SYMBIOSIS (2005) 40, 119–135 ©2005 Balaban, Philadelphia/Rehovot ISSN 0334-5114

Review article.

Fossil microorganisms and land plants: Associations and interactions

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(Received November 30, 2005; Accepted December 25, 2005)

Abstract
Microorganisms are critical in the bio- and geosphere today, and certainly performed similar functions in ancient ecosystems. Bacteria, cyanobacteria, microalgae, and various fungi and fungi-like organisms constitute a substantial component of these ancient communities, and have been responsible for the evolution and sustainability of the ecosystems in functions ranging from decomposition of metabolites to catalyzation of nutrient cycles. This review provides examples of associations and interactions between microorganisms and land plants, principally from the Devonian and Carboniferous. During this time span of approximately 150 myr, most of the vascular plant lineages evolved and radiated into new terrestrial niches. Several exceptionally well-preserved fossil communities are used to demonstrate a wide range of biological interactions. Although none of the land plant partners exist today, many of the microorganisms involved appear morphologically little changed. Moreover, some interactions suggest that the genetic code and biochemical pathways necessary for the associations and interactions to be successful evolved early in the lineages of microorganisms involved, and have seemingly remained unchanged to the present. The examination of microorganism/land plant associations (and interactions) provides another level of biological resolution that can be used to track coevolutionary processes and help formulate hypotheses designed to more fully understand the evolutionary history of ecosystems.

Keywords: Saprophytism, parasitism, mutualism, Paleozoic, Devonian, Carboniferous (=Mississippian, Pennsylvanian), fungi, bacteria, cyanobacteria, algae, ecology, interaction

1. Introduction

It is estimated that there are more than five million different kinds of organisms on Earth today, most of which are extremely small. These minute life forms are commonly termed 'microorganisms' or 'microbes', regardless of their biological affinities. In this review we adopt this broad definition and include bacteria, cyanobacteria, microalgae, and a variety of fungi and fungi-like organisms. Despite their small size, microorganisms are essential components of all ecosystems today, and they function as decomposers and as drivers of local and global nutrient cycles (e.g., Bottjer, 2005); moreover, photoautotrophic microorganisms (e.g., phytoplankton) represent an important source of oxygen to aquatic animals. During the last twenty-five years, one of the most profound achievements of microbiological and ecological research is the increasingly detailed documentation of how microbial life is involved in the various processes that characterize complex modern ecosystems, and how microorganisms drive the evolution and sustainability of these ecosystems (e.g., Staley and Reysenbach, 2002 and references therein).

Although microorganisms certainly played an equally important role in ancient ecosystems, only recently have they received increased attention when examining the fossil record. This is due in part to the fact that microorganisms generally are not readily preserved as fossils, and most sites that yield well-preserved macrofossils do not contain direct evidence for the presence of microorganisms other than perhaps decomposed plant and animal remains. Moreover, historically even in instances where microorganisms are preserved, the researchers often lacked appropriate microscopic techniques needed to adequately study these

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fossils. Further contributing to a lack of interest by most paleontologists in describing microorganisms was the fact that there remained many undescribed macrofossils available for study. In addition, research on microfossils today is still limited because many scholars unknowingly created an inherent bias against the evidence of microorganisms since the majority of specimens that they collected were selected because of their completeness. This has resulted in a significant underrepresentation of microorganisms and evidence of their activities and interactions in many collections since, by their very nature, microorganisms would most often be abundant in the incomplete, highly altered or degraded specimens. These are, of course, not the types of specimens typically used in defining land plant and animal species. Further contributing to the lack of a substantial body of information on fossil microorganisms is the fact that few paleontologists have training in microbiology, and thus lack the knowledge to adequately identify and interpret fossil microorganisms.

In spite of these limitations, there are a few early reports of microbial life in ancient ecosystems. Foremost among these are the studies by B. Renault on several Carboniferous and Permian cherts from France (a series of papers between 1885 and 1903), and the detailed descriptions by R. Kidston and W.H. Lang (1921) of microorganisms from the Lower Devonian Rhynie chert. This *in situ* silicified ecosystem is interpreted as a hot springs environment dominated by ephemeral fresh water pools that hosted a diverse assemblage of plants, animals, and microorganisms (e.g., Kerp and Hass, 2004; Trewin and Rice, 2004).

During the last 30 years, some of the limiting factors that adversely affected the study of microorganisms have changed. As a result, today there is an increasing body of literature on fossil microbial life, including some studies that document complex levels of biological interaction. In spite of advances in microscopy and imaging techniques, even for exceptionally well-preserved fossil microorganisms, it remains impossible in many instances to even broadly determine affinities and/or potential interactions. In other cases, the fossil record provides obvious examples of microorganisms interacting with land plants at the time they were preserved. For example, fossil epiphyllous fungi on leaves and parasitic chytrids in and on spores can easily be detected and fully analyzed today. In some instances there may be no obvious direct evidence of the fossil microbial partner; however, altered cells and tissue systems (e.g., necrotic areas, thickened cell walls) in the plant partner indicate that some level of interaction occurred. Lastly, the most common microbial interaction with land plants – saprophytism – is also the most difficult to document regarding the microorganisms involved.

Scope of the review

The purpose of this contribution is to review the current status of associations and interactions between microorganisms and land plants based on the fossil record. We focus on examples from the late Paleozoic (especially the Devonian and Carboniferous [=Mississippian and Pennsylvanian]) since these associations/interactions occurred in well understood ecosystems, in which both the geological and biological framework have been extensively documented (cf. Behrensmeyer et al., 1992 and references therein). Moreover, at the end of the Devonian, all major lineages of vascular plants, with the exception of the angiosperms, were present and, for the first time in geological history, provided a wealth of new micro-habitats and hosts for microorganisms (cf. Goodman and Weisz, 2002). One of the most important aspects of being able to accurately document fossil microorganism/land plant interactions concerns the three-dimensional preservation in which cells and tissues systems can be examined in great detail. Some of the most important fossil sites yielding this type of preservation are of Devonian and Carboniferous age. Another critical component in determining an interaction is *in situ* specimens that permit the examination of not only the individual partners (i.e. microorganisms and land plants), but also the various forms of evidence that denote their specific interactions.

We exclude from this review a variety of well documented reports that demonstrate microbial activity and possible interactions with other elements in the ecosystems based on indirect evidence, including sedimentary structures (Hagadorn and Bottjer, 1997), diagenetic processes (Petsch et al., 2005), biofilms (Krumbein et al., 2003 and references therein), and various geochemical traces (Verrecchia et al., 2003). Also excluded is information on dispersed microorganisms that appear in the palynological record since these data typically do not provide insight into interactions or associations with other organisms.

The following sections provide examples of microorganism/land plant associations (and interactions) that occur in the late Paleozoic fossil record and offer a perspective on the wealth of information that has been gathered to date from these ancient ecosystems.

2. Bacteria

Although bacteria (or bacteria-like prokaryotic organisms) are among the oldest life forms known on Earth and probably represent the principal decomposers in all Paleozoic ecosystems, they are generally the most difficult to identify and fully interpret based on the fossil record. Although there are a few earlier reports on what were regarded as bacteria associated with fossil plants, the first detailed descriptions of *in situ* bacteria are those provided by Renault (1894a,b, 1895b,c, 1896a,b,c, 1900). Renault described and illustrated several types of circular to slightly elongate bodies, sometimes in pairs or groups of three (each approximately 3–4 μm in diam), that occur in the cells of various Carboniferous and Permian vascular plants

anatomically preserved in cherts. The smaller forms were assigned to the genus *Micrococcus,* while the slightly larger forms were described as *Bacillus* (Fig. 1). Other species of these two genera were reported from petrified coprolites. Two of the forms originally described by Renault have later been re-figured by von Pia (in Hirmer, 1927) and interpreted as saprotrophs. Although it is highly probable that the majority of the structures that were originally interpreted as bacteria by Renault and subsequent workers represent microorganisms, improved microscopic techniques indicate that some represent inorganic particles. Approximately 25 years after publication of Renault's works, Kidston and Lang (1921) described and illustrated spherical colonial masses of unicellular bacteria from the Lower Devonian Rhynie chert. These occur freely in the matrix or on plant fragments and fungal hyphae. Other small spherical structures occur in thick-walled fungal spores in the Rhynie chert. Taylor et al. (2004) suggested that these bacteria-like bodies may have functioned in a similar manner to the bacteria-like organisms (BLO's) that have been reported in extant spores of some mycorrhizal fungi (cf. Bonfante, 2003).

