures (FIG. 2A–C) up to 45 μm diam, which closely resemble the oogonia of certain extant peronosporomycetes, especially species in order Saprolegniales. These fossils characteristically occur associated with microbial mats and plant debris and sometimes may be solitary but more frequently occur in clusters (Krings et al. 2007b). Despite the absence of attached antheridia, these Rhynie chert structures contain internal spore-like bodies that are morphologically identical to oospores and thus suggestive of peronosporomycete affinities. Each of these smaller bodies is approximately 12 μm diam and consists of a central opaque region that is surrounded by a delicate wall that typically is separated from the central opaque region (e.g. FIG. 2A).

There are several examples of fossil Peronosporomycetes that are slightly younger geologically. One of these is from the Middle Mississippian (ca. 330 000 000 y ago) chert of central France. This paleoecosystem is interpreted as a series of pools and small lakes within an open swamp forest in an environment dominated by active volcanism (Rex 1986). It is hypothesized that the chert originated in the pools and lakes. The fossil peronosporomycete consists of a single spherical oogonium (FIG. 2D, E) approximately 20 μm diam to which are attached two paragynous antheridia (Krings et al. 2010c). Extending from the surface is a conspicuous ornamentation composed of elongate subtle extensions, less than 0.5 μm wide and up to 14 μm long, which are regularly distributed over the surface and densely spaced (FIG. 2F). Most of the extensions are one to several times furcate and attached to a small, bulb-like swelling at the base (arrows in FIG. 2F). Another peronosporomycete with ornamented oogonia occurs as an endophyte in the sporangium wall of a specimen of the fern *Biscalitheca* cf. *musata* preserved in the Late Pennsylvanian (ca. 300 000 000 y ago) Grand-Croix chert from France (Krings et al. 2010b). The Grand-Croix chert is especially important because it contains a flora that represents one of only a few European equivalents to the Late Pennsylvanian coal ball floras from North America (Galtier 2008). This peronosporomycete, *Galtierella biscalthethecae*, is

composed of wide aseptate hyphae that extend along the inner surface of the host cell walls (FIG. 2G) to form spherical and typically terminal oogonia (FIG. 2H–J). Several oogonia possess what are interpreted as amphigynous antheridia at the neck region of the oogonial stalk (arrows in FIG. 2I, J). Some of these structures (especially FIG. 2J) are quite similar to amphigynous antheridia seen in certain extant forms such as some species in *Phytophthora*. Perhaps the best fossil interpreted as a peronosporomycete is preserved in a coal ball from the Lower Coal Measures (Lower Pennsylvanian, ca. 315 000 000 y ago) of Great Britain. This extraordinary fossil (FIG. 2K) occurs within the periderm of an arborescent lycophyte and is represented by an unornamented oogonium approximately 15 μm diam to which are attached four paragynous and declinous, club-shaped antheridia (Krings et al. 2010d). Three antheridia are still in attachment with their subtending hyphae or antheridial stalks. The septum between one of the antheridia and its parental hypha is illustrated (arrow in FIG. 2K). In the same host tissue are other spherical structures that are 20–35 μm diam, are variously ornamented and also show evidence of what might represent paragynous antheridia (FIG. 2L, M).

An especially interesting aspect of the geologic history of the Peronosporomycetes is the occurrence of *Combresomyces cornifer* in lycophyte periderm cells from the Middle Mississippian chert of central France (Krings et al. 2007a, Dotzler et al. 2008). This fossil is represented by stalked oogonia characterized by a compound surface ornament consisting of hollow papillations of the oogonial wall (FIG. 3A, B). The tip of each of these structures bears antler-like extensions that are believed to have formed as a result of the condensation of some mucilaginous extra-oogonial wall secretion (Dotzler et al. 2008). Within some of the oogonia are single spheres interpreted as aplerotic oospores. In other specimens are relatively large clavate and paragynous antheridia adpressed to the oogonial wall (FIG. 3C). While many robust hyphae in the host cells correspond in diameter to the base of the oogonial stalk, no hyphae have been found attached. It is interesting to note that a similar but slightly younger type of oogonium,

