

The importance of fungi in shaping the paleoecosystem

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Abstract

Although fungi have a long geologic history, many aspects regarding their origins and subsequent evolution remain impossible to document from the fossil record. As heterotrophs, fungi must interact with other organisms, and it is here that the fossil record can provide an important source of biological and paleoecological information about fungal interactions. Saprophytic, parasitic and biotrophic interactions among fungi and other organisms are ancient; examples of these interrelationships are discussed as they relate to the establishment and evolution of the biological and physical paleoecosystem.

1. Introduction

Although fungi were some of the first organisms to be reported as fossils, their geologic record is only now beginning to be fully appreciated. Several major groups can be traced well back into the Paleozoic (Taylor, 1993); for others, the record is far less precise, and none are known from sediments of Precambrian age. Perhaps the oldest fossil fungi are represented by non-septate filaments from the Cambrian that are believed to have been reef saprophytes (Kobluk and James, 1979). Filaments have also been reported from Early Silurian sediments (Pratt et al., 1978), while perforate-septate hyphae and multicellate spores are known from the Late Silurian (Sherwood-Pike and Gray, 1985). Despite the antiquity of these fungal remains, little is known about their organization, and even less about how they functioned in the paleoenvironment in which they lived.

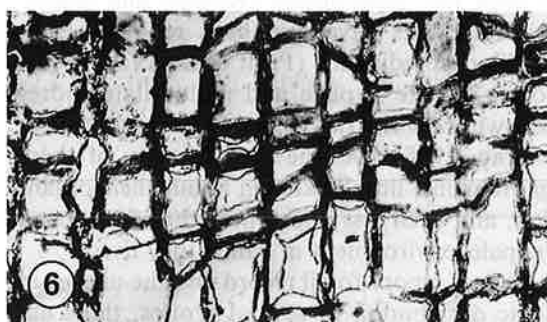
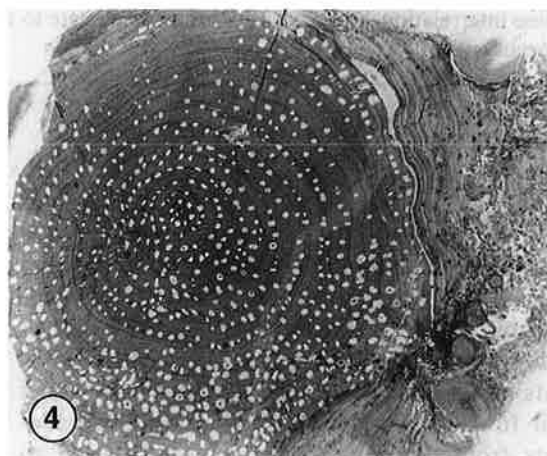
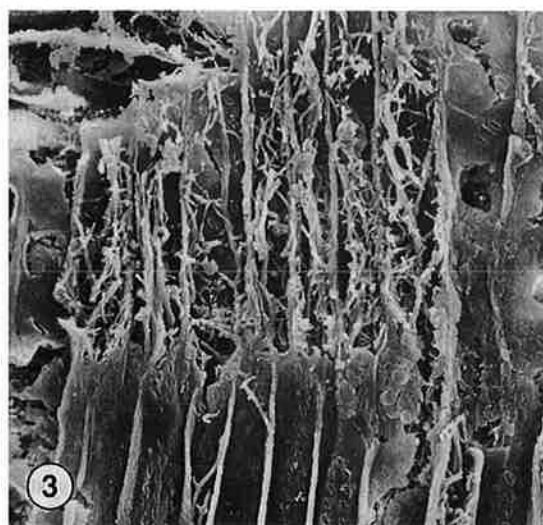
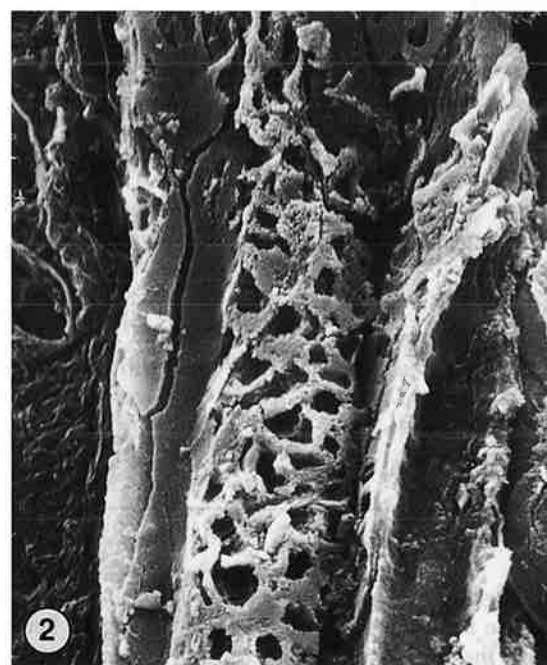
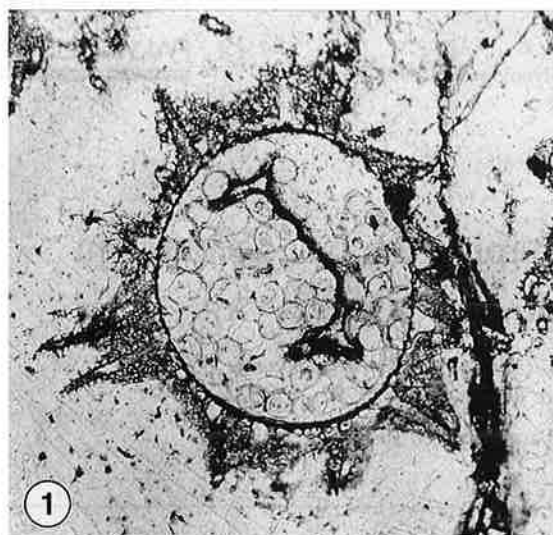
In spite of a poor fossil record and the uncertain geologic distribution of several groups, there are