Small enigmatic microspheres, 1–2.5 μm in diameter, termed cocci and diplococci occur in coalified vascular plant conducting cells of Late Carboniferous age (Lyons, 1991). These bacteria-like structures were interpreted as saprotrophs based on their occurrence in partially degraded plant material. Both microspheres and short filaments have also been described from other Late Carboniferous permineralized plant material and interpreted as filamentous bacteria (Smoot and Taylor, 1983). Some of the spheres, however, possess a preformed operculum and appear nearly identical to the zoosporangia produced by various Chytridiomycota (see below).

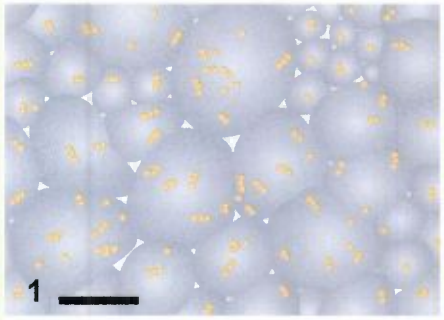
Despite the fact that there exist several reports of bacteria preserved in the fossil record, in some instances in association with plant tissues, it still remains a difficult task to determine precisely how they functioned in the processes that sustained the late Paleozoic ecosystems. While it is important to continually report the presence of bacteria and bacteria-like organisms in the fossil record, the development of both new techniques and imaging systems will be required before the role of these organisms in ancient ecosystems can be more accurately assessed. One potential avenue of research with fossil bacteria may be the identification of bacterial metabolites that in turn can be used to indirectly infer associations and interactions with land plants.

3. Cyanobacteria

The fossil record of cyanobacteria is extensive and appears to date back to the Late Archean; by the Neoproterozoic, there is also evidence of cyanobacteria entering into associations with other organisms (Yuan et al., 2005). However, the number of examples of fossilized associations between cyanobacteria and other organisms is low, and therefore our understanding of the evolutionary history of these partnerships continues to be incomplete. The only terrestrial Paleozoic ecosystem that provides some insights into associations and interactions between land plants and cyanobacteria is the Early Devonian Rhynie chert. Various free-living cyanobacteria, including *Archaeothrix oscillatoriformis*, *Kidstoniella fritschii*, *Langiella scourfeldii*, and *Rhyniococcus uniformis*, have been reported from this ecosystem (Kidston and Lang, 1921; Croft and George, 1959; Edwards and Lyon, 1983). Recently, there has also been a report of a direct association, which has been interpreted as a lichen-like mutualism. This association is composed of a dense fungal mycelium that forms shallow depressions along the upper surface, each of which contains a large number of coccoid *Gleocapsomorpha*-like cyanobacteria. Extending among the cyanobacteria are hyphae that form a net-like structure. One of the interesting questions that has been raised by the discovery of this fossil concerns the nature and degree of physiological interaction between the two potential partners, and how this interaction might be documented based on fossils (see Taylor et al., 1997). It is interesting to note that the thallus formed by the fungus/cyanobacterium consortium extends for several centimeters, always demonstrating an intimate proximity between the two partners. This consistent association suggests that the genetic code underlying the establishment and maintenance of the partnership had been in place relatively early in the evolutionary history of both fungi and cyanobacteria involved.

Other examples of associations between cyanobacteria and Rhynie chert organisms involve the charophyte *Palaeonitella cranii* and the land plant *Aglaophyton major*. In *P. cranii,* the association occurs in the form of a dense aggregate of cyanobacterial filaments that overgrow what appears to be a lateral branch of the alga (Fig. 2). Dense aggregations of filaments of *Archaeothrix*-type cyanobacteria have been discovered on prostrate axes of *Aglaophyton major* (Fig. 3). It is interesting to note that these aggregations only occur in areas where the axes are locally injured and, as a result of the injury, exuded some kind of wound secretion (Krings et al., in prep. a). This suggests that the wound secretion, preserved as black, opaque masses, contains substances that attract the cyanobacteria. On axes that show no evidence of wound secretion, single cyanobacterial filaments occur sporadically. Other filamentous cyanobacteria occupy spaces in the walls of empty and partially degraded sporangia of *A. major* (Figs. 4, 5).

The most complex cyanobacteria/land plant association in the Rhynie chert includes *Archaeothrix*-type filaments that colonize the prostrate mycorrhizal axes of *A. major*. The cyanobacteria enter the axes through the stomatal pores and initially colonize the substomatal chambers (Fig. 6).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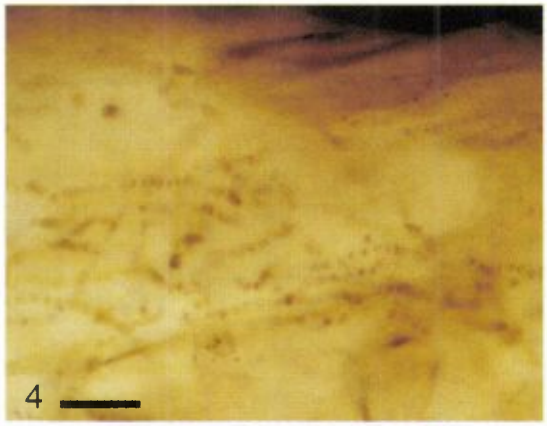
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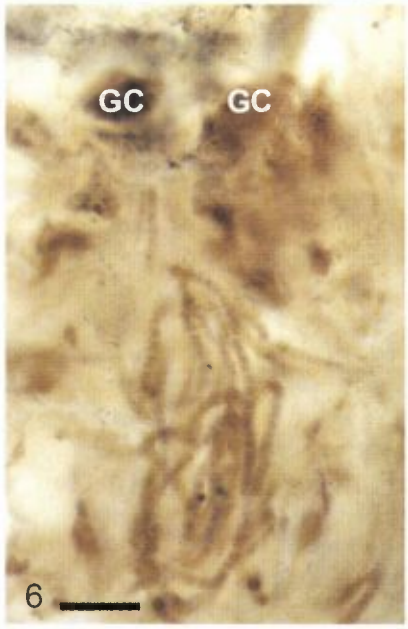
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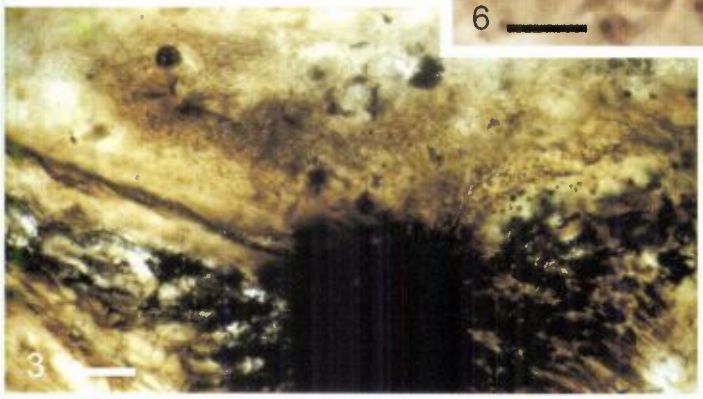
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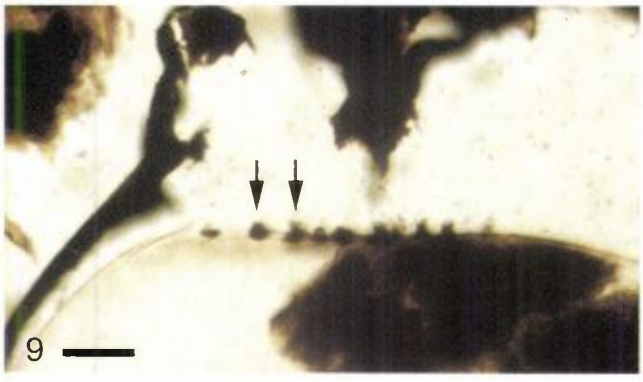
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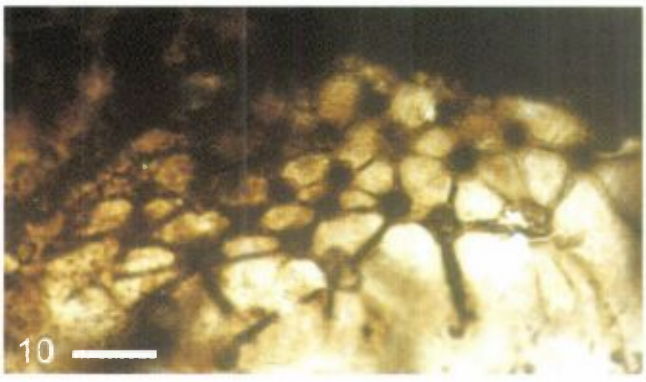
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From there, they spread as intercellular endophytes throughout the outer cortical tissues and mycorrhiza-zone by growing through the intercellular system. In dead ends of the intercellular system, the cyanobacterial filaments loop and continue growth in reverse direction (Figs. 7, 8). Near the mycorrhizal arbuscule-zone in the outer cortex, individual filaments or groups of filaments penetrate the walls of parenchyma cells, and become intracellular endophytes. Within cells, the filaments form characteristic coils. This association represents the oldest fossil evidence for endophytic cyanobacteria in land plants. One might speculate that colonization of ancient plant parts by filamentous cyanobacteria is a chance result of preservation in which a propagule (e.g., a hormogonium) was carried into the substomatal chamber and initiated growth. While this scenario is possible given the large number of vegetative propagules that were present in the Rhynie chert ecosystem, there is at least one alternative interpretation that is reflected in the pattern of cyanobacterial growth. In several sections of prostrate axes of *A. major* are cyanobacterial filaments extending through the intercellular spaces within the cortex that are also occupied by hyphae of the endomycorrhizal fungus. Like the fungal hyphae that penetrate specialized cortical cells to form arbuscules, the cyanobacterial filaments also penetrate individual cells and become coiled.

