

Chapter 1

Fungal Endophytes as a Driving Force in Land Plant Evolution: Evidence from the Fossil Record

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Plant–fungal interactions occur at multiple levels and help to shape plant communities and the ecosystems they comprise. Such interactions may involve competition, antagonism, and varying degrees of mutualism. Just as herbivores can impact the structure and dynamics of a plant community by overall decreasing fitness of interacting species, fungi bring about similar outcomes in the ecosystem (Dighton 2003). In addition, microorganisms, including fungi, drive the bio-geochemical cycles of nature as the principal decomposers of organic matter in the biosphere (e.g., Setälä et al. 1998; Fang et al. 2005; Taylor et al. 2009a). Fungi also impact the ecosystem in negative ways, ranging from parasites of plants and animals to pathogens and disease causative agents of these organisms.

Perhaps the most notable of plant–fungal interactions involve mutualistic relationships between certain fungi and the roots (or other parts) of land plants ranging from a bryophytic grade of evolution to angiosperms. This intimate association, termed a mycorrhiza, is the most prevalent symbiosis on Earth, and is estimated to occur in more than 80% of living land plants (e.g., Cairney 2000; Selosse et al. 2006). It demonstrates the coevolution of the two partners. In fact, this type of mutualistic symbiosis between an alga and fungal partners may have been the necessary prerequisite to the establishment of plant life in the terrestrial realm (Raven 1977; Selosse and Le Tacon 1998).

The purpose of this chapter is to demonstrate various fungal (in the broad sense, including members of the Oomycota (Peronosporomycetes) and Hyphochytridiomycota) endophytes, and land plant–fungal endophyte interactions from the fossil record. While fungal endophytes can be documented throughout the Phanerozoic, it is the Early Devonian and Carboniferous fossils that have been critically examined systematically. As a result, there are a number of well-documented examples for endophytic fungal associations with land plants from these periods. We have selected examples that demonstrate endophytic occurrences of fungi in shoot axes

(including rhizomes), leaves, and roots of fossil land plants, with special reference to plants from the Lower Devonian and Carboniferous.

1.1. HISTORICAL PERSPECTIVE

Fungi are ubiquitous on Earth today, and represent essential components of many ecosystems where they are involved in numerous vital processes (e.g., Dighton et al. 2005). While the activities in the fungal world obviously played similarly important roles in ancient ecosystems, systematic analyses of fungi in the fossil record represent a relatively new avenue of research, despite the fact that fossil plants and animals have been studied for more than 250 years. There are several reasons for this lack of focus on fossil fungi, and fungal associations and interactions with other organisms in ancient ecosystems. Perhaps the most important of these is the small size of most fungal fossils and the lack of specific diagnostic features that can be resolved at the level of transmitted light.

In addition, information about fossil fungi is based almost exclusively on the dispersed record, which generally does not produce these life forms in situ (e.g., Kalgutkar and Jansonius 2000). Moreover, the life history of many fungi is complex and generally cannot be fully reconstructed by fossil representatives because the record is typically composed of isolated stages such as (zoo-)sporangia, cysts, and (resting) spores (e.g., Krings et al. 2009a, 2009d). Today, however, various levels of inquiry in paleobiology require collaborative efforts from multiple disciplines of expertise. This is especially true of questions that focus on ecosystem interactions and community structure. Often in the study of fossil microbial life there is a historical separation between those scholars with interests exclusively in the extinct organisms (and perhaps their value as stratigraphic markers and index fossils), and their counterpart colleagues, who have the necessary knowledge about the biology and diversity of modern microorganisms.

Another reason for the under representation of descriptions of fungi in the paleobotanical literature certainly was the abundance of exquisite fossils of animals and plants that captured the attention of the scientific community of the day. Related to this aspect was the inherent collection bias in which only the most complete and showy specimens were brought to the attention of the paleobotanists, while the fragmented and scrappy remains—those with potential evidence for fungal activities—were left behind.

Despite these problems, there are a few remarkable early reports of exquisitely preserved late Paleozoic fungi and fungal associations or interactions with other elements of ancient ecosystems (e.g., Renault 1896, 1900; Kidston and Lang 1921). However, these studies are based on material preserved in a silicious chert matrix, a very special mode of preservation (see Section ‘Mode of Preservation’) in which even the most delicate structures and finest details may be faithfully fossilized. Because fossiliferous cherts were so locally restricted and distinct from other fossil sites, the organisms contained therein became a sought-after curiosity that attracted the attention of several prominent paleontologists at the time.

The increasing number of reports of Precambrian microbial life (see Tyler and Barghoorn 1954; Taylor et al. 2009b) then appears to have initiated a more general paleobiological interest in evidence of microbial activities from other, geologically younger paleoecosystems. Today, the importance of microbial, including fungal, life as a major constituent of ecosystem functioning is a primary focus of many disciplines (e.g., McArthur 2006). As a result, there has been a paradigm shift in the appreciation of the microbial world in time and space, including microbial associations and interactions with other organisms in ancient ecosystems.

1.2. MODE OF PRESERVATION

Success in documenting fossil fungi, and examining their associations and interactions with other ecosystem components, heavily relies on the way the fungi and their host(s) are preserved. Cherts represent one of the most important sources of evidence for fossil fungi (Taylor et al.

2011). Chert deposits occur at various points in geologic time and typically represent dense microcrystalline or cryptocrystalline sedimentary rocks. Some cherts may be fossiliferous and demonstrate three-dimensional and structural preservation of the organisms (sometimes even in situ), as well as details of individual cells and subcellular structures (e.g., multilayered cell walls, flagella, chromosomes, and nuclear cap; see Taylor et al. 2004). Although the process of fossil preservation in cherts is not fully understood, several modern analogs are being investigated today with regard to deciphering the taphonomic processes involved in the preservation of animals, plants, and microorganisms (e.g., Channing and Edwards 2009). As a result of the fidelity of fossil preservation, cherts provide an ideal matrix from which to extract information about fungi and their associations or interactions with other components of the ecosystem. Cherts provide the only source of direct evidence of the fungal world within the context of ecosystem complexity, versatility, and dynamics. Although various types of fungi have also been exquisitely preserved by other modes, including other types of silicification, coal balls, and amber (surveyed in Taylor et al. 2009b), in general, the ecological configuration within the community in which these organisms lived is less completely known.

Despite the diversity of microorganisms preserved in some chert deposits (e.g., bacteria, cyanobacteria, microalgae, and fungi in the Early Devonian Rhynie chert; see Taylor and Krings 2005), the fungi have received the greatest amount of attention to date for several reasons. One of these is the nutritional mode of fungi, which, as heterotrophs, require various levels of interaction with other organisms that may be dead or alive. As a result of the many ways used by fungi to obtain carbon, they are easier to recognize as functioning components in ancient ecosystems than, for example, a cyst or phycocyst of a unicellular type of planktonic alga (e.g., Dotzler et al. 2007).

1.3. FUNGAL ENDOPHYTES AND THE FOSSIL RECORD: PROBLEMS OF DEFINITION

The term fungal endophyte is used by mycologists for all fungi that exist in living plant tissues without causing observable disease symptom when they are detected. Colonization may be inter- or intracellular, localized or systemic (Schulz and Boyle 2005). However, identification of fungal endophytes (as defined in the preceding text) in fossil material is hampered by the inherent difficulty of determining the condition of the host at the time of colonization, that is, whether it was alive and functional or in the process of senescence or decay (Taylor and Krings 2005; Krings et al. 2009c). For example, intact fossil plant tissue systems containing fungi suggest an endophytic association, whereas fragmented and partially degraded tissue systems containing fungi may signal saprotrophism. However, it is difficult to determine whether the fragmentation and decay was initiated prior to or after fungal colonization, or the decay “symptom” is a preservational artifact. Moreover, modern fungal endophytes may become effective as saprotrophs after plant senescence (e.g., Zhou and Hyde 2001; Osono 2006; Hyde and Soyong 2008). Since plant-inhabiting fungi present in fossil plants may have utilized similar nutritional strategies, it is almost impossible to distinguish fungal endophytes from saprotrophs in the fossil record. Based on these considerations, Krings et al. (2009c) have suggested that, with fossils, the term fungal endophyte should be understood as strictly descriptive, and should be used for all fungi that occur within intact plant cells or tissues in which there are no visible disease symptoms. In fossil specimens where there is an obvious host response or disease symptom, or other structural evidence that may signal an interaction, the endophyte may be more specifically defined as a parasite, mutualist, or pathogen.