nevertheless unique contributions that can be made only through the investigation and evaluation of fossil fungi. One of the most important contributions considers the various biological interactions that occurred among fungi and other organisms through geologic time. In this paper we will discuss several of these interrelationships and consider how they may have affected the paleoecosystem in which they existed.

2. Saprophytic interactions

It has been suggested that as the atmosphere gradually evolved, the Earth experienced extensive fluctuations in temperature and terrestrially consisted of barren rock surfaces that were low in nutrients. As a result, there were few stable, moist environments in which organisms might flourish. As time progressed the land surface must have also included decaying algae and other organisms,

PLATE I



such as cyanobacteria, along shore lines and in shallow tidal pools. There can be little doubt that initially various microorganisms were the primary decomposers, and only later did fungi and pseudofungi assume this role.

Today the most obvious interaction among fungi and other organisms involves the decomposition of plant and animal tissues, a process that returns available nutrients back into the ecosystem. One would expect examples of saprophytic activity to be common in the fossil record; however, this is generally not the case. In the Carboniferous, for example, a high percentage of fungal remains are not preserved within plant tissue, but rather as hypogeous sporocarps in the surrounding matrix (Plate I, 1). Many of these fossils may represent endogonaceous Zygomycetes (White and Taylor, 1989a). Today this fungal group constitutes the major root symbionts (mycorrhizae) in the ecosystem, but during the Paleozoic these fungi may have been the principal decomposers in the ecosystem (Taylor and White, 1989). Today the principal cellulose and lignin decomposers in the ecosystem are Basidiomycetes. Although they have a fossil record that dates back to the Upper Devonian (Stubblefield et al., 1985), the fossil record of this group indicates that Basidiomycetes may have initially contributed only marginally as tissue decomposers. While it is difficult to document the actual fungi responsible for tissue decomposition, the activities of these organisms are represented in the fossil record as fragmented pieces of plant tissue that can be observed, especially in permineralizations (e.g. coal balls and silicified peats) (Plate I, 3). Not all material of this type can be traced directly to the activities of fungi; some fragments obviously reflect combined microbial decomposition together with mechanical

dissociation of plant material resulting from transport, deposition and diagenesis.