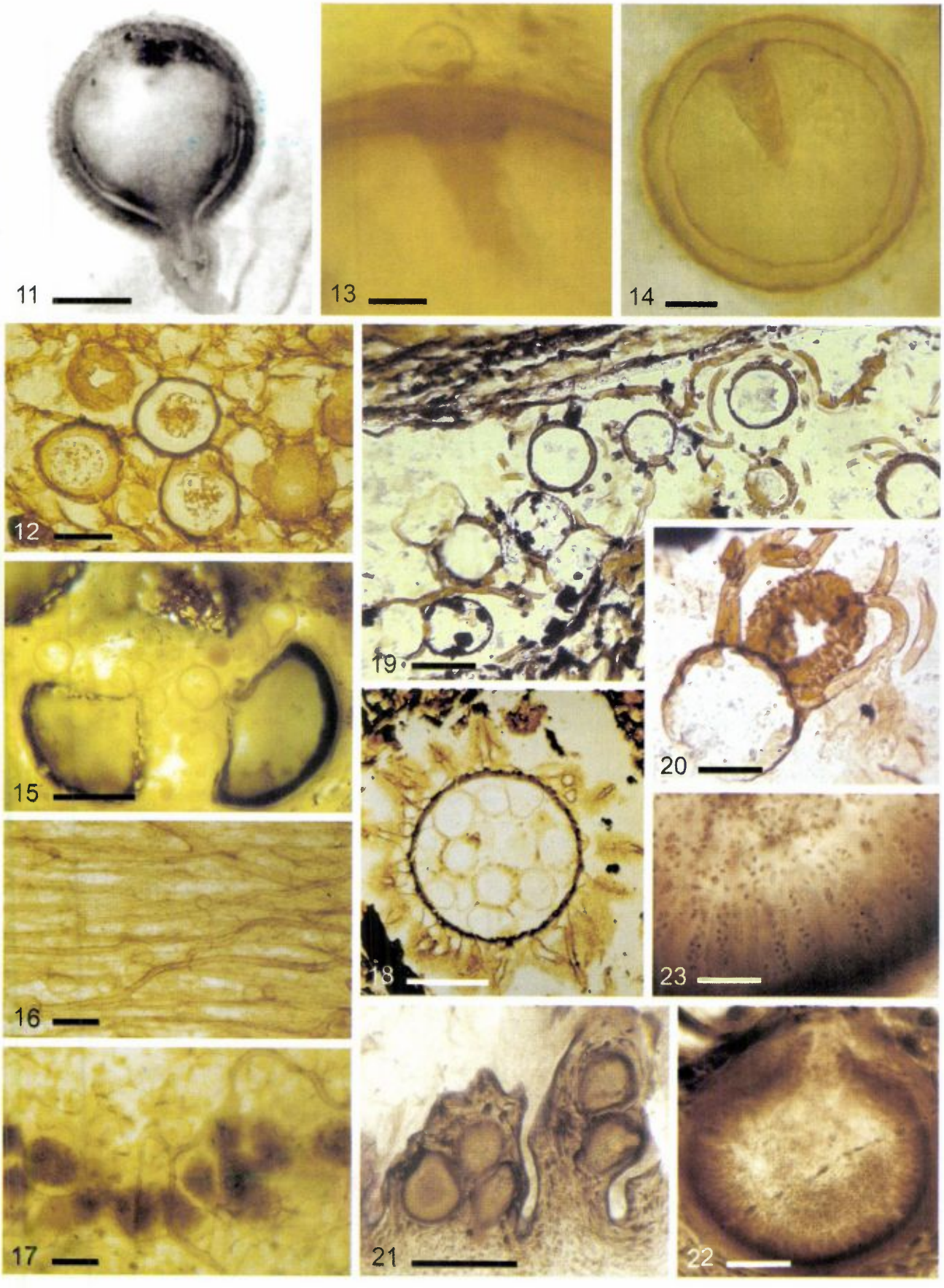
The fact that these coils regularly occur in the same organ (prostrate axis), are consistently formed in a well-defined region of the axes (i.e., the outer cortex), and have approximately the same shape in all of the infected cells suggests that this association is not accidental, but rather constitutes some level of physiological interaction. Moreover, the infected cortical cells do not differ in shape from uninfected cortical cells, which suggests that they remained intact after infection. Although we are uncertain as to the role of the cyanobacteria in this association, it is likely that they provided some form of benefit to the plants, perhaps regarding nitrogen fixation. A second scenario might include the role of cyanobacteria in the establishment of the mycorrhiza, and thus the *A. major*/mycorrhizal fungus/cyanobacterial consortium formed a tritrophic mutualistic interaction. Studies of extant mycorrhizal plants indicate that a variety of associated microorganisms play a significant role as "helpers" in the establishment and maintenance of the mycorrhiza (e.g., von Alten et al., 1993; Bowen and Theodorou, 1979; Garbaye, 1994; Tsavkelova et al., 2001, 2003), and it is in this capacity that perhaps these endophytic Rhynie chert cyanobacteria may have functioned.