1.4. EXAMPLES OF FOSSIL FUNGAL ENDOPHYTES

Molecular evidence (e.g., Heckman et al. 2001; Bhattacharya et al. 2009; Blair 2009) suggests that the major groups of Fungi, as well as certain fungal-like organisms (e.g.,

Peronosporomycetes), were already well diversified by the time the first land plants with conducting elements appeared on Earth during the Silurian (see Taylor et al. 2009b). Most of these early plants with conducting tissue were constructed of small prostrate and upright axes that were generally root- and leafless and that produced terminal or lateral sporangia (Kenrick and Crane 1997); a few forms, however, demonstrate a more complex organization in which there was a tendency toward organ differentiation (Bateman et al. 1998). Land plants with true leaves and roots became widespread during the Devonian (e.g., Beerling et al. 2001; Raven and Edwards 2001; Gensel 2008). However, fungal endophytes can be documented from the oldest structurally preserved land plants that lacked a differentiation of the plant body into shoot axes, leaves, and roots.

1.4.1. Rhizomes and Shoot Axes

Early Land Plants from the Lower Devonian Rhynie Chert

The Early Devonian Rhynie chert, an in situ silicified Early Devonian hot spring environment characterized by small, ephemeral freshwater pools scattered across the landscape, no doubt represents the most famous fossiliferous chert deposit. It contains exquisitely preserved direct evidence for fossil fungi and fungal associations and interactions with other elements of the ecosystem (Taylor et al. 2004). While there are numerous examples of fungal endophytes associated with the Rhynie chert land plants, most of these are represented by isolated parts or stages of the life cycle, and thus cannot be resolved in detail. Others, however, can be documented based on multiple examples that show a consistent spatial distribution of the fungi within the host.

Perhaps the best-documented example of fungal endophytism in an early land plant is the endomycorrhizal symbiosis that occurs in the sporophyte and gametophyte generations of *Aglaophyton major* (Figures 1.1A–D) (Taylor et al. 1995, 2005a; Remy and Hass 1996). One of the interesting aspects of the organization of *A. major* is the degree to which the prostrate axes are in contact with the substrate. Typically, in most land plants a substantially large portion of the plant body grows through the substrate in the form of roots or rhizomes. In *A. major*, however, the contact between the plant body and substrate is restricted to small areas of the sinuous prostrate axes that produce rhizoids (Edwards 1986; Remy and Hass 1996); no part of the plant body grows within the substrate, and all axes are stomatiferous. The stomata on the prostrate axes provide entrances for fungal endophytes, including the endomycorrhizal fungus *Glomites rhyniensis*, a member of the Glomeromycota (Taylor et al. 1995). From the substomatal chamber, the fungus spreads throughout the intercellular system of the outer cortex (Figure 1.1B). One of the unusual features of the *A. major* sporophyte-endomycorrhizal association is the occurrence of intracellular arbuscules (Figures 1.1C, D) exclusively within a well-defined narrow zone of tissue, one to two cells thick, between the outer and middle cortex (see Figure 1.1A (arrows)). In addition, the arbuscule zone, at least in the sporophyte generation, can be traced throughout the prostrate and upright axes, and is present nearly to the distal tips of the upright axes. While the gametophyte of *A. major* (= *Lyonophyton rhyniensis*) contains the same type of mycorrhizal system, the spatial distribution of the fungus in the gametophyte remains elusive because the morphology of the host continues to be incompletely known (Remy and Remy 1980; Remy and Hass 1996; Taylor et al. 2005a).

In contrast to *A. major*, *Nothia aphylla* (Figures 1.1E–I), another early land plant from the Rhynie chert, is characterized by prostrate axes that were bilaterally symmetrical in cross section (Figure 1.1E), and extended through the substrate much like the rhizomes of extant plants (Kerp et al. 2001; Daviero-Gomez et al. 2005). Studies of the anatomy of *N. aphylla* indicate that stomata were not produced on these subterranean axes, nor did the multilayered hypodermis contain an extensive intercellular system. Nevertheless, various fungal endophytes can be found in subterranean axes, including one type that is believed to be endomycorrhizal

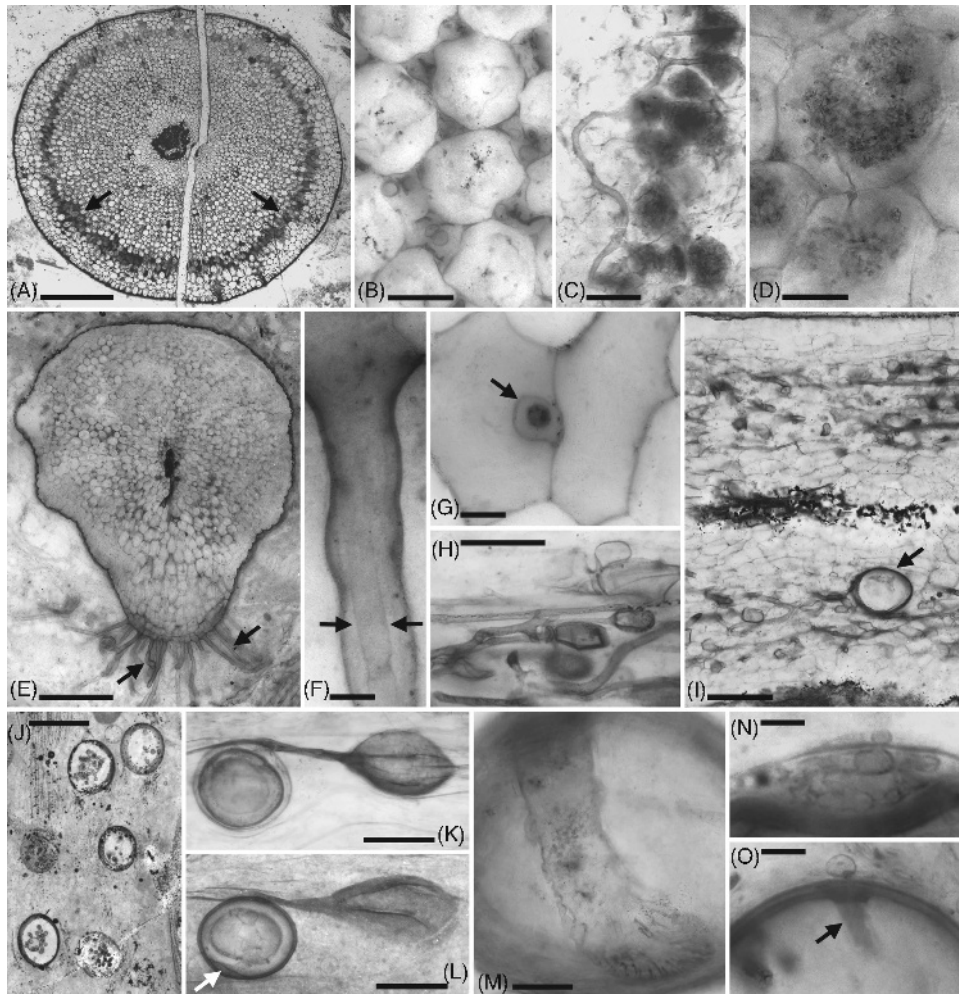


Figure 1.1. Fossil fungal endophytes from Lower Devonian Rhynie chert. (A) *Aglaophyton major* axis, transverse section, with mycorrhizal arbuscule zone (arrows). PBO; bar, 1 mm. (B) Fungal hyphae in intercellular spaces of *A. major* outer cortex. PBO; bar, 30 μm . (C) *A. major* arbuscule zone with trunk hyphae and arbuscules. PBO; bar, 50 μm . (D) Two cortical cells of *A. major*, each containing an arbuscule. PBO; bar, 20 μm . (E) Rhizomatous axis of *Nothia aphylla*, transverse section, with rhizoids (arrows) extending from ventral rhizoidal ridge. PBO; bar, 0.5 mm. (F) Fungal hypha (between arrows) entering *N. aphylla* through a rhizoid. PBO; bar, 20 μm . (G) Hypha in *N. aphylla* hypodermal cell (section view), encasement layer (arrow). PBO; bar, 20 μm . (H) Intercellular hyphae and vesicles in cortex of *N. aphylla*. PBO; bar, 100 μm . (I) *N. aphylla* prostrate axis, horizontal longitudinal section, with hyphae, vesicles, and a thick-walled spore (arrow) in cortex. PBO; bar, 200 μm . (J) Cluster of glomeromycotan spores in degraded land plant axis. BSPG; bar, 200 μm . (K, L) Spore-saccule complexes. PBO; bars, 200 μm . (L) Germination shield (arrow). (M) Tongue-shaped germination shield. PBO; bar, 50 μm . (N) Microfungus inhabiting the wall of a large fungal spore. PBO; bar, 5 μm . (O) Chytrid-like microfungus on a glomeromycotan spore with a papilla (arrow) on the inner spore wall surface. PBO; bar, 10 μm .