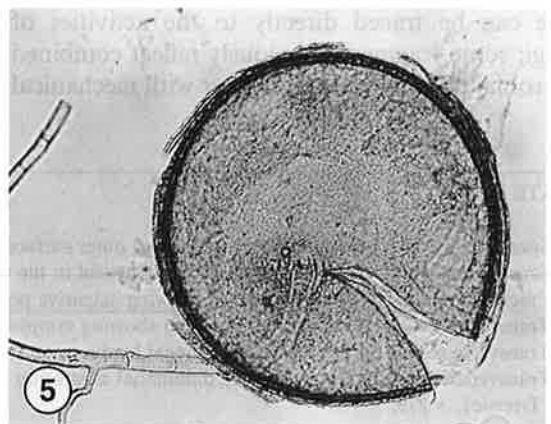
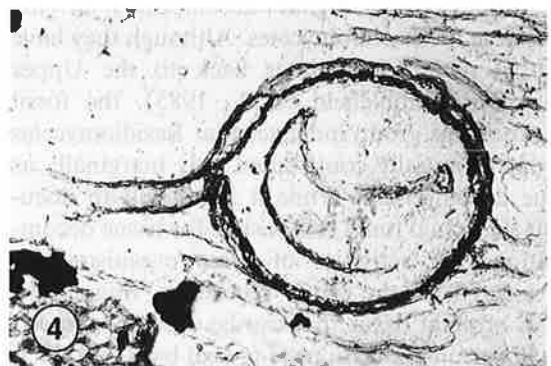
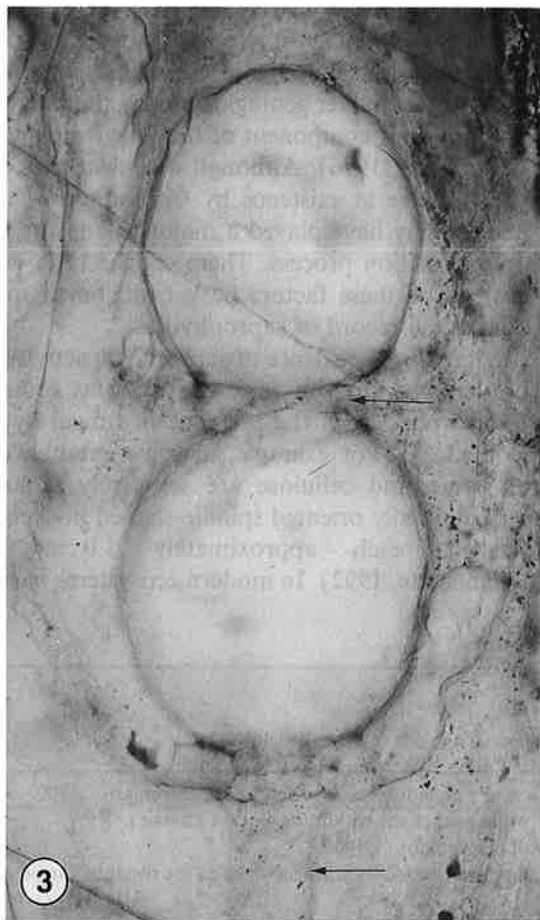
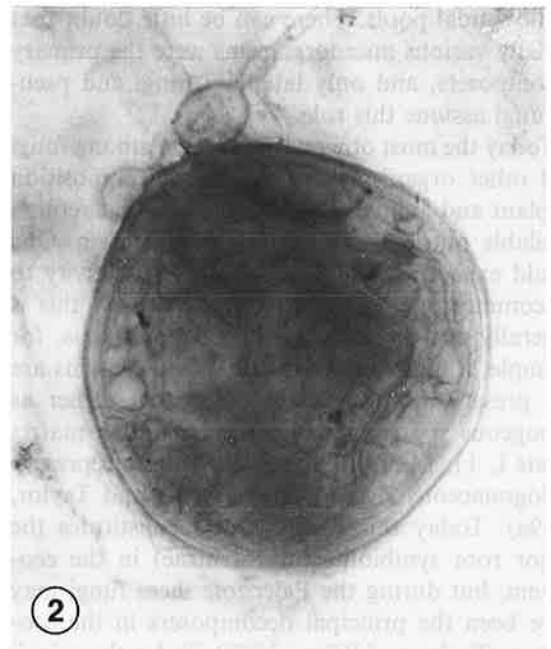
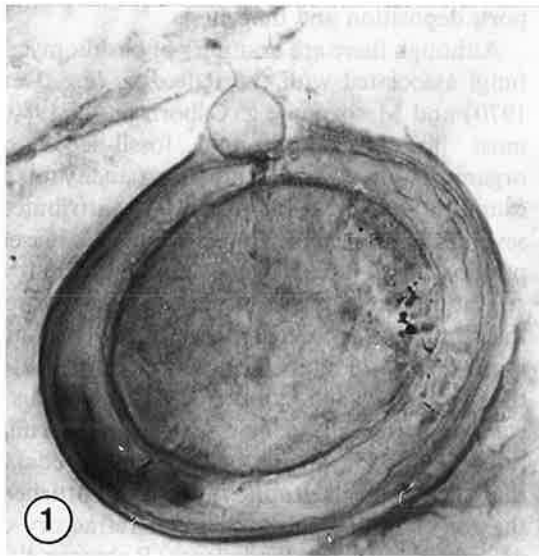
Although there are examples of basidiomycetous fungi associated with the Paleozoic (e.g. Dennis, 1970) and Mesozoic (e.g. Osborn et al., 1989), in most instances the actual fossil-decomposing organisms are not present. The paucity of good examples of these fungi may be attributed to several factors. For example, it may be biased by preservation, reflect some environmental constraint on fungal growth such as acidity, or reflect the fact that such decomposers initially inhabited more upland habitats. It has been suggested that the seemingly small number of Carboniferous saprophytes is directly related to the large accumulations of organic carbon in the form of coal, and that such deposits are the result of a bottleneck in the recycling of lignin and other refractory compounds produced by land plants (Robinson, 1990). This hypothesis is largely consistent with the historical belief that ascomycetes and basidiomycetes, the two principal lignin decomposers today, evolved much later geologically, and thus were not an important component of the Paleozoic mycota (Pirozynski, 1976). Although it is clear that both groups were in existence by Carboniferous time, neither may have played a major role in the total decomposition process. There can be little doubt that all of these factors have contributed to the poor fossil record of saprophytism.

More direct evidence of saprophytic activity can be demonstrated by various symptoms found in fossil wood, or in the presence of fungal hyphae (Plate I, 5). For example, in some extant woods as lignin and cellulose are selectively removed, longitudinally oriented spindle-shaped pockets are formed, each approximately 1.0 cm long (Blanchette, 1992). In modern ecosystems basidio-

PLATE I

1. Sporocarp of *Traquairia* showing ornamented outer surface and spores (?) inside (Carboniferous). $\times 120$.
2. Erosion troughs in the secondary wall of a tracheid in the wood of *Callixylon* (Devonian). $\times 2000$.
3. Fractured section of *Callixylon* wood showing extensive penetration of fungal hyphae into tracheids (Devonian). $\times 200$.
4. Transverse section of *Araucarioxylon* stem showing symptoms of white pocket rot within the wood (Triassic). $\times 0.7$.
5. Transverse section of a tracheid with fungal hypha penetrating wall (Devonian). $\times 1000$.
6. Transverse section of wood showing differential separation of primary and secondary tracheid walls as the result of fungal attack (Triassic). $\times 275$.