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extensions (from Krings et al. 2010c: FIG. 2B); bar = 2 μm . G–J. Hyphae and oogonia of *Galtierella biscalthethecae* from the Pennsylvanian of France; specimens I and J with putative antheridia surrounding neck region (from Krings et al. 2010b: FIG. 1c, e, f and l); bars: G, I, J = 10 μm ; H = 5 μm . K. Oogonium with four attached antheridia from the Pennsylvanian of Great Britain; large arrow indicates attachment of oogonial stalk, small arrow shows septum between antheridium and antheridial hypha (from Krings et al. 2010d, FIG. 2C); bar = 5 μm . L and M. Spherical structures showing attachment of smaller spheres (antheridia?) from the Pennsylvanian of Great Britain; arrows (M) indicate separate subtending hyphae (unpubl material, Max Hirmer slide collection, BSPG, Munich, Germany); bars = 10 μm .

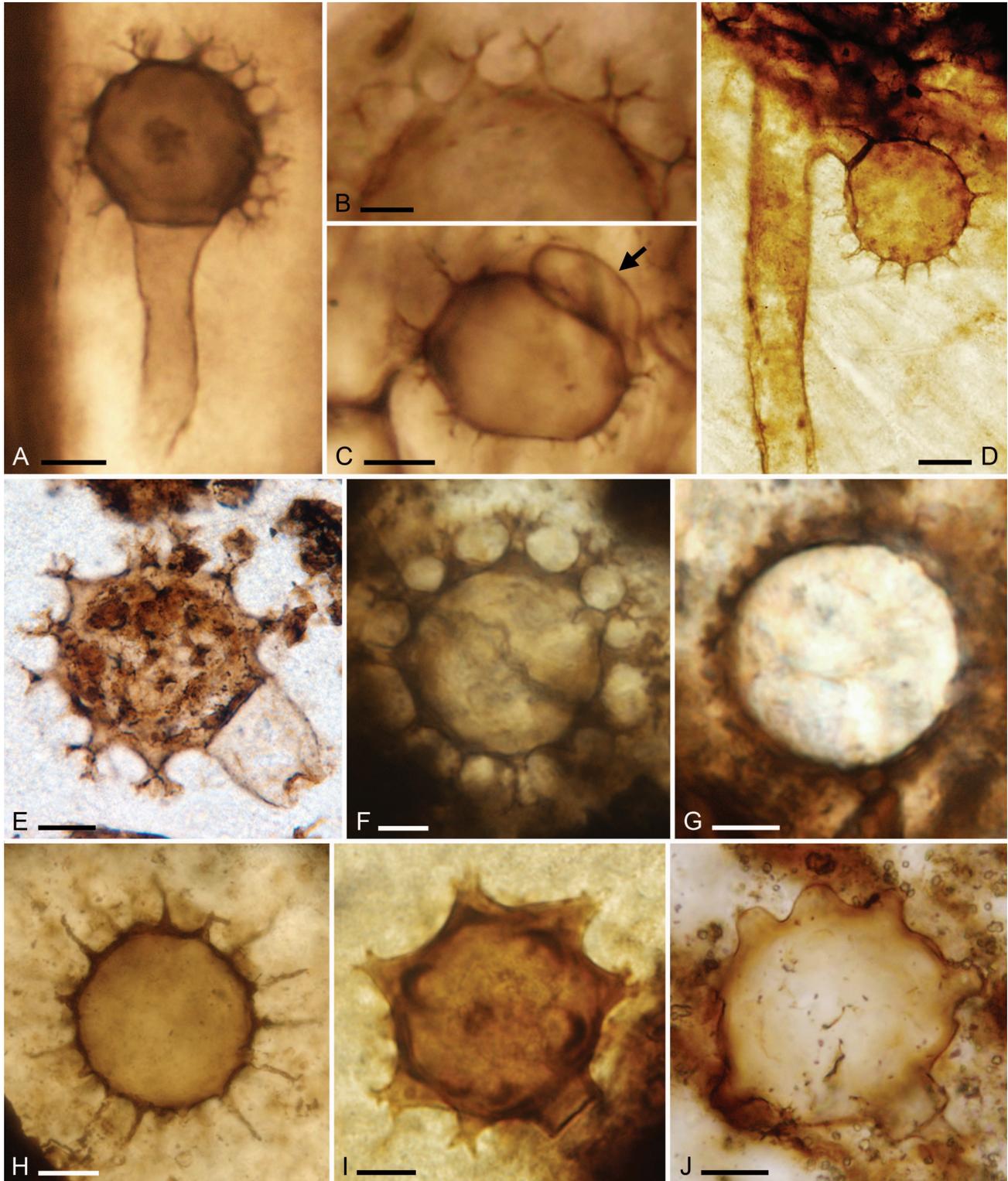


FIG. 3. A–C. *Combresomyces cornifer* from the Mississippian of France. A. Oogonium on stout subtending hypha. B. Detail of surface ornament. C. Specimen with attached antheridium (arrow) (from Dotzler et al. 2008: FIGS. 1N, K and 2B); bars: A, C = 10 μ m; B = 5 μ m. D. *Combresomyces williamsonii* from the Lower Pennsylvanian of Great Britain (from Strullu-Derrien et al. 2010: FIG. 2a–i); bar = 35 μ m. E. *Combresomyces cornifer* from the Triassic of Antarctica (from Schwendemann et al. 2009: pl. 1, FIG. 1); bar = 20 μ m. F–H. Various ornamented spherical microfossils in coal balls from the Lower Pennsylvanian of Great Britain (unpubl material, Max Hirmer slide collection, BSPG, Munich, Germany); bars: F, G = 10 μ m; H = 20 μ m. I. Putative

Combresomyces williamsonii, has been found in the cortical tissues of a seed fern from the Lower Coal Measures of Great Britain (Strullu-Derrien et al. 2010). These specimens, some of which occur in organic attachment to hyphae up to 40 μm wide (FIG. 3D), differ from *C. cornifer* in the size (they are up to four times larger