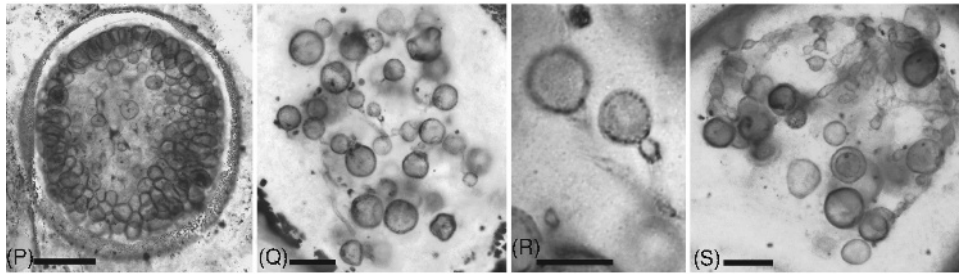


Figure 1.1. (Continued) (P) Fungal spore containing numerous small spores of a microfungus. BSPG; bar, 100 μm . (Q) Thallus of a microfungus inhabiting a glomeromycotan spore. BSPG; bar, 20 μm . (R) Detail of (Q) with apophysate zoosporangia; bar, 10 μm . (S) Microfungal thallus in a glomeromycotan spore, showing catenulate swellings of hyphae. BSPG; bar, 20 μm . Source: BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; PBO, Paleobotanical Collection of Westfälische Wilhelms-Universität, Forschungsstelle für Paläobotanik, Münster, Germany.

(Krings et al. 2007b, 2007c). Since the prostrate axes of *N. aphylla* lack stomata, the putative endomycorrhizal fungus enters the axes through the rhizoids (Figure 1.1F) that occur on the ventral side along the so-called rhizoidal ridge (Figure 1.1E (arrows)). Apparently, because intercellular spaces are virtually absent in the hypodermis, the fungus extends through this tissue as an intracellular endophyte until it reaches the cortex where intercellular spaces are present. In the cortex, the fungus forms an extensive intercellular network of hyphae, and produces vesicles (Figure 1.1H) and large, thick-walled spores (Figure 1.1I). The most interesting aspect of this putative endomycorrhizal association is that the intracellular growth of the fungus in the hypodermis is somehow controlled by the host through the production of cell wall sheaths around the fungal hyphae (Figure 1.1G). As a result, the fungus appears to be “guided” through the hypodermis without being able to extract nutrients from the host, and into the cortex where intracellular penetration is no longer possible. To date, arbuscules have not been identified in either the sporophyte or gametophyte generations of *N. aphylla*.

Although the other early land plants from the Rhynie chert (for an inventory, see Kerp and Hass 2004) have not been examined in sufficient detail to document the presence of mycorrhizal symbioses, there is a strong indication that Glomeromycota were in some way associated with all Rhynie chert land plants. One type of evidence occurs in the form of glomeromycotan spores within the cortical tissues of these plants (e.g., Figure 1.1J). Often associated with the spores are hyphae that terminate in thin-walled vesicles. In modern Glomeromycota, spores of various species differ in size, coloration and thickness of the spore wall, the number and thickness of individual wall layers, as well as in the presence or absence of associated structures such as bulbous swellings of parental hypha or sporiferous saccules (see <http://invam.caf.wvu.edu>). Moreover, some spores are characterized by a distinct mode of germination in which germ tube formation is preceded by the development of a germination shield (e.g., Walker and Sanders 1986). Spore morphology, color, and wall composition are important features in characterizing extant arbuscular mycorrhizal fungi, with more than 200 species delimited to date. Molecular studies suggest that an even larger number is present (Redecker and Raab 2006). Three types of glomeromycotan spores have been described from the Rhynie chert. One resembles the genus *Glomus* (Taylor et al. 1995); the second is similar to the extant genus *Scutellospora* with the presence of a prominent, circular germination shield with a lobed margin (Dotzler et al. 2006). In the third type, the germination shield is usually tongue-shaped with infolded margins (Figure 1.1M). Moreover, the spores are borne laterally in the neck of a sporiferous saccule (Figures 1.1K, L). This Early Devonian spore-saccule complex conforms most closely with the

spore–sacculle complexes seen in the modern genus *Acaulospora* (Dotzler et al. 2009). Based on these observations, we believe that Glomeromycota were relatively diverse by Rhynie chert time, and well established as a group even before true roots evolved since all of the Rhynie chert plants and many other early land plants at the time lacked roots. The recent description of a *Glomites* species (i.e., *G. sporocarpoides*) producing spores in sporocarps from the Rhynie chert adds further support to the early diversification of Glomeromycota (Karatygin et al. 2004).

Some glomeromycotan spores in the Rhynie chert contain evidence of colonization by various types of other fungi (Figures 1.1N–S). One example is the presence of inwardly directed pegs or papillae that arise from the inner spore wall and that contain a central canal (Figure 1.1O (arrow)). The papillae are constructed of concentric layers of newly synthesized wall material, and represent a host response aimed at encapsulating the parasite; in some instances, the parasite is still present on the spore surface (Figure 1.1O). Similar host responses in the form of papillae have been documented in extant glomeromycotan spores (e.g., Boyetchko and Tewari 1991), as well as fossil spores from the Carboniferous (Krings et al. 2009a). While this example of a host response can be interpreted as indicative of a distinctly parasitic association, there are various types of microfungi residing in the walls (Figure 1.1N) or in the interior (Figures 1.1P–S) of glomeromycotan (and other fungal) spores in the Rhynie chert that cannot be identified as to the nutritional mode because there is no observable host response (Taylor et al. 1992; Hass et al. 1994; Krings et al. 2009b, 2010a). However, resolving the nutritional mode(s) of these associations would be particularly interesting with regard to better understanding the dynamics within the Rhynie paleoecosystems because, if the intrusive microfungi were parasites, they most likely impacted the number of viable glomeromycotan spores (see Purin and Rillig 2008), and thus reduced the number of mycorrhizal inoculations and therefore altered the structure of this early land plant community.

Most of the plant–fungal associations/interactions reported to date from the Rhynie chert consist of a single fungus interacting at some level with a single host. On the other hand, more complex association systems involving several fungi that (simultaneously) enter into qualitatively different relationships with one host and sometimes also interact with one another have been detailed in a single instance (Krings et al. 2007c). In this example, three types of fungal endophytes colonize the subterranean rhizomatous axes of the land plant *N. aphylla*. While one of these endophytes was most probably endomycorrhizal, the other two (Figures 1.2A, B) were likely parasites based on the presence of several characteristic cell and tissue alterations and host responses, including bulging of infected rhizoids, separation of infected from noninfected tissues by secondarily thickened cell walls (Figure 1.2C), and the local disintegration of cells by the parasite or as a response on attack (Figure 1.2D).

While we have highlighted examples from the Rhynie chert because of the extraordinary preservation, there are other reports of structurally preserved early land plants that contain evidence for endophytic fungi. These associations include clusters of large spores within the cortical tissues of the trimerophyte *Psilophyton dawsonii* that show similarities to the spores produced by extant Glomeromycota (Stubblefield and Banks 1983).