PLATE II



mycetes are responsible for this type of decay pattern, commonly known as white pocket rot (Plate I, 4). The oldest known occurrence of this type of decay is from the Permian and Triassic of Antarctica (Stubblefield and Taylor, 1986). Pocket rot fungi are also believed to be responsible for wood rot in Upper Triassic tree trunks in North America (Creber and Ash, 1990). Interestingly, the pockets in both modern and fossil woods are identical suggesting that the diffusion rates of fungal enzymes through the cellulose and lignin are also identical. Less dramatic effects of fungal activity can be identified in woods by examining preservational differences in the primary and secondary walls of tracheids (Plate I, 6). Various extant wood-rotting fungi selectively destroy cellulose and lignin at different rates (Plate I, 2). An analysis of these differences, both qualitative and quantitative, may ultimately provide a basis for distinguishing the type of fossil fungal rot (e.g. white rot, soft rot, brown rot) and thus the fungus responsible. At the present time, however, there is insufficient evidence to document the extent of these fungal interactions, and which ones played the major role in wood degradation. In many instances the fungi were saprobes of dead trees, while in other cases alterations in the cell walls indicate that the trees were alive when infection initially took place.

3. Parasitic interactions

Within living biological systems the difference between parasitic and mutualistic symbioses are often difficult to distinguish. Although a great deal has been written about the theoretical evolution of these interactions (e.g. Lewis, 1974), only recently have good examples of parasitic inter-

actions been documented from the fossil record. While it remains impossible to document the dual movement of nutrients in this type of symbiosis using fossils, the presence of an observable host response does indicate an antagonistic interaction.

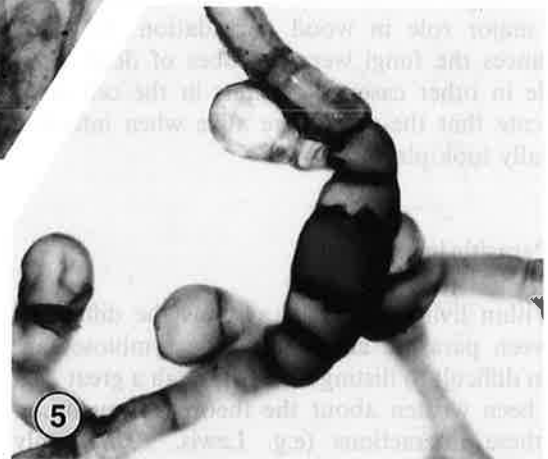
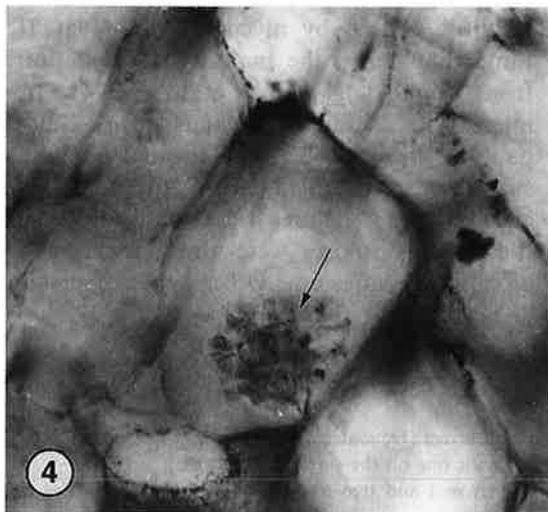
The earliest examples of a host response involved by fungal parasites comes from the Devonian Rhynie chert. One such example includes the charophyte *Palaeonitella* (Taylor et al., 1992). In this alga, cortical cells of the axis typically range from 30 to 70 μm ; occasionally abnormal cells occur. These are much larger, ranging up to 300 μm in diameter (Plate II, 3). These large, hypertrophied cells represent a direct host response. Similar responses are common in extant plants, including charophytes, when infected by certain aquatic fungi (Karling, 1928). Associated with such infections in modern charophytes is an increased production of large starch grains in the plastids. Interestingly, in some of the infected, fossil charophyte cells there are clusters of dark, granular bodies that may be indicative of this response. It is impossible to gauge the longevity of this parasitic interaction in the fossils. In particular did it represent a biotrophic nutritional mode in which the alga was not significantly altered by the fungus, or was the interaction necrotrophic, ultimately resulting in the death of the alga?

Another parasitic interaction detected in the Early Devonian paleoecosystem involves a host response caused by mycoparasites (Plate II, 1), fungi that derive the majority of their nutrition from other fungi (Hass et al., 1994). In this interaction, distinct thickenings termed callosities, papillae, or lignitubers are formed on the inner surface of thick-walled chlamydospores. The presence of these structures in the fossils indicates that the chlamydospores were alive for some period after fungal infection. Other types of mycopara-

PLATE II

1. Chlamydospore showing chytrid mycoparasite developing between wall layers (Devonian). $\times 1000$.
2. Chlamydospore containing endobiotic mycoparasite and possible epibiotic one on the surface (Devonian). $\times 1000$.
3. Portion of *Palaeonitella* axis showing normal cortical cells of axis (arrows) and two hypertrophied cells infected by chytrids (Devonian). $\times 150$.
4. Stalked chlamydospore. (Carboniferous). Compare with modern *Glomus* chlamydospore in 5. $\times 200$.
5. Chlamydospore of extant *Glomus*. $\times 200$.