4. Algae

There are numerous reports of algae throughout the geologic record, with the vast majority of these represented by forms that cause calcium carbonate to secrete in and around the thallus, and thus increase the potential of being preserved. Although non-calcifying algae have also been reported, they are distinctly under-represented in the fossil record. It is predominantly these latter forms, however, that today enter into various associations with other organisms. Extant examples of such associations include small spheroid consortia formed by cyanobacteria, diatoms, and chemoorganotrophic bacteria that occur in North Sea microbial mats (Brehm et al., 2003), mutualistic partnerships of zooxanthellae and zoochlorellae with marine cnidaria (e.g., Douglas, 1988), parasitic algae in land plants (Joubert and Rijkenberg, 1971; Chapman and Waters, 1992), and a host of algal pathogens on animals and humans (e.g., Nelson et al., 1987; Modly and Burnett, 1989). Perhaps the most widespread association involving algae is the lichen symbiosis, which represents an intimate consortium formed by one to several fungi (mostly ascomycetes) and one or more species of cyanobacteria and/or algae. The low degree of preservation potential of symbiotic algae makes it generally unlikely that these associations can be realized in the fossil record.

To date we are aware of only a single late Paleozoic example that demonstrates a land plant/algal association. This association includes the colonial alga (likely with affinities in the Chlorophyta) *Lageniastrum macrosporae* that resides inside late Early Carboniferous lycophyte

Figures 1–10: Bacteria, cyanobacteria, and the colonial alga *Lageniastrum macrosporae* in association with land plants. Fig. 1: *Bacillus*- and *Micrococcus*-type bacteria in land plant tissue from the Carboniferous of France (redrawn from Renault, 1896, Fig. 102); Bar = 40 μm. Fig. 2: Filamentous cyanobacteria growing on a lateral branch of *Palaeonitella cranii* from the Rhynie chert; Bar = 100 μm. Fig. 3: Aggregation of cyanobacteria on a prostrate axis of *Aglaophyton major*. Note the black, opaque wound secretion below the cyanobacterial mass; Bar = 180 μm. Figs. 4–8: Endophytic *Archaeothrix*-type cyanobacteria in *Aglaophyton major* from the Rhynie chert. Fig. 4: Cyanobacteria in the wall of an empty and partially degraded sporangium; Bar = 60 μm. Fig. 5: Detail of Fig. 4, showing cyanobacterial filaments; Bar = 12 μm. Fig. 6: Cyanobacterial filaments in a substomatal chamber. Note the pair of guard cells (GC); Bar = 60 μm. Fig. 7: Cyanobacterial filaments forming loops within dead ends of intercellular system; Bar = 70 μm. Fig. 8: Detail of Fig. 7, focusing on the loops; Bar = 35 μm. Figs. 9, 10: The *Lageniastrum macrosporae/Sublagenicula nuda* association from the Lower Carboniferous of France. Fig. 9: Young colony with cells arranged in a single plane. Arrows indicate individual, pear-shaped algal cells; Bar = 50 μm. Fig. 10: Older colony with characteristic protoplasmic strands that interconnect adjacent cells; Bar = 30 μm.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megaspores of the *Sublagenicula nuda*-type (Renault, 1894b, 1896a,b, 1900; Grewing et al., 2003; Krings et al., 2005). Like most of the associations of microorganisms with land plants that are reviewed here, the algal endophyte is not a single instance, but rather is represented by multiple occurrences in megaspores. Moreover, the alga demonstrates consistency with regard to spatial arrangement of the colony within the spore wall, located just beneath the suture on the proximal surface. In addition, several developmental stages of the algal colony within the confines of the megaspore can be distinguished. Young *L. macrosporae* colonies consist of a few cells that are arranged in a single plane (Fig. 9). In slightly older algae, increasing cell numbers result in the colony assuming a dome-like, three-dimensional configuration by expanding toward the base of the spore along the inner surface of the spore wall.

There is a striking similarity in structure and organization between the fossil and some species of the extant chlorophyte genus *Volvox* (e.g., *V. globator*). Perhaps the most extraordinary morphological correspondence between *L. macrosporae* and extant *Volvox* species is the presence of radiating protoplasmic strands that interconnect adjacent cells in the colony (Fig. 10); the protoplasmic strands are the result of incomplete cytokinesis in extant *Volvox* (cf. Ikushima and Maruyama, 1968; Kirk, 1998). In contrast to modern *Volvox*, however, *L. macrosporae* lived as an endophyte, at least during part of the life cycle. *Lageniastrum macrosporae* occurred in a highly dynamic environment characterized by small lakes and pools scattered across a landscape, dominated by active volcanism (Rex, 1986). In such unstable conditions it is reasonable to speculate that the ephemeral nature of the ecosystem provided the selective pressure for *L. macrosporae* to become endophytic. In many modern algae, thick-walled resting cells serve as one of several strategies that permit the population to survive during unfavorable environmental conditions (Coleman, 1983; Kirk, 1998). Perhaps *L. macrosporae* did not produce resting cells, but rather utilized the thick-walled and resistant lycophyte megaspores as a strategy to overcome harsh environmental conditions.

5. Oomycota

Initially, the Oomycota were thought to be related to the algae, but later were treated as a separate group of fungi or pseudofungi. Today these organisms are termed Straminipiles and classified as Peronosporomycetes (Dick, 2001). Oomycetes were likely among the first eukaryotes on Earth; however, the fossil record of the group has remained problematic. There are several late 19th and early 20th century descriptions of fossil coenocytic hyphae, "oogonia", and/or various types of spores (e.g., Smith, 1877; Cash and Hick, 1878; Williamson, 1888) as well as trace fossils in animal remains dating back to the Precambrian (e.g., Wedl, 1859; Duncan, 1876) that have been interpreted as oomycetes (literature surveyed in Tiffney and Barghoorn, 1974; Pirozynski, 1976; Johnson et al., 2002). For example, Pirozynski (1976) notes that the ascus-like microfossil described by Schopf and Barghoorn (1969) from the Upper Precambrian of Australia is virtually indistinguishable from intercalary oogonia seen in modern members in the Saprolegniales. More recently, however, Johnson et al. (2002) suggested that all of these fossils are questionable and cannot be attributed to the Oomycota with confidence.

In the Early Devonian Rhynie chert are small spore-like structures morphologically similar to the oogonia/oosporangia of certain extant oomycetes (Taylor et al., submitted). Some of these arise on coenocytic hyphae, and when mature possess a single oosphere/oospore within a highly ornamented oogonium/oosporangium (Fig. 11). The features seen in these fossils suggest affinities with certain

Figures 11–23. Two fossil peronosporomycetes and various fungi in association with land plants. Fig. 11: Oogonium/oosporangium from the Rhynie chert; Bar = 10 μm. Fig. 12: *Albugo*-like peronosporomycete in the seed-like structure *Nucellangium glabrum* from the Upper Carboniferous of North America; Bar = 100 μm. Fig. 13: Chytrid parasitizing a thick-walled glomeromycetous clamydospore; Bar = 6 μm. Fig. 14: Host response of the clamydospore in the form of elongate, concentrically layered papillae that extend into the spore lumen and encase the chytrid rhizoids; Bar = 15 μm. Fig. 15: Chytrid zoosporangia extending from spores of *Aglaophyton major* from the Rhynie chert; Bar = 30 μm. Figs. 16, 17: The glomeromycete *Glomites rhyniensis*, the mycorrhizal fungus of *Aglaophyton major* from the Rhynie chert. Fig. 16: Hyphae running through the intercellular system of the plant, occasionally forming vesicles; Bar = 100 μm. Fig. 17: The mycorrhizal arbuscule-zone where the fungus forms intracellular arbuscules (dark tufts) in cortical cells; Bar = 100 μm. Fig. 18: *Traquairia williansonii* from the Upper Carboniferous of North America; Bar = 165 μm. Figs. 19, 20: *Protoascon missouriensis*, a zygomycete from the Upper Carboniferous of North America. Fig. 19: Several azygo- or zygosporangium-suspensor complexes within the confines of the seed-like structure *Nucellangium glabrum*; Bar = 50 μm. Fig. 20: Detail of Fig. 19. Individual azygo- or zygosporangium-suspensor complex. Note the suspensor appendages that form a basket-like structure around the sporangium; Bar = 25 μm. Figs. 20–23: *Palaeopyrenomycites devonicus*, an endophytic ascomycete in *Asteroxylon mackiei* from the Rhynie chert. Fig. 21: Several perithecia in the cortex of *A. mackiei*; Bar = 500 μm. Fig. 22: Individual perithecium, longitudinal section; Bar = 85 μm. Fig. 23: Detail of Fig. 22, showing paraphyses and asci with ascospores; Bar = 40 μm.