Carboniferous Land Plants

In contrast to the plant life in the Early Devonian, the Carboniferous vegetation was characterized by far greater biodiversity and morphological variability (Kerp 2000 and references therein). During the Early Devonian, plants were small, relatively simple, and probably short-lived, but in the Carboniferous, many plants were long-lived, arborescent, and complex in morphology. They had developed various types of secondary growth, and formed complex, stratified forest ecosystems that provided a much larger number of ecologically distinct (micro-)habitats for fungal endophytes. Moreover, the vast coal-swamp forests of the Carboniferous were highly productive ecosystems, which provided an increasing amount of biomass for saprotrophic organisms. As a result of this increased availability of distinct habitats and accessible nutrition, one would

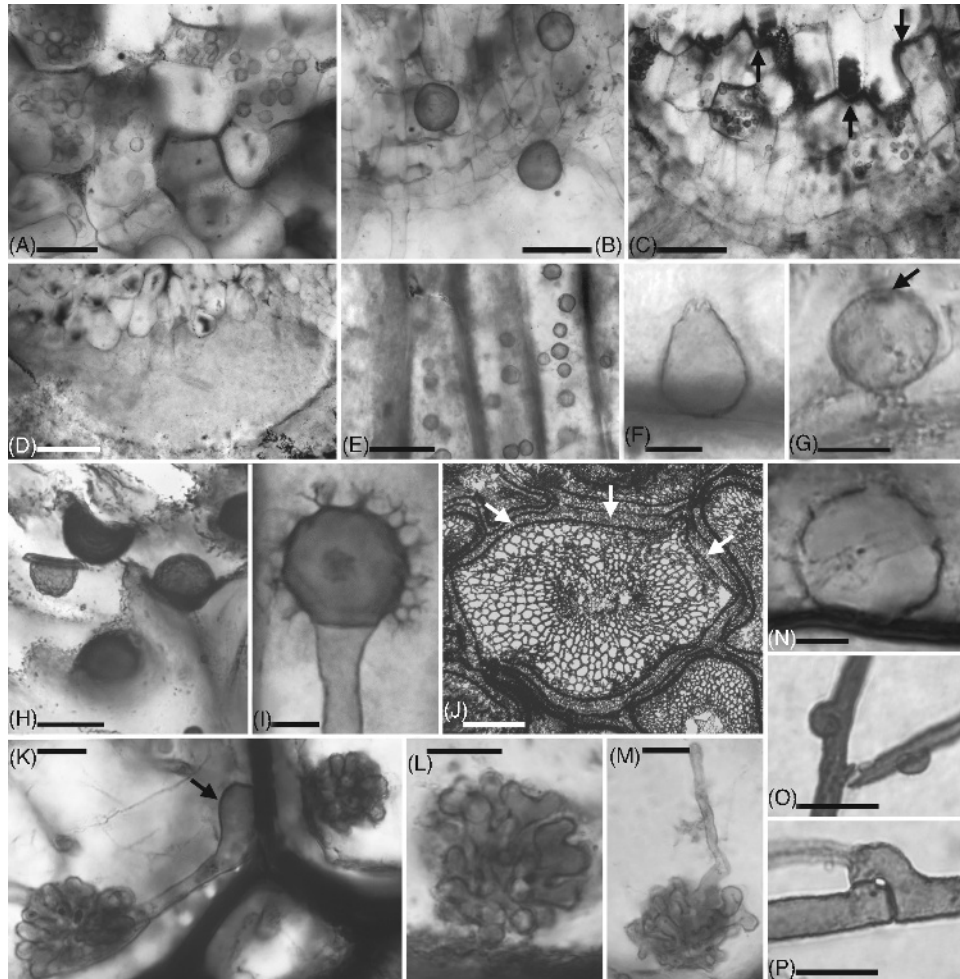


Figure 1.2. Fossil fungal endophytes from Lower Devonian Rhynie chert, Carboniferous cherts from France, and Early Permian silicifications from Germany. (A)–(D) Fungal endophytes in *Nothia aphylla* from the Rhynie chert. (A) A fungal endophyte in hypodermal cells. PBO; bar, 50 μm . (B) A second endophyte as in (A). PBO; bar, 150 μm . (C) Rhizoidal ridge (see (E)) showing hypodermal cells with secondarily thickened walls (arrows). PBO; bar, 100 μm . (D) Rhizoidal ridge with large void that may represent a host response or fungal degradation. PBO; bar, 250 μm . (E)–(I) Fungal endophytes in lycophyte wood and periderm from the Carboniferous of France. (E) Unidentified microfungal remains in tracheids. REN; bar, 30 μm . (F)–(G) Zoosporangium-like structures attached to tracheid and periderm cell walls; note distal, cleft-like discharge opening in Figure 1.2F and pore-like opening in Figure 1.2G (arrow). REN; bars, 10 μm . (H) Bowler hat-shaped putative chytrid zoosporangia. ROC; bar, 20 μm . (I) *Combre-somyces conifer* oogonium in a periderm cell; note conspicuous surface ornamentation. REN; bar, 10 μm . (J)–(P) Fungal endophytes in a *Psaronius* root mantle from the Lower Permian of Germany. (J) Root, transverse section, showing organization of tissue systems; cortical tissues contain arbuscule-like structures (arrows) (see Figures 1.2K–M). BSPG; bar, 2 mm. (K)–(M) Hyphae and arbuscule-like structures in cortical cells of *Psaronius* roots; note appressorium on host cell wall (arrow in Figure 1.2K). BSPG; bars, 10 μm . (N) Putative multiporate chytrid zoosporangium in *Psaronius* root cortex cell. BSPG; bar, 5 μm . (O)–(P) Basidiomycetous hyphae with clamp connections in *Psaronius* root aerenchyma. BSPG; bar, 10 μm .

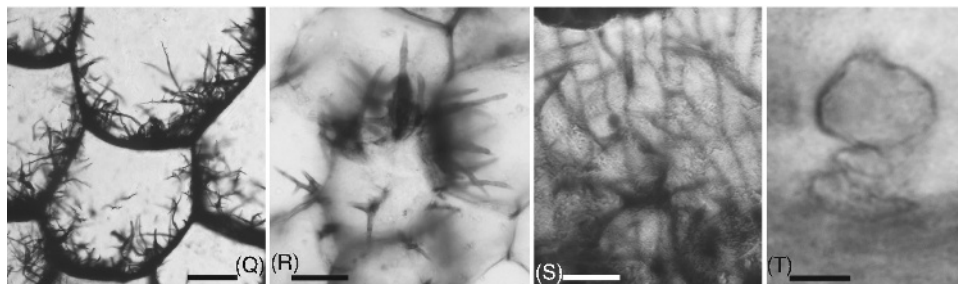


Figure 1.2. (Continued) (Q–T) Fungal endophytes in calamite rootlets from the Carboniferous of France. (Q) Endophyte infection on numerous cortical cells; note absence of intracellular fungi on inner periclinal walls. REN; bar, 50 μm . (R) Localized endophyte infection. REN; bar, 30 μm . (S) Anastomosing hyphae of the endophyte extending through host apoplast. REN; bar, 20 μm . (T) Apophysate putative chytrid-like zoosporangium attached to wall of cortical cell. REN; bar, 5 μm . *Source:* BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; PBO, Paleobotanical Collection of Westfälische Wilhelms-Universität, Forschungsstelle für Paläobotanik, Münster, Germany; REN, Collection Renault and ROC, Collection Roche, Museum d'Histoire Naturelle, Paris, France.

expect to see an increase in the diversity of fungi in the Carboniferous. Unfortunately, reports of fungi from this period of time are not widespread. This is due primarily to the fact that many early paleobotanical studies focused on impression/compression modes of preservation, which do not normally provide sufficient resolution to detect fungi associated with plants. In instances where plant remains are preserved in a chert matrix or otherwise permineralized, associated fungi have sometimes been noted and documented to some extent (e.g., Renault 1896, 1900). It is interesting to note in this context that the most common mode of structural preservation of Carboniferous plant remains in the form of calcium carbonate coal balls (for details on coal balls, refer to Scott and Rex 1985), which has been responsible for a considerable amount of detailed information on plant life in the Carboniferous (Taylor et al. 2009b), has yielded relatively few studies of fungi. Although there are various reasons for this paucity of attention to the fungal component of the Carboniferous coal ball floras, certainly one important reason is the commonly used technique to study coal ball plants—the cellulose acetate peel technique (for methodology, see Galtier and Phillips 1999). Since this technique relies on the acid digestion of the coal ball matrix, many of the fungi embedded in the matrix are lost during preparation (Taylor et al. 2011). In spite of this, there exist a few studies reporting on Carboniferous fungi that suggest an enormous, yet largely unrealized fungal diversity during this period of time.