than *C. cornifer*), general organization of the surface ornament and the presence of both paragynous and hypogynous antheridia. Another report of *C. cornifer* comes from the Triassic (ca. 215 000 000 y ago) of Antarctica (Schwendemann et al. 2009). While these oogonia (FIG. 3E) are morphologically identical to those from the Mississippian of France, they are appreciably larger ($\sim 100 \mu\text{m}$ diam) and do not occur endophytically but instead are isolated within degrading plant material. Several specimens also have been found between the seed coat and megagametophyte of a conifer seed containing a well developed embryo (Schwendemann et al. 2010).

PUTATIVE REMAINS OF PERONOSPOROMYCETES

Numerous examples of fossil microorganisms are abundant in the rock record for which the biological affinities remain unresolved. Especially interesting are several types of small, prominently ornamented spherical structures (FIG. 3F–J) that occur in abundance in coal balls from the Lower Coal Measures of Great Britain (Williamson 1878, 1880, 1883) and that also have been discovered in coal balls and chert deposits elsewhere (e.g. Krings et al. 2009). One of the more common types (FIG. 1F, G) initially was named *Zygosporites* (Williamson 1878, 1880), a genus that was interpreted as a type of land plant spore because some of the specimens occurred clustered within a sporangium (FIG. 1D, E). Later, Williamson (1883) termed *Zygosporites* as superfluous and suggested that the genus be deleted from the record. Some of the fossils that might have been included in *Zygosporites* are characterized by surface ornamentation patterns that are remarkably similar to those of *Combresomyces* (e.g. cf. FIG. 3F and 3A, D), whereas others if found dispersed might be assigned to the acritarchs or remain unresolved (e.g. FIG. 3G, H). None of these structures have been found with attached antheridia, but some display the typical truncated, collar-like extension of the oogonium