peronosporomycetes, especially certain species in the extant genus *Pythium*. A number of small spheres also occur in the Carboniferous. One of these has been found in a specimen of the seed-like structure *Nucellangium glabrum* from North America and interpreted as an oogonium of an *Albugo*-like oomycete (Fig. 12; Stidd and Cosentino, 1975). What is perhaps most interesting about this fossil is the fact that the host response seen in the tissues of *N. glabrum* is similar to that produced by extant flowering plants infested with the parasitic oomycete *Albugo*.

6. Fungi

In contrast to the paucity of fossil associations and interactions involving bacteria, cyanobacteria, and algae, there are numerous examples of fungi associated with land plants in the fossil record (e.g., Taylor, 1990). In many instances, these associations are recognizable based only on the presence of vegetative hyphae in plant remains, and it is therefore difficult to determine the systematic affinities of the fungal partner and nature of its interaction with the plants (i.e. saprophytism, parasitism, mutualism). On the other hand, there are several excellent examples of fungus/land plant interactions in which the affinities of the fungal partner can be determined based on vegetative and reproductive characteristics. Other evidence of fungus/land plant interactions can be assessed based on structural features seen in the host.

The substantial body of literature dealing with fossil fungi from the late Paleozoic, in part earlier surveyed by Tiffney and Barghoorn (1974), Pirozynski (1976), Stubblefield and Taylor (1988), Taylor (1993), Taylor and Taylor (1997, 2000), and Kalgutkar and Jansonius (2000), provides examples of associations and interactions with land plants from all major groups of fungi (cf. McLaughlin et al., 2001; Schüssler et al., 2001).

Chytridiomycota

Chytridiomycota are considered the basal group of fungi. Extant members are found in a wide variety of habitats, ranging from aquatic environments to the guts of various mammals; most forms, however, are parasites of plants, animals, and other fungi. Because chytrids are the only true fungi that produce motile, flagellate cells, they are sometimes difficult to be distinguished from other organisms based on fossils.

Some of the oldest fossil chytrids come from the Lower Devonian Rhynie chert. Illman (1984) described and illustrated several forms in the spores of the bryophyte-like land plant *Horneophyton lignieri*. More recently, other chytrids have been described from the Rhynie chert, which are not only morphologically comparable to modern forms, but also illicit the same host responses (Taylor et al., 1992b). They occur as both epi-and endoparasites, and are associated with several of the land plants and their spores, as well as charophytes and other fungi. While in many of these associations it is difficult to directly examine the parasite, evidence for the biological interaction occurs in the form of specific host responses. For example, Hass et al. (1994) report chytrids infecting the thick-walled chlamydospores of mycorrhizal glomeromyetes (Fig. 13). The host response to these parasites occurs in the form of elongate, concentrically layered structures (papillae) that extend into the spore lumen (Fig. 14) and represent newly synthesized wall material that functions to keep the parasite from extracting nutrients from the spore protoplast. Another host response to chytrid infection involves enlarged cells (hypertrophy) seen in the charophyte *Palaeonitella cranii* (Taylor et al., 1992a). There is also direct evidence for parasitic chytrids that attacked various land plants in the Rhynie chert ecosystem. For example, many spores of *Aglaophyton major* have chytrid zoosporangia extending from the spore wall and from the germinating gametophyte (Fig. 15). Other chytrids can be found attached to the walls of cortical cells in several Rhynie chert plants (Boullard and Lemoigne, 1971; Taylor et al., 1992b).

A morphologically more complex chytrid from the Rhynie chert is the saprophyte *Palaeoblastocladia milleri* (Remy et al., 1994), in which two stages of the life history are preserved in association with partially degraded axes of the land plant *Aglaophyton major*. *Palaeoblastocladia milleri* produces vegetative hyphae in the cortex of the plant and dense tufts of upright, fertile axes protruding from the epidermis. These terminate in either zoosporangia or thick-walled resting sporangia. On other axes that represent the gametothallus are chains of 2–3 gametangia. The presence of these two phases in the life history of this fungus is indicative of a true alternation of generations, which is unusual in fungi today and found in only a small number of modern forms within a single order of the Chytridiomycota, i.e. the Blastocladiales.

Representatives of the Chytridiomycota are also known from Carboniferous and Permian deposits. Among these are some of the first late Paleozoic chytrids to be accurately identified. *Grilletia spherospermii* and *Oochytrium lepidodendri* occur in seeds of the Carboniferous gymnosperm *Spherospermum oblongum* and anatomically preserved tissues of the arborescent lycophyte *Lepidodendron* sp. (Renault and Bertrand, 1885; Renault, 1895a, 1896a). Not only did these authors relate these fossils to modern chytrid genera, but also suggested that these fungi were parasites. Chytrid zoosporangia were also discovered attached to the inner surface of specialized phloem cells of the fern *Botryopteris tridentata* preserved in a Pennsylvanian coal ball from Kentucky (USA) (Smoot and Taylor, 1983). What are interpreted as parasitic chytrids have also been recorded for several permineralized plant remains from the Permian of Antarctica (García-Massini, 2004). Today chytrids are routinely collected by placing pollen grains in an aquatic ecosystem to serve as "bait".

Studies of spores and pollen macerated from Carboniferous coal balls also indicate that these grains were often parasitized by endophytic chytrids (Millay and Taylor, 1978).