As with the Early Devonian, chert deposits represent the most important sources of evidence for Carboniferous fungi and fungal associations and interactions with other organisms. Several Carboniferous cherts from central France have produced numerous structurally preserved specimens of various types of plant parts (i.e., shoot axes and stems, roots, leaves, and reproductive organs) that represent a broad spectrum of the floras (e.g., Galtier 1970, 1971, 2008; Doubinger et al. 1995). Regardless of whether the fossils consist of entire plant organs, fragments, or highly degraded plant matter, associated with virtually all of these remains are various types of fungal endophytes. Especially interesting are pieces of lycophyte (i.e., *Lepidodendron*) wood and periderm preserved in Viséan (Middle Mississippian) cherts of Combres and Esnost that contain a diverse assemblage of Peronosporomycetes, chytrid-like organisms, and other fungal remains (Krings et al. 2007a). Evidence of chytrid-like organisms occurs in the form of variously shaped structures that resemble resting spores (Figure 1.2E) and zoosporangia (Figures 1.2F, G); associated with many of these structures are tenuous filaments or hyphae that may represent parts of rhizomycelial systems (Krings et al. 2009a). In some of the periderm cells and

tracheids, there is a specific host reaction in the form of conical callosites. These structures are identical to those present in certain fungal spores (see Section ‘Early Land Plants from the Lower Devonian Rhynie Chert’). Despite the close association of callosites and putative chytrid zoosporangia, these structures have not been observed in organic connection. Other structures resembling chytrid zoosporangia occur within largely degraded plant material. One of these structures is hemispherical in shape and superficially resembles a bowler hat with an enrolled rim that surrounds a wide opening (Figure 1.2H).

Also present in several specimens of the Visean lycophyte periderm is a highly unusual intracellular endophyte, *Combresomyces cornifer*, which is interpreted as a Peronosporomycete based on the presence of specimens displaying oogonia with attached paragynous antheridia (Dotzler et al. 2008). Peronosporomycetes (Oomycota) are believed to be among the oldest eukaryotes on Earth (Pirozynski 1976); however, the fossil record of this group has remained inconclusive (Johnson et al. 2002). The characteristic oogonium–antheridium complexes that occur during the sexual reproduction process represent the only structural feature that can be used to positively identify fossil Peronosporomycetes (Dick 1969). *C. cornifer* is one of only a few Carboniferous microorganisms showing this feature (reviewed in Krings et al. 2011a). Moreover, the oogonium of *C. cornifer* possesses a complex surface ornamentation composed of branched, antler-like processes that arise from hollow papillations of the oogonium wall proper (Figure 1.2I). This type of surface ornamentation is unknown in extant Peronosporomycetes. A similar but slightly younger type of oogonium, *Combresomyces williamsonii*, has been found in the cortical tissues of a seed fern from the Lower Pennsylvanian of Great Britain (Strullu-Derrien et al. 2011). These specimens differ from *C. cornifer* in the size, general organization of the surface ornament, and the presence of both paragynous and hypogynous antheridia. Moreover, shortly after the discovery of *C. cornifer* from the Carboniferous of France specimens of this organism were reported from permineralized peat from the Triassic of Antarctica (Schwendemann et al. 2009). This suggests that this Peronosporomycete existed morphologically unchanged for a period of nearly 90 million years, and even survived the end-Permian mass extinction event. Of further significance is the fact that, although the vegetations of the Carboniferous and Triassic were quite different, this Peronosporomycete obviously had the capacity to adapt to changes in host quality.

1.4.2. Roots

It is generally assumed that by the middle Devonian all of the major groups of higher land plants possessed elaborate root systems, which served for anchorage and conduction (Gensel et al. 2001; Raven and Edwards 2001). Since several of the rootless Early Devonian land plants already possessed complex mycorrhizal associations, it is assumed that mycorrhizal fungi colonized root systems soon after they evolved. However, it is important to note that between the Early Devonian and Middle Triassic (see Phipps and Taylor 1996) there is little known about either the fungi or the root systems of the plants that they may have inhabited. There are several reasons for this, including the general absence of well-preserved extraxylary tissues where mycorrhizal fungi would typically be found, and the general paucity of detailed studies of plant roots from this period of time. Further contributing to this lack of information about the evolution of interactions between land plant roots and mycorrhizal fungi in the late Paleozoic is the scarcity of fungal evidence from Carboniferous plants, despite the fact that there is abundant plant diversity that has been documented from a large number of exquisitely preserved specimens. As a result, there have been just a few reports noting the presence of fungi in Carboniferous roots and other below-ground plant organs, including a few that suggested the presence of mycorrhizal associations (e.g., Weiss 1904; Osborn 1909; Halket 1930; Andrews and Lenz 1943; Agashe and Tilak 1970). Many of these reports have later been challenged or remain inconclusive (e.g., Cridland 1962; Taylor and Krings 2005; Strullu-Derrien and Strullu 2007). A recent reexamination of cordaite rootlets from the Upper Pennsylvanian of Grand-Croix (France) initially prepared by Octave Lignier, Rudolph Florin, and Alfred Carpentier

describes arbuscule-like structures in a well-defined area of the cortex (Strullu-Derrien et al. 2009). Arbuscule-like structures have recently also been documented in the ultimate units of the belowground organs of arborescent lycopsids (Lepidodendrales) from the Lower Pennsylvanian of Great Britain (Krings et al. 2011b).

One of the most interesting root systems that existed during the Carboniferous and Early Permian is the root mantle of the marattitalean tree fern *Psaronius*. Although other ferns, both fossil and extant, possess a root mantle, that of *Psaronius* is unusual in several ways. It consists of several layers of intertwining aerial roots (Figure 1.2J) that at some levels fuse by proliferation of the cortex. As a result of this developmental pattern, the root mantle forms an ensheathing structure around the actual stem that may become extensive over time. *Psaronius* root mantles were widely inhabited by other plants and animals, and thus represented a special habitat (e.g., Rothwell and Scott 1983; Labandeira 1998; Rössler 2000). It is reasonable to expect that fungi would be components of this habitat as well. In thin sections, initially prepared by Karl Mägdefrau of an Early Permian *Psaronius* stem from eastern Germany, ongoing research has discovered more than 15 types of intra- and intercellular fungal endophytes (Figures 1.2K–P), ranging from chytrid-like zoosporangia (Figure 1.2N) to basidiomycetous hyphae with clamp connections (Figures 1.2O, P) (Barthel et al. 2010). One of the most interesting fungal associations in these roots is an intracellular mycelial system of uncertain affinity that extends through large portions of the (proliferating) root cortex. It consists of hyphae that form prominent appressoria on host cell walls (Figure 1.2K (arrow)) and arbuscule-like structures in the cell lumen (Figure 1.2M). Although the nutritional interaction between this fungus and its host remain unknown, the fungus has features in common with modern endomycorrhizal fungi, including the apparently ephemeral nature of the arbuscule-like structures.

While the *Psaronius* example documents fungal endophytes in aerial roots, the general organization and functioning of substrate roots is quite different. One of the inherent difficulties in studying substrate roots in the fossil record, irrespective of the quality of preservation, is their generally disarticulate occurrence that makes it difficult to determine the source plant, especially if the roots contain only primary tissues. It is precisely these roots in which one would expect to find evidence of the colonization by endophytic fungi, especially endomycorrhizae. A recently discovered example of what may represent another complex land plant root–fungal interaction occurs in narrow calamite (arborescent plants related to modern *Equisetum*) rootlets preserved in Late Pennsylvanian cherts from Grand-Croix, central France. This fungus (Figures 1.2Q–S) consists of branched hyphae that appear to enter the host from the outside and initially extend through the apoplast of the cortical cells (Figure 1.2S). At some point, however, the hyphae invade individual cortical cells, but are confined to only the outer periclinal and anticlinal cell walls. The extent of intracellular penetration is variable among the specimens of roots. While some roots display extensive intracellular presence of the fungus with almost all of the cortical cells affected (Figure 1.1Q); others show more localized infections in which one to few adjacent cells contain hyphae (Figure 1.1R). At this point, we are uncertain as to whether this pattern of infection is developmental or represents a more specific type of interaction. Although this fungus is the most conspicuous endophyte in these calamite rootlets, there are other fungal remains in the rootlets as well, many of which resemble chytrids (e.g., Figure 1.2T).