PLATE III



sites completely fill the host cell (Plate II, 2). In these, however, there is no apparent host response in the fossil suggesting that the cells were rapidly killed. Mycoparasites are widespread in nature today, and are found in all major groups of fungi. Although the interactions of these fungi in modern ecosystems remains poorly understood, their universal occurrence indicates that some fungal/plant diseases are naturally controlled by this type of antagonism. The presence of mycoparasites that infect chlamydospores of extant endophyte fungi (Plate II, 5) suggests that mycoparasitism might have negatively impacted the production of viable chlamydospores and thus reduced the incidence of mycorrhizal infections in certain paleoecosystems.

Chlamydospores can be identified as early as the Lower Devonian (Plate III, 2), and are relatively common in many Carboniferous peat swamp deposits (Plate II, 4) (Wagner and Taylor, 1982). In spite of their rather frequent occurrence, however, none have been found infected by mycoparasites. This is particularly surprising because one would expect to observe chytrids in the supersaturated soils on the Carboniferous peat swamps as they are found in wet soils today (Sylvia and Schenck, 1983). Moreover, many extant chytrids that have been isolated from the spores of arbuscular mycorrhizae are facultative and can function as saprobes. In the Carboniferous, it may be that the pH of the peat swamps inhibited fungal growth. The absence of both in-situ mycoparasites and detectable host responses in these peats provides additional support for this hypothesis.

Parasitic fungi have also been described on certain fossil reproductive organs. For example, Stidd and Cosentino (1975) described a fungal parasite within the seed *Nucellangium*. Characterizing this interrelationship was based on

the morphological similarity of the fossil fungus to the modern, obligate parasite *Albugo*, and the pattern in which the seed tissues were disrupted. Examples of pollen grains parasitized by chytrids are also known from the Carboniferous (Millay and Taylor, 1978). While it is impossible to determine the extent of which parasitic fungi affected the reproductive biology of fossil plants, if present in sufficient numbers these pathogens could certainly have exerted extensive selective pressure on the community. In other instances, certain types of reproductive propagules show a consistent absence of fungal interaction. For example, *Lepidocarpon*, a water-disseminated megasporangium, has never been reported to be infected by aquatic fungi. By comparison, other lycopod reproductive organs from the same Carboniferous sites show evidence of extensive tissue disruption as a result of fungal activity (Stubblefield and Taylor, 1984) (Plate III, 1). Additional evidence of this type may provide a basis for eventually suggesting that certain plants were better adapted to withstand fungal infection.

Parasitic interactions have also been observed on the vegetative parts of fossil plants, particularly in the form of epiphyllous fungi (Plate III, 5). Although almost all incidences of these fossil fungi are known from Tertiary angiosperm leaves, at least one infection has been reported on a conifer (Alvin and Muir, 1970). At some localities the number of epiphyllous fungi is large with infection taking place on many taxonomically different hosts (Dilcher, 1965). In some of these, it is possible to reconstruct the complete life history of the fungus. This provides the opportunity both to detail the infection process and, perhaps, analyze host specificity (Daghlian, 1978). One potentially rewarding

PLATE III

1. Lycopod megasporangium containing several chlamydospores (arrows); note the disrupted megagametophyte tissue (Carboniferous). $\times 50$.
2. Chlamydospores and hyphae in Rhynie chert axis (Devonian). $\times 100$.
3. Arthropod cuticle (arrow) with numerous trichomycete thalli attached to its inner surface (Triassic). $\times 200$.
4. Cortical cell of *Aglaophyton* axis containing arbuscule (arrow) (Devonian). $\times 600$.
5. Multiseptate spore of an epiphyllous fungus that has germinated to produce several hyphae (Eocene). $\times 450$.
6. Alveolar organization of a paleosol. This is believed to demonstrate a pattern of biomineralization (Carboniferous). $\times 1000$.

area of study may involve the use of epiphyllous fungi as indicators of past climates (Lange, 1978).

Although the phylloplane has been in existence since the Middle Devonian, there is not a great deal of evidence of fungi on leaves earlier than the Cretaceous. Barthel (1961) described hyphae on foliage of *Mariopteris*, and Schaarschmidt (1966) illustrated what are interpreted as apothecia and asci on the Triassic leaf *Pterophyllum*. While the general absence of such occurrences may reflect a failure to document these structures, it also may be that pre-Cretaceous fungi were unable to penetrate the cuticle on leaf surfaces. Studies of extant parasitic fungi indicate that penetration of a leaf is principally mechanical, although chemical degradation is also paramount. Perhaps the cuticles of pre-Cretaceous plants were simply too thick for hyphal penetration, or the chemical composition may have been significantly different in some early plant groups (Tegelaar et al., 1991). Another postulate regarding the absence of epiphyllous fungi prior to the Cretaceous may be related to the essentially hypogeous habitat of these early fungi. For example, although biotrophic, parasitic and saprophytic nutritional modes were established early in the fossil record, the group(s) that eventually became epiphyllous parasites may have inhabited the soil where organic molecules were more easily obtainable. Only when there was extensive competition for edaphic nutrients, or when some modification of the fungal life history evolved (e.g. production of air-borne spores), did leaf surfaces become a potential nutrient source that eventually became exploited. Various chemical and mechanical plant defenses may have also served as deterrents to the colonization of leaves by fungi before the Cretaceous. Thus, it may have taken a considerable period of time for fungi to evolve the appropriate enzyme systems (e.g. cutinase) to enter the plant.