Glomeromycota

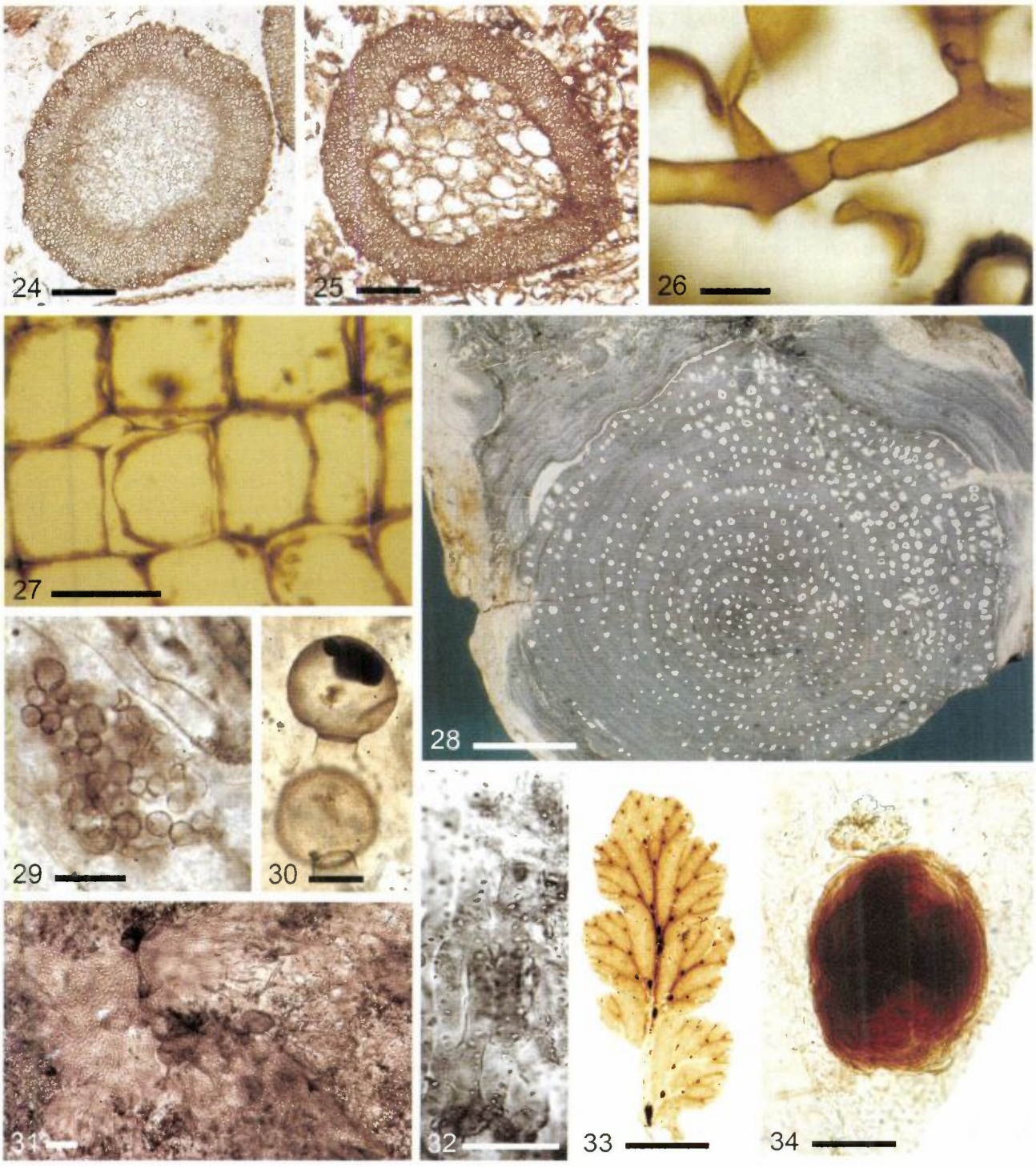
Today the Glomeromycota circumscribes one of the major groups of mycorrhiza-forming fungi that historically were included in the Zygomycota (cf. Schüssler et al., 2001). These fungi form highly specialized interactions with a large number of land plants, including bryophytes, ferns, gymnosperms, and angiosperms. The oldest putative fossil evidence for the existence of glomeromycetes includes thick-walled chlamydospores that have been reported from Precambrian sediments (Pirozynski and Dalpé, 1989); similar spores (*Palaeoglomus grayi*) are known from the Ordovician of North America (Redecker et al., 2000, 2002). However, in none of the accounts is there any information relative to associations of these fungi with land plants, and hence the role that they played in the ancient ecosystems. Chlamydospores, suggestive of those produced by fungi involved in arbuscular mycorrhizae, have also been reported from plant tissues of Devonian (Stubblefield and Banks, 1978) and Carboniferous age (Wagner and Taylor, 1982). Moreover, hyphae or hypha-like structures, aggregated in cortical tissues of the underground parts of several Carboniferous plants, have variously been interpreted as arbuscules (e.g., Weiss, 1904; Osborn, 1909; Halket, 1930; Andrews and Lenz, 1943; Cridland, 1962; Agashe and Tilak, 1970); however, most of these reports have later been questioned (cf. Stubblefield and Taylor, 1988). Arbuscule-like structures (*Glomites cycestris*) are also known in roots of the Triassic cycad *Antarcticycas schopfii* (Phipps and Taylor, 1996).

To date the oldest unequivocal evidence for the existence of interactions between the Glomeromycota and land plants occurs in the form of arbuscular mycorrhizae from the Lower Devonian Rhynie chert (Kidston and Lang, 1921; Boullard and Lemoigne, 1971; Taylor et al., 1995). The fungal partner, *Glomites rhyniensis*, consists of aseptate hyphae that enter prostrate axes of various land plants and extend through the intercellular spaces within the cortex (Fig. 16). While there are a number of reports of fungal hyphae in cortical tissues of late Paleozoic plants, it is the presence of intracellular arbuscules (Fig. 17) within a well defined area of the cortex (termed mycorrhizal arbuscule-zone) that substantiates these fungi as endomycorrhizal. Arbuscules have also been discovered in the gametophyte generation of several Rhynie chert macroplants (Taylor et al., 2005). While it remains impossible to demonstrate that a physiological interaction actually took place between a fossil mycorrhizal fungus and a land plant, the morphological similarity between modern and fossil arbuscules, in addition to a variety of characters, including a consistent and well-defined area in the cortex where the arbuscules are formed, clearly indicates that these fungi and the host plants formed a mutualistic association. Molecular data and inferred molecular clock hypotheses (cf. Berbee and Taylor, 2001) further underscore the existence of such mutualistic interactions as occurring at least 400 million years ago, or even earlier (Heckman et al., 2001). Taken together, all of these data add support to the hypothesis advanced by Pirozynski and Malloch (1975) that endomycorrhizal fungi were essential in the colonization of the terrestrial realm.

Zygomycota

Modern zygomycetes are widespread and abundant in a variety of habitats, with most forms occurring as saprophytes, but some as parasites of plants, animals, and other fungi. The group is characterized by the production of thick-walled zygospores, a feature that might be recognizable in the fossil record. Nevertheless, it has been difficult to identify fossil members of this group. Within Carboniferous permineralized peat from North America are a variety of small spherical structures, including some that are ornamented, which have collectively been termed sporocarps (Davis and Leisman, 1962). Based on size, morphology, and surface ornamentation, a number of morphogenera have been introduced for these sporocarps, including *Dubiocarpon*, *Mycocarpon*, *Sporocarpon*, and *Traquairia* (Fig. 18). The fungal affinities of these structures are based on the wall that consists of tightly compacted anastomosing hyphae that, in some forms, may be subdivided into two distinct layers. The central lumen may contain one to several spherical structures, however, the number and occurrence of these internal structures is variable. Historically, the sporocarps have been interpreted as fruiting bodies of ascomycetous fungi (Stubblefield and Taylor, 1988); the internal spherical structures as either asci, or, in a few instances, asci containing ascospores. More recently, however, an alternative interpretation of the sporocarps has been presented (White and Taylor, 1989). These authors consider some of the internal spheres as mycoparasites, probably with affinities in the Chytridiomycota. The one common feature of all sporocarps is a thick-walled spore that lines the inner surface of the lumen. In this interpretation, the spore represents a zygospore, similar to those produced in mycelial sporocarps of certain modern Mucorales. The fungi that produced the sporocarps have not been identified to date, but they were most likely saprotrophs of plant tissues based on their common occurrence in partially degraded plant material (Taylor and White, 1989). Other Carboniferous fungal remains suggested as representing fossil zygomycetes include vesicles of various types within the cortex of the seed fern stem *Lyginodendron oldhamium* (Ellis, 1918). Some of these vesicles are intercalary and interconnected to each other by short aseptate hyphae.