1.4.3. Leaves

Although leaves constitute a harsh habitat for fungi because nutrient availability is transient, and leaves undergo extreme fluctuations in humidity, temperature, gas exchange gradients, and ultraviolet radiation (Goodman and Weisz 2002), leaf endophytes represent a major component of fungal associations with plants (e.g., Arnold 2007; Rodriguez et al. 2009; Wang et al. 2009). Like roots, true leaves (microphyllous and megaphyllous types) had evolved by the end of the Early Devonian (Gensel 2008). Although it is reasonable to expect that endophytic fungi rapidly exploited these new niches, fungal remains in leaves are rarely reported in late Paleozoic and

Mesozoic fossils, despite the fact that foliage fossils are perhaps the most intensively studied plant organs. The absence of a well-defined record may result from several factors, perhaps most important is that the majority of foliage fossils are preserved as impressions and compressions, which do not normally lend themselves to the presence of microscopic remains on the surface or in the interior. In addition, the role of collection bias (i.e., only retrieving complete or well-preserved specimens) no doubt has filtered out numerous examples of fungal leaf parasitism and pathogenicity. This paucity of information has led some to speculate that fungal leaf endophytes did not evolve until much later, perhaps in conjunction with the origin and diversification of flowering plants in the Early Cretaceous.

However, research indicates that fungal leaf endophytes were present at least by the Carboniferous. A structurally preserved fern pinnule fragment from the Late Pennsylvanian Grand-Croix cherts of central France contains an intracellular endophytic fungus of uncertain affinity that inhabits the cells of the hypodermis (Krings et al. 2009c). The fungus consists of branched, septate hyphae that produce long-necked hyphal swellings (Figure 1.3C) and structures that probably represent conidia (Figure 1.3D). A few other fungal leaf endophytes have been discovered in compression fossils through cuticular analysis (for details on methodology, refer to Kerp and Krings 1999). The evidence for the presence of fungi in these leaves consists of hyphae and spores in the parenchymatous mesophyll and conducting tissues (e.g., Barthel 1961; Krings 2001). The inability to place these fungi within the context of life history biology precludes their affinities and details about the nutritional mode.

Other structurally preserved Carboniferous leaf fragments contain microscopic remains that are somewhat similar to structures seen in extant fungi, but cannot be assigned to the fungi with certainty. One recently discovered example from the Upper Pennsylvanian of France includes a variety of unusual structures that mostly occur as intracellular endophytes in hypodermal cells of several fern pinnules (Figures 1.3E–H) (Krings et al. 2010d). Some of these structures have a superficial similarity to fungal microsclerotia (Figures 1.3G, H), while others are reminiscent of resting spores (Figures 1.3E, F). Although the systematic affinities, and sometimes even the biological nature, of these structures remain equivocal, their presence offers an important source of information about the degree of vascular plant leaf colonization by other types of organisms in the late Paleozoic.

While we have presented examples of endophytes associated with true leaves, there is also an excellent example of a fungal endophyte associated with an early land plant that lacked leaves, but had small, unvascularized but stomatiferous leaf-like appendages. The upright axes of *Asteroxylon mackiei* from the Upper Devonian Rhynie chert were densely covered with leaf-like appendices, some of which were colonized by an endophytic ascomycete, *Palaeopyrenomycites devonicus*, that produced perithecia within the host tissue, usually beneath the stomata (Figure 1.3A) (Taylor et al. 2005b). The morphology and internal organization of these perithecia is relatively complex (Figure 1.3B). This supports the hypothesis, based on molecular data, that the Ascomycota were established as a diverse group of fungi by the Early Devonian (e.g., Heckmann et al. 2001; Berbee and Taylor 2001; Taylor and Berbee 2006).

1.4.4. Reproductive Structures

Evidence to date indicates that all early land plants were homosporous and produced large quantities of relatively simple spores (e.g., Kerp and Hass 2004; Wellman et al. 2006). Upon germination, the spores developed into free-living, multicellular gametophytes (surveyed in Kerp et al. 2004). All of the examples that have been presented in the preceding text on fungal endophytes in early land plants relate to occurrences in the sporophyte. However, there also are several examples from the Early Devonian Rhynie chert of fungal associations with the gametophyte generation of early land plants. Those that have been studied in detail indicate that the gametophyte generation was endomycorrhizal and displayed the same complement of structures (e.g., arbuscules, vesicles, and trunk hyphae) as the sporophyte (Taylor et al. 2005a).

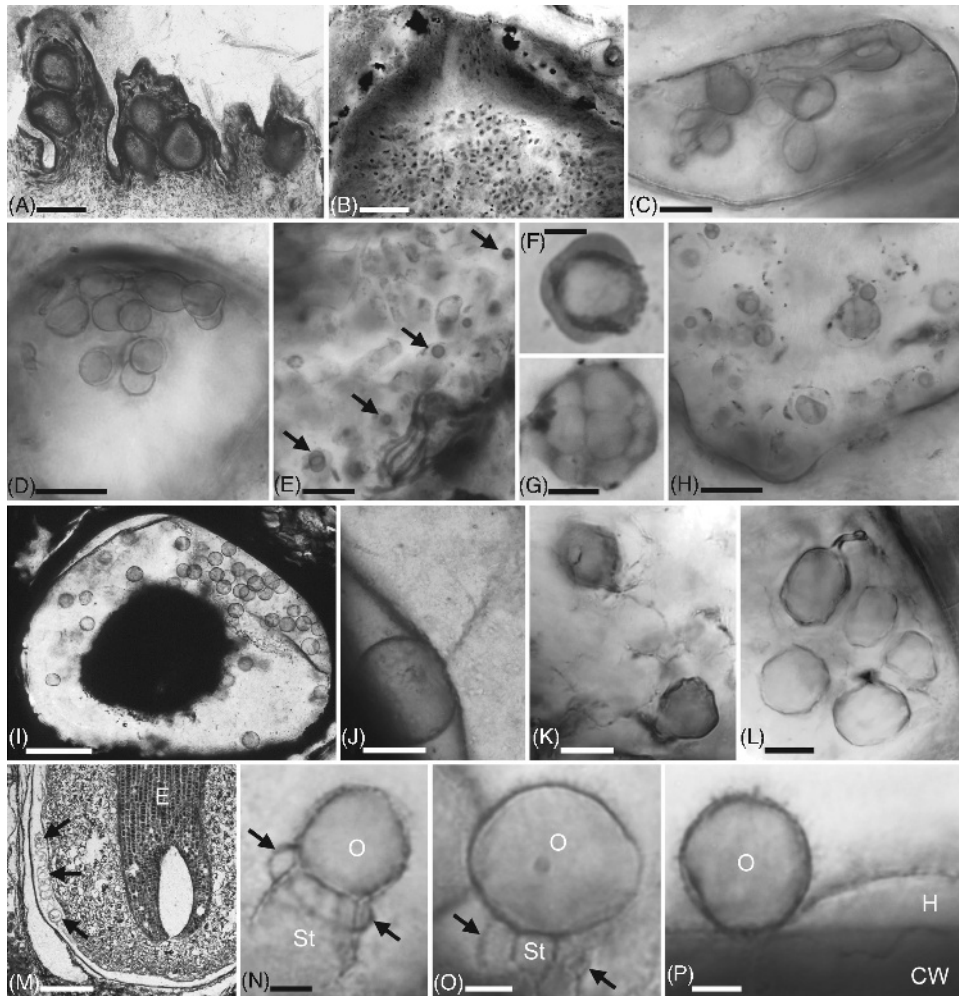


Figure 1.3. Fossil fungal endophytes from Lower Devonian Rhynie chert, Carboniferous cherts from France, North American Carboniferous coal balls, and Triassic silicified peat from Antarctica. (A) Perithecia of *Paleopyrenomycites devonicus* in enations of the land plant *Asteroxylon mackiei* from the Rhynie chert. PBO; bar, 0.3 mm. (B) Detail of perithecial ostiole of *P. devonicus*. PBO; bar, 50 μm . (C, D) Long-necked hyphal swellings and putative conidia in hypodermal cells of a fern pinnule from the Carboniferous of France. REN; bars, 10 μm . (Figure 1.3C) and 20 μm (Figure 1.3D). (E–H) Microscopic structures in hypodermal and cortical cells of fern pinnules from the Carboniferous of France. REN; Figures 1.3E, F: structures resembling resting spores (arrows in Figure 1.3E). Bars, 50 μm (Figure 1.3E) and 5 μm (Figure 1.3F); (G, H) microsclerotium-like structures. bars, 5 μm (g); 30 μm (H). (I, J) Chytrid-like organisms in lycophyte megaspores from the Carboniferous of France. ROC; bars, 150 μm (I); 30 μm (J). (K–L) Chytrid-like organisms from the degrading cortex of a Carboniferous fern reproductive structure from France. REN; bars, 10 μm . (M) Triassic seed (longitudinal section) containing an embryo and fungal sporocarps (arrow) between megaspore membrane and megagametophyte tissue. KU; bar, 100 μm . (N–P) Putative peronosporomycete from the wall of a Carboniferous fern sporangium from France (St, subtending hypha or stalk; O, oogonium; arrows, amphigynous antheridium). REN; bars, 5 μm . (P) Mature oogonium (O) and subtending hyphae (H) on host cell wall (CW); bar, 5 μm .