where the parental hypha was attached (e.g. FIG. 3I, J). One form (FIG. 3I) initially was found dispersed but also later was found in the space between the integument and megasporangium of a silicified *Stephanospermum akenioides* seed from the Upper Pennsylvanian of France (Krings et al. 2010a). Within the seed are coenocytic hyphae that are identical in diameter to the collar-like extension of the ornamented structure, suggesting that both might belong to the same organism. We continue to advance the hypothesis that at least some of these enigmatic microfossils represent peronosporomycete oogonia or oospores. Because of the indisputable similarity of many of these forms to structures that, if found in the dispersed record, would readily be placed within the acritarchs we are inclined to give some merit to the largely ignored hypothesis that certain acritarchs are peronosporomycetes initially advanced by Pirozynski (1976a).

DISCUSSION

Despite the fact that there are relatively few records of bona fide fossil Peronosporomycetes (TABLE I), the record appears to suggest that at least by the Carboniferous a considerable number of members of this group of organisms lived as endophytes within the tissues of land plants. Plant organs colonized by fossil peronosporomycetes include seeds, extraxylary (cortical) tissue of lycophytes and a seed fern and the sporangia of a fern. In none of these host tissues and organs is there any evidence of a host reaction or other anatomical features that might indicate disease. Moreover only one of the endophytes (i.e. *Combresomyces williamsonii*; Strullu-Derrien et al. 2010) shows structural features (i.e. haustoria) suggestive of parasitism. This might suggest that most Carboniferous Peronosporomycetes lived as saprotrophs. As far as is known none have been reported associated with roots or other types of below ground anchoring and absorbing organs.

While Dick (2001) suggested that some morphogenetic patterns of oogonial wall ornamentation in Peronosporomycetes might have phylogenetic value, ornament development in fossil peronosporomycete oogonia cannot be resolved with sufficient clarity to provide a character that can be used in phylogenetic analyses (Dotzler et al. 2008). Krings et al. (2010c)

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oogonium discovered within a seed from the Pennsylvanian of France; note truncated extension that represents the attachment point to the parental hypha (from Krings et al. 2010a: pl. 1, FIG. 9); bar = 15 μm . J. Putative oogonium showing truncated attachment point to the parental hypha from the Mississippian of France (unpubl material, paleobotanical collection, Université Montpellier II, France); bar = 15 μm .

note that the two fossil forms from the Mississippian of France (i.e. the unnamed form illustrated in FIG. 2D, E and *Combresomyces cornifer* in FIG. 3A–C) both possess complex oogonial ornaments that differ in morphology from those in extant Peronosporomycetes. While acknowledging the uncertain value of this feature with regard to peronosporomycete phylogeny, they hypothesize that fossil groups or lineages of Peronosporomycetes might have existed that were characterized by various features (and developmental patterns) or combinations of features (and developmental patterns) unknown in any extant groups.

It is perhaps not surprising that the evolutionary history of a group of fungus-like organisms such as the Peronosporomycetes, in which most of the primary diagnostic features are difficult to recognize as fossils, has a poorly understood fossil record. There are several reasons for this situation. One has been mentioned already and concerns the idea that the preservation potential of these organisms is far too low to provide a reliably identified fossil record. A second reason for the limited fossil record is the preparation technique used to study fossil organisms of this type. The cellulose acetate peel technique, the standard procedure used in examining Carboniferous coal ball plants (Galtier and Philipps 1999), is inadequate compared to the more traditional time-consuming preparation of thin sections (Hass and Rowe 1999). One additional limitation is the obvious fact that, while the paleobotanical community has the fossil specimens but mostly lacks the ability to identify the organisms, the mycological community has the experience but normally lacks the fossil specimens.

As we have attempted to demonstrate in this paper, organisms such as the Peronosporomycetes are represented in the fossil record and recognizable if the preservation is adequate and the techniques used to prepare the material allows for appropriate resolution. We hope that this review stimulates the further exchange of ideas so as to enable paleobiologists to better appreciate the wealth of information that is contained in the microorganisms present with their megafossils. Concomitantly the mycological community might profit from incorporating paleobiological data in their approaches to understanding the biology and evolution of microorganisms in time and space.

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