Perhaps the most interesting fossil assigned to the



Figures 24–34. Devonian, Carboniferous, and Triassic fungi, and pathological alterations in land plants inflicted by phytopathogenic fungi. Figs. 24, 25: *Palaeosclerotium pusillum* from the Upper Carboniferous of North America; Bars = 200 μm. Fig. 26: *Palaeofibulus antarctica* from the Triassic of Antarctica. Hypha with clamp connection; Bar = 10 μm. Fig. 27: *Araucarioxylon* wood from the Permian of Antarctica in which lignin and cellulose degradation by fungi has led to the removal of the secondary cell walls; Bar = 30 μm. Fig. 28: *Araucarioxylon* specimen from the Permian of Antarctica, showing spindle-shaped regions where cellulose and lignin are completely degraded (pocket rot) by phytopathogenic fungi; Bar = 1.9 cm. Figs. 29, 30: Unidentified fungal remains associated with decaying plant material from the Rhynie chert; Bars = 40 μm (Fig. 29) and 30 μm (Fig. 30). Fig. 31: Epiphyllous mycelium of an unidentified fungus growing on a pinnule of the seed fern *Blanzyopteris praedentata* from the Stephanian of France; Bar = 60 μm. Fig. 32: Detail of Fig. 31, showing several hyphae; Bar = 12.5 μm. Fig. 33: Cleared pinnule of *Helenopteris paleaui*, a seed fern from the Stephanian of France, with numerous dark spots; Bar = 3.5 mm. Fig. 34: Lysigenous secretory cavity with crystallized contents of the seed fern *Dicksonites pluckenetii* from the Stephanian of France; Bar = 50 μm.

Zygomycota, which has historically also been difficult to interpret, is *Protoascon missouriensis* (Batra et al., 1964; Baxter, 1975). The description of this fungus is based on more than 50 specimens inside the megaspore of a partially degraded seed-like structure *Nucellangium glabrum* (Fig. 19). The fungus consists of a swollen, bulb-like structure, up to 150 μm in diameter, with up to 12 elongate, aseptate appendages arising in a whorl from one end (Fig. 20). The appendages form a basket-like structure that surrounds a highly ornamented sporangium containing a single thick-walled spore. As the generic name implies, *Protoascon missouriensis* was initially believed to be an ascomycete. However, subsequent studies (Pirozynski, 1976; Taylor et al., 2005b) have reinterpreted the bulb-like structure and associated appendages as a suspensor of a zygomycete and the enclosed sporangium containing a single spore as an azygo- or zygosporangium like those seen in modern zygomycetes (e.g., *Absidia*). Although found within a partially degraded reproductive structure, it is impossible to state whether *P. missouriensis* was a saprotroph or some form of endoparasite.

Ascomycota

The Ascomycota are probably the largest group of fungi, with more than 30,000 species recognized today. Among other features, the ascomycetes are characterized by simple septate hyphae and sexual reproduction that involves the production of ascospores in specialized structures termed asci. Ascomycetes were initially believed to have evolved in the Mesozoic (Pirozynski, 1976), and in fact there are a number of excellent examples of Mesozoic members of this group (e.g., Alvin and Muir, 1970; Daghlian, 1978; Kar et al., 2004; van der Ham and Dortangs, 2005). Today, however, based on specialized cells (phyllides) suggestive of ascomycete conidia, the group is dated back to at least the middle Silurian (Sherwood-Pike and Gray, 1985), and other specimens documenting diversity in the late Paleozoic (Taylor, 1994). Despite the ancient lineage of the group, there are relatively few reports of late Paleozoic ascomycetes in association with land plants. One putative ascomycete/land plant association consists of thyrothecia on the surface of the enigmatic Early Devonian plant *Orestovia petzii* from Siberia (Krassilov, 1981); another is spherical ascoma (*Mycokidstonia sphaerialoides*) from the Rhynie chert (Pons and Locquin, 1981). Recently, an exceptionally well-preserved ascomycete, *Palaeopyrenomycites devonicus*, in association with the land plant *Asteroxylon mackiei* (Fig. 21) was reported from the Rhynie chert (Taylor et al., 2005a). This fungus produced globose perithecia, each approximately 500 μm in diameter, which are characterized by a small distal ostiole (Fig. 22). Extending from the inner surface of the perithecium are closely spaced paraphyses and asci that each contain up to 16 ascospores (Fig. 23). On the surface of the host axes are tufts of condia. It is interesting to note that the ascocarps often are positioned within the substomatal chambers of the plant with the ostiole directly beneath the stomatal pore. Based on this latter feature, we submit that *P. devonicus* was a parasite that colonized *A. mackiei* while it was alive.

Palaeosclerotium pusillum is a Carboniferous fungus that appears to share affinities with several fungal groups (Rothwell, 1972). Within what is interpreted as a cleistothecium are asci containing ascospores (Figs. 24, 25); also present are septate hyphae with clamp connections. The affinities of *P. pusillum* remain conjectural; some have interpreted the fungus with a unique combination of features that link ascomycetes and basidiomycetes (McLaughlin, 1976), or as an ascomycete that has been parasitized by a basidiomycete (Singer, 1977). Another late Paleozoic fungus that has been interpreted as an ascomycetous plant parasite is *Protomyces protogenes*, a form that occurs in the underground axes of the arborescent lycophyte *Lepidodendron* sp. (Smith, 1884).

Basidiomycota

The vegetative phase of most basidiomycetes is characterized by regularly septate (doliporous septa) hyphae, which possess so-called clamp connections and externally produced sexual spores. Historically, there were a number of reports of late Paleozoic (mostly Carboniferous) fossils that were interpreted as basidiomycetes, including *Dactyloporus archaeus, Incolaria securiformis, Polyporites bowmanii, Pseudopolyporus carbonicus*, and *Rhizomorpha sigillariae* (cf. Lindley and Hutton, 1831–37; Lesquereux, 1877; Herzer, 1895; Hollick, 1910). However, almost all of these early reports were later questioned and the specimens reinterpreted as nonfungal (cf. Pirozynski, 1976). As a result, the late Paleozoic fossil record of the Basidiomycota remains remarkably poor. The apparent absence of these fungi in association with land plants is interesting in light of the fact that today basidiomycetes are the primary decay agents of cellulose and lignin (Hibbert and Thorn, 2001).

One example of a late Paleozoic basidiomycetous fungus is *Palaeancistrus martinii* Dennis, 1969, 1970). This organism consists of a mycelium displaying several features that are similar to those found in modern basidiomycetes; especially noteworthy are distinct clamp connections and intercalary and terminal chlamydospores. Hyphae with clamp connections have also been reported from the Devonian of North America (Stubblefield and Taylor, 1986), and the Permian (Stubblefield et al., 1985) and Triassic of Antarctica (Fig. 26; Osborn et al., 1989).

Although the Late Silurian-Early Devonian enigmatic trunk-like organism *Prototaxites* sp. has been suggested as a basidiomycete (Hueber, 2001), there is at present no compelling evidence to demonstrate the presence of typical basidiomycetous reproductive structures (i.e. basidia). It is especially difficult to envisage a heterotrophic organism the size of *Prototaxites* (some "trunks" reached more than 1 m in diameter) existing in a terrestrial environment inhabited

by a relatively sparse vegetation consisting of land plants only several centimeters tall. Rather, *Prototaxites* may represent an example of an ancient mutualistic association that combined both heterotrophy and some level of the lichen-like nutritional mode (Selosse, 2002). It may be that cyanobacteria and/or chlorophytes inhabited the distal and outer parts of the organism and have simply not been found, or not recognized.