Fungi may have also been inhibited from colonizing leaves as a result of the presence of other fungi, shoot-inhibiting endophytes, in particular. An interesting hypothesis has been presented by Wilson (1993). He suggested that in extant mutualistic symbioses the above-ground fungal endophytes may have evolved to become the primary defense against herbivory as a result of their ability

to produce certain toxic compounds. As a result of the interactions between mycorrhizae and herbivores the structure of the community may be altered since plants vary in their tolerance to herbivory and dependence on mycorrhizae (Gehring and Whitham, 1994). For example, in modern ecosystems it has been suggested that under high light and low nutrient availability, mycorrhizal infection alters the carbon/nutrient balance in the plants so that there is an increase in allocation of carbon based defenses against herbivory (Gange and West, 1994). While such fungal/animal interactions probably existed in paleoecosystems, they will certainly be impossible to document from the fossil record. It is possible that as the endophytes became more highly evolved and localized, their defensive influence on leaves and other foliar organs became diminished; this may have been the stimulus needed for parasitic fungi to move onto leaf surfaces. The spatial relationships of host tissues may have also played a major role in the timing of fungi occupying foliar surfaces. Although there is no direct evidence from the fossil record to date, various types of fungal parasites may have initially entered the reproductive organs of the plant and then later colonized the leaf. In other situations parasites may have initially entered through plant roots. Although there is little evidence in fossil roots and other underground organs indicative of pathogen penetration (e.g. tissue disruption), there are some anatomical characters in many fossil plants that are identical to those regarded as mechanical barriers to pathogens in extant plants (e.g. periderm layers). For example, Banks and Colthart (1993) illustrated wound tissue in the Devonian plant *Psilophyton* that anatomically resembles necrophyllic periderm. In some extant plants this periderm develops as a result of fungal invasion (Woodward, 1992).

It is interesting to note that in many modern plants waterlogging is the impetus for the ingress of root-invading fungi. It is clear that such conditions were common in Carboniferous swamp communities. Nevertheless, there is little evidence of fungal activity in the roots and underground organs of these plants. Is the absence of this interaction the result of a chemical defense of the

plants that inhabited these swamps, the result of our inability to identify these responses in the fossil record, or simply the fact that such interactions did not evolve until much later? The antiquity of various types of fungal interactions (as documented from the Devonian Rhynie chert) suggests that the absence of fungal activity in the underground organs of Carboniferous plants is probably the result of fungi being excluded from specific ecosystems by certain abiotic constraints, such as water acidity.

4. Biotrophic interactions

Biotrophic interactions may be defined as those interrelationships between a fungus and its host in which there is a continual source of carbohydrates directed to the fungus. Minimal tissue damage and morphological alteration in the host are also characteristics of biotrophic associations (Lewis, 1974). Such mutualistic fungal/plant interactions have been hypothesized as being ancient, and perhaps the catalyst for the terrestrialization of the Earth by land plants (Jeffrey, 1962; Pirozynski and Malloch, 1975). Only recently, however, has the sine qua non of biotrophy, the fungal arbuscule (Plate III, 4), been demonstrated in the early land plant *Aglaophyton major* (Remy et al., 1994). The fossil arbuscules consist of a specialized hyphal trunk that repeatedly dichotomizes within the plant cell to form a highly branched structure that is considered the site of physiological exchange between the fungus and host in extant systems (Bonfante-Fasolo, 1984). Although phosphorous may have been readily available to aquatic, land plant ancestors, this may not have been the case in the oxidative, terrestrial environment. Because modern arbuscular mycorrhizae are known to increase the uptake of host phosphorous, the advantages of this type of biotrophic interaction in a presumably nutrient-poor environment is obvious. However, mycorrhizae may also transfer other nutrients to the host and some of these may have been especially critical early in the evolution of mycorrhizal symbioses (Pate, 1994). But arbuscular mycorrhizae are also known to increase nitrogen uptake (Tobar et al., 1994), an equally

important ecological advantage in increasing biomass. Thus, this biotrophic symbiosis and the evolution of the arbuscule may have evolved in response to this selective pressure. Recently, Garbayé (1994) commented on the importance of certain types of bacteria in the establishment of mycorrhizae. Such helper bacteria are suggested to be involved in: recognition and receptivity between the fungus and host, germination of the fungal spores, enhancement of fungal growth, and as a modifier to the physico-chemical properties of the soil. Few bacteria have been identified in the fossil record and none with mycorrhizae, however, the apparent widespread occurrence of bacteria in extant mycorrhizae suggests that they could have been important in the initial evolution of biotrophic symbioses.

Extant arbuscular fungi also function to protect host roots from pathogens, increase the solubility of soil minerals, and produce plant growth hormones; all of which would contribute substantially to the establishment and maintenance within an ecosystem. The fact that arbuscular mycorrhizae are widespread today in their association with flowering plants has been the basis for suggestions regarding the antiquity of this biotrophic symbiosis. In extant plants, these root-inhabiting endosymbionts are represented by approximately 100 species of Zygomycetes, all classified within the Glomales (Morton and Benny, 1990). The morphological similarity between modern and the Early Devonian arbuscules indicates that the physiological exchange structure in this symbiosis has remained stable for a considerable period of geologic time. However, the fact that these endophytes are so widespread today suggests that the biochemistry of the fungal enzyme system is also highly evolved. There is, however, one distinct difference between the Early Devonian arbuscules and those of extant mycorrhizae. In living plants, arbuscules are extremely ephemeral, and once degeneration takes place host cells revert back to their normal function. In *Aglaophyton*, it appears that once arbuscules no longer functioned as physiological exchange sites, the host cells collapsed and new cells were formed in the cortex (Taylor et al., 1995).