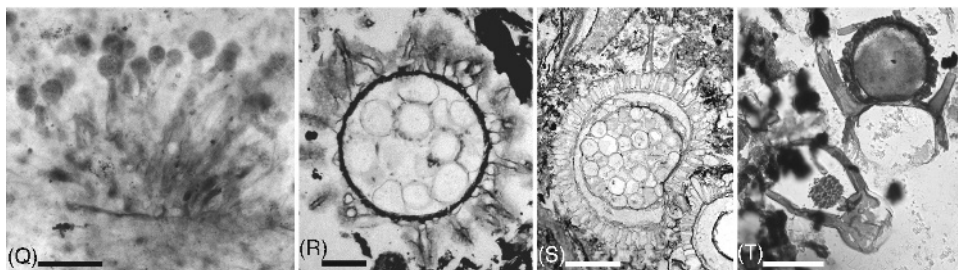


Figure 1.3. (Continued) (Q) Tuft of sporothalli of *Palaeoblastocladia milleri* arising from the surface of a decaying Rhynie chert axis. PBO; bar, 50 μm . (R–S) Two types of sporocarps associated with degrading plant material in Carboniferous coal balls. KU; bars, 10 μm (R); 20 μm (S). (T) Two (a-)zygosporangium-suspensor complexes in a Carboniferous seed. KU; bar, 30 μm . Source: KU, University of Kansas Paleobotanical Collection, Lawrence, Kansas, USA; PBO, Palaeobotanical Collection of Westfälische Wilhelms-Universität, Forschungsstelle für Paläobotanik, Münster, Germany; REN, Collection Renault and ROC, Collection Roche, Museum d'Histoire Naturelle, Paris, France.

By far, the most frequently found fossil fungal association with early land plant reproductive structures are spores colonized by various types of chytrid-like organisms. Many land plant spores from the Rhynie chert show a dense epibiotic population of (putative) zoosporangia on the spore surface, often close to the germination suture. Others occur between the individual layers of the spore wall, and still others are endophytic and inhabit the spore lumen (Taylor et al. 1992; Krings et al. 2009b). The absence of any response in the form of a structural alteration of the host makes it impossible to evaluate the nutritional mode of the fungi and also the impact of these organisms as driving forces in the evolution of early land plant communities. Similar associations between chytrid-like organisms and land plant spores have also been documented from the Carboniferous (surveyed in Krings et al. 2009a). In addition to homosporous plants such as ferns and some sphenophytes, some Carboniferous plant groups, most notably the lycophytes, had evolved heterospory, in which large female spores (megaspores) and small male spores (microspores) are formed (Bateman and DiMichele 1994). That these spore types represented an increased source of nutrients available to the fungi is supported by examples of epibiotic and endobiotic colonization of Carboniferous (mega-)spores by numerous types of microfungi, most of which in some degree resemble chytrids (e.g., Figures 1.3I, J). Chytrid-like organisms are known to have colonized the spore-producing organs of a Late Pennsylvanian zygopterid fern from France (Krings et al. 2009d). In this example, four types of structures similar to chytrid zoosporangia occur in the degraded cortex of the small axes that produced the sporangia (e.g., Figures 1.3K, L). Moreover, the sporangium walls of this fern contain what we interpret as an intracellular endophytic Peronosporomycete that produced amphigynous antheridia (Figures 1.3N–P) (Krings et al. 2010c). As seed plants evolved and diversified during the Late Devonian, additional types of microhabitats for fungal endophytes also became available. Not only did these include the large encapsulated seed megaspores, but also the reduced microgametophyte phase in the form of pollen grains. In fact, infected seeds, spores, and pollen grains represent the most frequent evidence of chytrid-like microfungi in the fossil record (e.g., Renault and Bertrand 1885; Oliver 1903; Daugherty 1941; Millay and Taylor 1978; Krings et al. 2009a, 2009d), suggesting that these stages in the life history of land plants represented suitable hosts and habitats for these microorganisms as they do today.

1.4.5. Saprotrophic Fungi in Decayed Plant Material

While it is obvious that the most common interaction between land plants and fungi in ancient ecosystems was saprotrophism, distinguishing saprotrophic relationships from the various

biotrophic relationships that existed between plants and fungi in the past is extremely difficult. One of the reasons for this difficulty is the lack of detailed information about the fungal life history, which could be used to determine the systematic affinities of the fungus, and thus infer the nutritional mode. One fossil fungus that is known in extraordinary detail, including the life cycle, is *Palaeoblastocladia milleri* from the Rhynie chert (Remy et al. 1994). In this fungus, there is a distinct alternation of haploid gametothalli and diploid sporothalli (Figure 1.3M) that is nearly identical to that in certain extant members of the Blastocladiomycota. Since the extant forms are so distinct and possess a saprotrophic nutritional mode, the hypothesis has been advanced that the vegetative system of the fossil fungus, which extends throughout the cortical tissues of degrading axes of the early land plant *A. major* supported the fungus through decomposition of host tissues.

Permineralized peat, including Carboniferous coal balls and silicified peat from Antarctica, are additional sources of information about fossil saprotrophic fungi because this preservational mode includes numerous stages of plant degradation. For example, in some coal balls, there are various types of spore-like bodies, termed sporocarps (Figures 1.3R, S), that consist of interlaced hyphae surrounding a central cavity; the external surface of some may possess elaborate types of ornamentation (Davis and Leisman 1962). In some sporocarps, there are internal spherical structures that were at one time thought to be asci and ascospores (see Stubblefield and Taylor 1988). Today, these fungi are believed to belong to the Zygomycota (Krings et al. 2010b), and the internal spheres are interpreted as some form of chytrid-like mycoparasite (White and Taylor 1989). A possible clue as to the interaction between at least one type of sporocarp-producing fungus and its host is the recent discovery of these structures between the megaspore membrane and megagametophyte tissue of a Triassic seed (Figure 1.3M).

Another putative zygomycete that occurs in Carboniferous permineralizations is *Protoascon missouriensis* (Figure 1.3T) (Batra et al. 1964). While the generic name indicates that this fungus was originally interpreted as an ascomycete, recent research views it as an (a-)zygosporangium-suspensor complex of a zygomycete, perhaps most closely related to the Mucorales (Taylor et al. 2005c). Also in these permineralizations are thick-walled spores that resemble the chlamydospores of various Glomeromycota (Wagner and Taylor 1982). Although the size and complex wall organization of these spores is comparable to those of some Early Devonian and extant glomeromycotan spores, the precise affinities of the structures remain unclear because other aspects of the life history continue to be unknown.

Although relatively unexplored to date for fungal remains, the permineralized peats from the Permian and Triassic of Antarctica have provided some evidence of fungi associated with land plants. For example, a putative endoparasitic chytrid (García-Massini 2007a) and clusters of terminal and intercalary *Glomus*-type chlamydospores (García-Massini 2007b) have been reported from (decaying) plant remains preserved in these cherts.

1.5. DISCUSSION

The examples that have been used to illustrate fossil fungal endophytes chiefly from the Devonian and Carboniferous represent a very small segment of the total level of endophytic fungal associations and interactions with land plants that existed in late Paleozoic ecosystems. Nevertheless, as we have noted in the preceding text, the extraordinary preservation within a chert matrix does make it possible to examine several types of land plant–fungal associations and interactions in great detail. These associations and interactions provide the basis for our current understanding of the roles that fungi have played in shaping and sustaining ancient ecosystems, and driving their subsequent evolution.