Some fossil microorganism/land plant interactions can be deduced even when there is no direct evidence of the fungal partner, because the pathological symptoms present in the plant partner are identical to those produced in modern plants by certain extant phytopathogenic fungi. For example, there are a number of examples of basidiomycete-induced symptoms that can be observed in fossil wood. Cell wall swellings (appositions) that extend into the lumina of wood cells in the Devonian progymnosperm *Callixylon newberryi* are identical to alterations seen in the cell walls of modern plants (Stubblefield et al., 1985). A pathological alteration presumably caused by a parasitic basidiomycete, also occurs in Permian gymnosperm wood (*Araucarioxylon* sp.) from Antarctica (Stubblefield and Taylor, 1986). Here lignin and cellulose are degraded, ultimately leading to the removal of the secondary cell wall (Fig. 27); this symptom is typical of white-rot in extant woody plants (cf. Blanchette, 1980a). In other *Araucarioxylon* specimens from Antarctica, spindle-shaped regions are formed (Fig. 28) where lignin and cellulose are completely degraded (Stubblefield and Taylor, 1986). This late Paleozoic symptom is identical to wood degradation and bleaching observed in some hardwoods and conifers and is caused by the basidiomycete *Phellinus pini* (cf. Blanchette, 1980b). It is interesting to note that, while the hosts of these fungi have changed several times during the course of land plant evolution, the pathological alterations produced by the fungi are identical to those seen in wood today. While this does not necessarily mean that the same fungus species has been responsible for these interactions in both modern and fossil woods, it does again suggest that the underlying genetic code and biochemical processes manifested by the fungi have either remained unchanged, or less likely, have evolved several times.

All of the major fungal phyla have been reported from the Rhynie chert with the exception of the Basidiomycota. Perhaps this reflects that the group had not evolved by the Early Devonian, or was an inconspicuous component of this Early Devonian ecosystem. Or that these fungi possessed a compliment of structural features that make them difficult to recognize because of a different nutritional mode. Finally, do features typical of extant basidiomycetes, including enzyme systems, reflect evolutionary adaptations that coevolved with major changes in the habit of land plants, especially the evolution of lateral thickening meristem that made it possible to increase the production of wood (lignin) during the rise of arborescence in the Middle Devonian?

Fungal remains with uncertain affinities

Throughout the late Paleozoic there is abundant evidence of fungi/land plant interactions in the form of vegetative hyphae, mycelia, isolated spores, and/or other fungal remains scattered throughout degraded plant tissues (e.g., Figs. 29, 30), sometimes so concentrated that it forms a coal maceral (i.e., funginite, cf. Benes, 1956; Benes and Kraussová, 1964; Lyons, 2000). In other instances, fungal hyphae and/or spores occur in the tissues of land plants and/or on the surfaces of leaves (e.g., Magnus, 1903; Renault, 1903; Barthel, 1961; Krings, 2001). While these structures are obviously fungal in origin, they have largely been neglected since many lack diagnostic features. In recent years, however, compression specimens of fossil plants have become an increasingly important source of information about the diversity of late Paleozoic ecosystems.

One of the principal reasons for this resurgence is the examination of compression fossils in the form of cuticular analysis (i.e. the examination of the epidermal anatomy based on cuticles). During the chemical preparation of cuticles, fungi become visible (e.g., Figs. 31, 32) and, as a result, represent an expansive source of new information about associations of endophytic and epiphyllous fungi with land plants that were previously unknown. In retrospect, this revelation is not surprising since the analysis of Cenozoic epiphyllous fungi is based primarily on chemically cleared compressed leaves, which have for many years been a routinely used material (e.g., Dilcher, 1965; Phipps and Rember, 2004).

Small, opaque spots are relatively common on the surfaces of compressed fossil foliage throughout the late Paleozoic (e.g., Fig. 33). Based on size, shape, color, and spatial arrangement, numerous morphospecies have been named and described (cf. Pirozynski and Weresub, 1979). Such structures are often interpreted as necrotic areas caused by phytopathogens or as fruiting bodies of endophytic or epiphyllous fungi (e.g., Oliver, 1903; Castro, 1997; Wagner and Castro, 1998). Recent studies based on cuticular analysis, however, indicate that some of these structures on Late Carboniferous seed fern foliage are not fungal remains, but rather the crystallized contents of secretory cavities (Fig. 34; Krings, 2000, 2001).

Although numerous anatomically preserved and compressed Carboniferous fern and seed fern foliage types have been studied to date, there are relatively few reports of fungal endophytes associated with these leaves. Several hypotheses might be advanced to explain why these associations are rarely documented. One might simply be the inability to recognize the fungi, or lack of interest in such leaf borne organisms. The physical constraints of the environment may have also played a role in defining where microorganisms were able to colonize. Finally, certain secondary metabolites produced by these plants in secretory cells, cavities, and ducts may have served to prevent or

reduce colonization by fungi because of fungicidal properties they possessed.

7. Conclusions

Although information on late Paleozoic fossil microorganisms has been relatively slow to accumulate, there is to date an increasing appreciation of the diversity of these organisms and how they interacted with the other components of ancient ecosystems. This has resulted in a number of contributions, which have reinforced or refuted theories with regard to the evolutionary history of microbial life based on molecular and genetic analyses of extant microorganisms. One of the interesting questions raised by both microbiologists and ecologists concerns the time of appearance of complex interactions between microorganisms and other biological systems (e.g., Goodman and Weisz, 2002). Typically, these questions are framed within the context of molecular and genetic studies using living organisms. In many cases the results from these studies are supported by the fossil record (e.g., Simon et al., 1993). Some aspects, however, remain insufficiently understood. For example, although the Glomeromycota are now suggested to be at least Ordovician in age based on the fossil record (Redeker et al., 2000), it remains uncertain when these fungi actually entered into complex mutualistic associations with other organisms including land plants. Although this latter aspect cannot be adequately addressed at present based on molecular and genetic studies, the fossil record provides unequivocal evidence that these associations were in place at least 400 million years ago. At a finer scale of resolution are a host of questions focusing on processes that occur during cellular interactions. The evolution of some of these processes can be indirectly examined in the fossil record. Such host responses as hypertrophy and hyperplasia, and various alterations in the integrity of cell walls, as well as the synthesis of new wall material, stimulated by an external agent such as a parasite, can be directly assessed based on fossil evidence.

It is obvious from the foregoing that the key to unraveling microorganism/land plant associations and interactions is based on the extraordinary three-dimensional preservation found in certain fossil assemblages, although other preservation types can occasionally also yield important information about microorganism/land plant interactions. While the Rhynie chert is perhaps the best known example for an *in situ* silicified late Paleozoic ecosystem, there are a number of other late Paleozoic ecosystems that have been preserved in a similar manner, but to date have received considerably less detailed attention relating to the microbial life. Among these are the silicified cherts from the Carboniferous of France, which were initially studied by Renault. Since the original descriptions (i.e. Renault, several papers between 1885 and 1903) there has been only a single subsequent report on the microorganisms from these cherts (Taylor et al., 1994). To a large degree the reassessment of the complex *Lageniastrum macrosporae/Sublagenicula nuda* association initially described some 100 years ago (Renault, 1894b, 1896a, 1990), by Grewing et al. (2003) and Krings et al. (2005) has served as a catalyst for establishing the next level of *in situ* fossil microbial research directed at associations with other organisms and biological interactions (Krings and Taylor, 2004). The discovery of Permian, Triassic, and Jurassic cherts from Antarctica, as well as cherts from younger silicified ecosystems (e.g., the Eocene Princeton cherts from Canada, cf. Currah et al., 1998; LePage et al., 1994), and numerous microorganisms preserved in amber (e.g., Poinar et al., 1993; Dörfelt, et al., 2000, 2003; Rikkinen et al., 2003; Schmidt, et al., 2004; Schmidt and Schäfer, 2005), offer additional excellent opportunities to not only document the diversity of microbial life through time, but, perhaps more important, address a broad range of questions relating to the evolutionary history of associations and interactions between microorganisms, land plants, and animals through time.

Acknowledgments

Financial support for part of the research referred to here was provided by the Alexander von Humboldt-Foundation, the Deutsche Forschungsgemeinschaft (DFG), and the National Science Foundation (NSF). We are indebted to Hans Kerp and Hagen Hass (Münster, Germany) for collaboration, valuable discussion, and access to some of the data presented here. Special thanks to Frank Baron and the Max Kade-Society for German-American Studies (Lawrence, KS, USA) for continuing support.

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