Generally absent from discussions of biotrophy in the fossil record is any consideration of ectomycorrhizae. Modern ectomycorrhizae are relatively common and represented by more than 5000 species of Basidiomycetes. These fungal symbionts infect root tips, with some hyphae extending into the outer zone of the cortex to form an extensive network termed the Hartig net. Root hairs do not develop in this region, and the root is characteristically short overall. Many ectomycorrhizae induce the production of short, knobby lateral roots. Although it would appear that this type of mycorrhizal infection could easily be detected in the fossil record, to date there are only a few examples. One of these consists of both nodular and abbreviated lateral roots in a Cretaceous conifer that are morphologically identical with those formed in ectomycorrhizal associations of the Pinaceae (Cantrill and Douglas, 1988). Fungi suggested as being ectomycorrhizal have also been reported in several Middle Eocene permineralized organs of *Metasequoia* (Basinger, 1981). However, the presence of hyphae in cortical cells of these roots and absence of a Hartig net suggests that these fungi were not ectomycorrhizae, but rather saprobes. LePage et al. (1995) have recently discovered well-preserved ectomycorrhizae in permineralized Eocene pine roots. Root hairs are absent from the lateral roots; however, knobby structures are present, two host responses to the ectomycorrhizal infection. Also present is evidence of a Hartig net. The fossil fungus is compared with the extant genus *Rhizopogon*, a common ectomycorrhiza of conifers, in particular pines. Indirect evidence of ectomycorrhizal activity has also been suggested based on the presence of needle-fiber calcite found associated with root encrustations (Wright, 1986).

5. Fungal/animal interactions

Less frequently encountered in the fossil record, but certainly common, are numerous fungal interactions with animals. The most common of these, no doubt, were saprobic, but there were other interrelationships as well. One example includes the Trichomycetes, a specialized group of obligate zygomycetous fungi that today live in the hind gut

of many aquatic arthropods (Lichtwardt, 1986). The first fossils from this fungal group were reported from the Triassic of Antarctica and consist of elongate thalli that are attached to an insect cuticle by a holdfast (White and Taylor, 1989b) (Plate III, 3). Although nothing is known about the animal that contained these fungi, the morphology of the fossil fungus provides details about this interaction. Arthropods are known from the Early Devonian, but to date none of these has been described in fungal associations. Fungi have, however, been described from older sediments (Late Silurian) that are suggestive of a possible arthropod/fungus interaction. These include fossils that are considered to be coprolites, each composed of a mass of fungal hyphae; the hyphae are interpreted as evidence for the presence of fungivores (Sherwood-Pike and Gray, 1985). Although fungal/animal interactions will continue to be difficult to document in the fossil record, they constitute an important component of modern ecosystems, and were certainly significant in the geologic past.

6. Lichens

Lichens represent another modern biological interaction in which fungi play a critical role. In this symbiosis, the photobiont is generally a green alga, while the fungal component (mycobiont) is generally an Ascomycete; two groups that have a long geologic record. Because of the antiquity of both groups, and because the lichen thallus should be easily fossilized, it is surprising that this type of interaction is not well represented in the fossil record. Rather, there are just a few reports of lichens throughout geologic time (e.g. Sherwood-Pike, 1985). It is generally assumed that the absence of fossil lichens can be attributed to several factors, including the dry habitats in which they commonly grow today and/or the fact that this type of symbiosis has only recently evolved.

As a result of information now known about fungal/plant interactions in the Early Devonian, it is highly probable that algal/fungal symbioses in the form of lichens are also ancient. The recent report of the extant cyanobacterium *Nostoc puncti-*

forme endosymbiotically associated with an endogonaceous fungus that is closely related to *Glomus* (Kluge et al., 1992) provides some evidence that early fossil interactions with Zygomycetes were possible. The extensive record of cyanobacteria throughout the Precambrian adds additional support that these organisms and fungi may have formed early symbioses.

Perhaps the best explanation for the apparent absence of fossil lichens is simply the inability of paleobiologists to recognize them in the fossil record. There are numerous so-called, enigmatic organisms that first appear in the Ordovician; these clearly represent the level of evolution seen in extant lichens. Recently, Stein et al. (1993) suggested that the Middle Devonian, thalloid fossil *Spongiophyton* is a lichen. Nothing is known about the internal structure of this organism, although cell outlines on the inner surface of the cuticle may represent the impression of fungal hyphae. Edwards and Rose (1984) have hypothesized that the pores in another enigmatic plant, *Nematothallus*, may have functioned in gas exchange similar to pseudocyphellae in the epicortex of certain types of lichens (Hale, 1981). Another possibility is that the various pores in many of these problematic plants represent pockets that contained cyanobacteria similar to those found in certain extant bryophyte symbioses (Sprent and Raven, 1985). In this association, not only would the cyanobacterium provide a source of carbohydrates to the fungal partner, but it might also function in nitrogen fixation. If the photobiont in early lichen symbioses was a cyanobacterium, then it may be even more difficult to distinguish filaments of the photobiont from those of the fossil fungus.