What is striking is that some of the relationships between endophytic fungi and Early Devonian land plants (e.g., endomycorrhizae) are remarkably complex, and appear similar structurally to the associations between fungi and land plants found today. This suggests that the genetic information and biochemical pathways to make these interactions work were in place ~400 million

years (Ma) ago, and that, in some instances, the signaling mechanisms and morphological adaptations that allowed these interactions to function remained largely unchanged to the present. It is remarkable that, despite the apparent stasis of fungi, various host plants have evolved multiple adaptations to maintain stable relationships or to control the fungi. Documentation of fungal endophytic associations and interactions in the Early Devonian and Carboniferous provides an ideal reference point that allows direct comparisons to be made between fungi and the changing floral elements at two especially interesting points in geologic time. While the Rhynie chert land plants are often referred to as the most primitive forms of higher land plants, it is well established that the first unequivocal terrestrial plants existed in the Early Silurian, and perhaps even earlier (see Kenrick and Crane 1997; Taylor et al. 2009b). Some molecular clock estimates (e.g., Heckmann et al. 2001) suggest that all major fungal lineages have diverged well before the first evidence of land plants. Based on these estimates, it is reasonable to conclude that fungi and land plants had already coevolved for a long period of time prior to the Early Devonian Rhynie chert. The assumption that fungi and land plants coevolved, and that the fungal partner was necessary for the transition of plant life from water to land, initially postulated by Pirozynski and Malloch (1975), has subsequently been rediscovered and elaborated. The complexity present in some of the Early Devonian Rhynie chert land plant–fungal associations adds further credibility to this hypothesis if we assume that, for example, the full complement of biological interactions necessary in a mycorrhizal symbiosis took millions of years to become established.

In spite of the well-documented details about the land plant–fungal associations in the Rhynie chert, it is important to understand that these examples likely represent only a small percentage of the total number of fungal associations and interactions that have existed in this paleoecosystem. Reasons for the incomplete representation of the actual fungal ecosystem during this time include the low number of specimens of some of the associations, unfamiliarity of some workers with fungal life history and potential host responses, and the overriding principle that morphological similarity does not always equal relatedness, especially in the context of geologic time.

In contrast to the Early Devonian Rhynie chert land plants, which all had a basic morphological uniformity (i.e., they were relatively small, generally naked, rootless, clonal, and only produced primary tissues), Carboniferous floras were much more diverse with reference to size, morphology, and reproductive biology of the plants, as well as with reference to plant community structure. It would seem obvious that, because of this increased biodiversity and morphological complexity there would be a marked increase in the diversity of fungi associated with these floras, as well as the number of specific plant–fungal associations or interactions. Although relatively few Carboniferous plant–fungal associations or interactions have been documented, our research indicates that the underrepresentation of biological interactions in the Carboniferous cherts from France does not reflect an actual paucity of associations and interactions in these paleoecosystems (Krings et al. 2007a, 2009a, 2009c, 2009d), but rather represents a study bias that has resulted from the more intensive screening for interactions in the Rhynie chert to date.

It is increasingly clear that in modern ecosystems many of the fungi involved in interactions with land plants simultaneously interact with a host of other (micro-)organisms. As a result, many associations that historically have been considered relatively simple are now known to be highly complex systems that involve multiple organisms (e.g., multitrophic relationships among land plants, cyanobacteria, mycorrhizal fungi, and bacteria). While it is difficult to resolve multitrophic levels of interaction in the fossil record, the close and consistent co-occurrence of different microbial endophytes within the same host may suggest a more complex association or interaction system. For example, several prostrate mycorrhizal axes of the land plant *A. major* from the Rhynie chert contain a filamentous cyanobacterium that appears to be abundant close to the mycorrhizal arbuscule zone (Krings et al. 2009e). Although the presence of cyanobacteria in *A. major* is a very rare occurrence, the close proximity of the cyanobacteria to the mycorrhizal fungus suggests some interaction between the two endophytes. This example underscores the importance of fully documenting the microbial diversity in and on other organisms within the fossil record. In this way, some of the less conspicuous elements of the microbial realm of

the past may be discovered and perhaps incorporated in our understanding of biocomplexity levels within ancient ecosystems.

In spite of the incredible diversity of fungal endophytes in leaves today, it is intriguing that leaf endophytes are not well documented in the fossil record prior to the Cretaceous. However, the few examples that have been described clearly indicate that these fungi were present in pre-Cretaceous plants (e.g., Oliver 1903; Barthel 1961; Krings 2001; Krings et al. 2009c). This fact contradicts the suggestion that fungal leaf endophytes may have initially evolved concomitantly with flowering plants, but rather suggests that these organisms may have actually been a rare element in late Paleozoic and Mesozoic ecosystems or simply overlooked. Another potential reason why this element of the fungal record is so rare may be related to the manner in which leaves are preserved as fossils in the form of impressions or compressions. It has also been suggested that certain plant groups during the late Paleozoic may have possessed physical or chemical defense mechanisms that inhibited or reduced fungal colonization (Taylor and Osborn 1996). Conversely, it is also possible that certain groups of fungi that are today commonly found as leaf endophytes had not yet developed the sufficient means to become established on or in leaves, or only a reduced portion of the life cycle persisted in or on leaves. As with the examples of root endophytes, we predict that, as more structurally preserved leaves are examined, there will be a substantial increase in the number of leaf endophytes reported.

1.6. CONCLUSIONS AND A FUTURE PERSPECTIVE

There are numerous examples of plant–fungal associations or interactions in younger sediments that have been important in assessing the distribution of fungi and fungal associations or interactions with land plants in time and space. These include a wide variety of symptoms on Cretaceous and Cenozoic leaves and other plant parts thought to be caused by fungi (e.g., Meschinelli 1898; Watanabe et al. 1999; Van der Ham and Dortangs 2005; Jasinski and Payette 2007), as well as fungal vegetative and reproductive structures on leaf surfaces (e.g., Dilcher 1965; Kar et al. 2004b; Phipps and Rember 2004; Phipps 2006). In addition, there are chert deposits from the younger Mesozoic and Cenozoic (e.g., the Eocene Princeton chert) that have been informative and hold great potential because of their excellent preservation and obvious interactions with a diverse flora (e.g., Le Page et al. 1994, 1997). The same may be said for silicified wood containing fungal remains that occur throughout the geologic column (e.g., Stubblefield et al. 1985; Pujana et al. 2009). There are also examples of indirect evidence of plant–fungal interactions such as structurally preserved basidiocarps of polyporous fungi (e.g., Fleischmann et al. 2007) and remains of phytoparasitic fungi in the dung of herbivorous dinosaurs (Kar et al. 2004a; Sharma et al. 2005) that document the presence of an interaction. Although known to contain a diverse biota, including fungi, for more than 100 years, fossilized plant resins (collectively termed amber) have produced only a few examples of plant–fungal associations/interactions (e.g., Dörfelt and Schmidt 2007).

Despite the large number of fungal remains in the fossil record, including those that provide direct or indirect evidence of an association or interaction with land plants, the discipline of paleomycology is at an early stage of development. It is interesting that despite studies by Renault (1896) more than 100 years ago, and the great interest in permineralized plant remains in Europe and North America, including studies of Carboniferous coal balls, fossil fungi were largely ignored. Moreover, when fungi were reported they were rarely placed within a broader context. A similar hiatus can be seen between the first description of fungi in the Rhynie chert by Kidston and Lang (1921) and subsequent reports of Rhynie chert fungi and land plant–fungal associations and interactions as the primary focus of the study. During the last 20 years, however, there has been an increasing awareness of fossil fungi and their importance in ancient ecosystems, which has been stimulated by a generally growing scientific interest in the microbial world and the interrelatedness of all organisms today.

Paleomycology today largely consists of descriptive studies. This inventory of the fossil microbial world is critical to subsequent studies aimed at understanding how these organisms functioned as integral parts of ecosystems. Inventories of fossil organisms provide a source of information to more accurately calibrate molecular clocks. While these calibration points will be important in helping to define minimum ages for various fungal lineages, some may also contribute to a more accurate assessment of the evolutionary history of specific plant–fungal associations and interactions, and how these relationships may have affected plant viability, and functioned as driving forces in land plant evolution.

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