Several additional Paleozoic plants with uncertain systematic affinities may also represent a level of evolution that has its closest analogue with modern lichens. These include, for example, *Prototaxites*, *Nematothallus*, and *Nematasketum*, all constructed of interwoven tubes of differing sizes. Some tubes have unusual septal pores, whereas irregular thickenings may be present in others. Moreover, the amorphous layer that covers many of these fossil organisms may be analogous to the mucilage that is produced by some living

lichens. To date, it has not been possible to identify the photobiont in any of these fossil organisms, but this may simply reflect the fact that none has been seriously considered to represent a lichen.

The antiquity of fungi, cyanobacteria, and green algae would suggest that the lichen symbiosis evolved quite early. It is evident that fungi were involved in various types of complex nutritional modes with other organisms early in geologic time. This fact provides additional evidence to support the hypothesis that the lichen symbiosis was not only present, but was a critical component of the early terrestrial ecosystem.

7. Abiotic interactions

Although the principal focus of this paper is the biological interrelationships among fungi and other organisms, it is important to point out that fungi have also played an important role in the sediment cycle. For example, fungal borers together with algae are important in the production of carbonate fines (Schneider, 1977). Micritization, the process by which carbonate skeletal material is dissolved and replaced by micrite, also involves the activities of fungi (Plate III, 6) (Kobluk and Risk, 1974). Furthermore, fungi are necessary in both the formation of soils and the processes involved in biomineralization. One major problem in interpreting the activities of fungi in this geologic context is the fact that the fungus is rarely fossilized, and when it is preserved it is difficult to distinguish hyphae from endolithic algae (Scott, 1981). Measuring the activities of fungi within a physical context will continue to remain a difficult task; however, the importance of these organisms in the formation of soils and other substrates is now only beginning to be fully appreciated. Unravelling some of the complex interactions in which fossil fungi have played an important role will require not only new insights, but an appreciation of the full spectrum of activities found in modern ecosystems. These can then be measured against evidence extracted from the rock record.

8. Conclusions

The question is no longer whether there is an adequate assemblage of fungi in the fossil record, but rather how these heterotrophs interacted with other organisms. Although it is becoming increasingly apparent that all major groups of fungi are very ancient, deciphering the levels of interaction is far more difficult. Currently the Devonian Rhynie chert represents the oldest paleoecosystem in which fungal interactions have been documented. The chert contains examples of saprophytic, parasitic and biotrophic interactions that involve fungal associations with land plants, algae, and other fungi. The presence of various host responses indicates that many of these interactions are also ancient. The fact that there is evidence of some nutritional balance between a fungus and its host strongly suggest that symbiotic interactions in the form of lichens may also be common in the fossil record. We suggest that in the years ahead it is studies of fungi that will play an increasing role in understanding the evolution of the terrestrial biota.

As fossil fungi continue to be described it will be especially important to document the full range of their interactions in both the biotic and abiotic environments. For example, there has been a great deal of speculation regarding the evolution of various fungal nutritional modes (saprotrophic, necrotrophic, biotrophic), including which constitutes the primitive condition (Lewis, 1974). The fact that such interactions are all well represented in the oldest anatomically preserved land plants necessitates that geologically older assemblages of organisms be critically analyzed for such interactions.

Despite the difficulties and constraints encountered when studying fossil fungi, there are important inferences that the oldest fungal/plant interactions can provide. For example, we know that some Rhynie chert endophytes had the enzyme systems capable of penetrating the host cell wall, but not the plasmalemma during the formation of arbuscules. Initially these fungi may have been saprobes that had the ability to penetrate both moribund and dead cells. A heterotroph with such an invasive mycelium would have obviously had

some advantage in its ability to obtain nutrients located well within plant tissues. As these fungal/plant interactions continued to form, perhaps the fungi overcame the plant's defensive mechanisms so that parasitic and, eventually, biotrophic interrelationships evolved.

In certain types of ancient fungal interactions the opportunity exists to evaluate more biological dimensions, such as host specificity. If enough host symptoms can be identified from the fossil record, it may be possible to assemble details about cellulose and lignin degradation processes, and thus evaluate this important component of fungal activity through geologic time. The distribution and evolution of fossil fungal forms can only be adequately evaluated based on comparisons of their vegetative and reproductive structures with those of modern groups. Moreover, the phylogenetic relationships of an increasing number of modern fungal groups is being proposed based on nucleotide sequences of small subunit ribosomal RNA (Hibbett, 1992). In some instances these data confirm more traditional patterns of classification, while in others the relationships are not as clearly defined. Despite the importance of these new types of molecular data sets, identifying the diversity, abundance, and distribution of fungal groups in time and space can only be determined based on the analysis of the fossil record.

The next major frontier in paleomycology must be the documentation of fungal interactions with algae and cyanobacteria. We would predict that there should be a recoverable record of these interactions because there are numerous exquisitely preserved Precambrian biotas around the world. The reports of diverse microbiotas from several upper Proterozoic sites (e.g. Knoll and Swett, 1985; Butterfield et al., 1990), increases the probability that fungal remains are also preserved in these assemblages. The analysis of these microbial biotas may provide the earliest details about the evolution of fungal nutritional modes in time and space.

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