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FUNGI FROM THE LOWER DEVONIAN RHYNIE CHERT: MYCOPARASITISM[1]

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Several examples of mycoparasitism are described from the Lower Devonian (Siegenian) Rhynie chert. These fungal interactions include thick-walled chlamydospores and vesicles in which epibiotic fungi are attached to the outer surface of the spore. Other fossil spores are characterized by mycoparasites developing between the layers of the spore wall or within the lumen. The presence of callosities extending from the inner surface of some fossil spores demonstrates that the hosts were alive when parasitized. This response by the mycohost is identical to that found in certain modern mycoparasitic symbioses involving vesicular arbuscular mycorrhizae that are parasitized by various aquatic fungi. The presence of mycoparasitism in a 400-million-year-old ecosystem underscores the potential significance of the fungal genome early in the evolution of other organisms.

Mycoparasites are fungi that derive the majority of their nutrients from other fungi. The terms hyperparasitism, direct parasitism, interfungus parasitism, and fungicolous fungi are sometimes used to describe this form of mycosymbiosis (Boosalis, 1964). Mycoparasitic fungi may be further subdivided based on the nature of their nutritional mode. In necrotrophic mycoparasitism nutrition is derived from nonliving host cells that may be killed prior to penetration and invasion; many of these fungi can also exist as saprophytes. Other mycoparasites are involved with the host in a biotrophic symbiosis. Here a balanced nutritional relationship has evolved in which the mycohost continues to grow and provide nutrients for the parasite. Depending upon the parasite, nutrients may be derived by the production of haustoria within host cells, dissolution of the host cell wall, or the formation of specialized absorbing cells at the tips of mycoparasitic hyphae (Barnett, 1964). Some authorities consider the commensualistic external contact between ascomycetes and basidiomycetes as an additional form of mycoparasitism (Pirozynski and Hawksworth, 1988). All major taxonomic groups of fungi contain species that are mycoparasitic (Sparrow, 1960; Lumsden, 1981), and a number of species are adapted to parasitize various types of fungal spores including those produced by vesicular-arbuscular mycorrhizae (VAM) (Boyetchko and Tewari, 1991). A few fungi are known that are self-parasitic (Nolan, 1975).

Although fungal remains have been described from Precambrian sediments, and no doubt existed during the early history of the earth, none of these specimens is now unequivocally regarded as fungal (Schopf and Klein, 1992). There are a few reports of early Paleozoic fungi based on traces and borings in carbonate shells, but these may just as likely represent the ancient activities of endolithic algae. To date the oldest fungal remains come from Silurian sediments in the form of hyphae and several types of spores (Pratt, Phillips, and Dennison, 1978; Sherwood-Pike and Gray, 1985). In these examples, however, nothing is known about the morphology or structure of the fungus, or its nutritional mode.

Recently, an extensive mycoflora of Lower Devonian age has been described in the freshwater ecosystem represented by the famous Rhynie chert locality (Taylor, Remy, and Hass, 1992a). All of the fungi described from this locality consist of different chytridiomycete morphotypes that are now included in the form class Palaeomastigiomycetes (Taylor, Hass, and Remy, 1992). The excellent preservation of these fungi has provided a unique opportunity to investigate several levels of fungal/host interaction that existed in this 400-million-year-old ecosystem, including parasitism of the green alga *Palaeonitella* (Taylor, Remy, and Hass, 1992b). It is the intent of this report to document the existence of several forms of mycoparasitism among the Rhynie chert fungi, including responses by the mycohost.

MATERIALS AND METHODS

The fungi from the Rhynie locality are preserved as permineralizations in this Lower Devonian (Siegenian) chert. Fungi were examined in thin sections prepared by cementing pieces of chert to standard microscope slides and subsequently grinding the rock to a thickness of 50–150 μm using silicon carbide powder. Fungi were located and photographed using oil immersion objectives directly on the polished surface of the rock. All slides are deposited in the Paleobotanical Collection of Professor Winfried Remy, Westfälische Wilhelms-Universität, Forschungsstelle für Paläobotanik, Münster. Slide numbers are noted in the figure descriptions.

DESCRIPTION

Almost all of the examples of mycoparasitism in the Rhynie chert consist of fungal interactions with various types of fungal spores and vesicles initially described as species of *Palaeomyces* by Kidston and Lang (1921). Spores and vesicles occur in axes of *Aglaophyton major* in the

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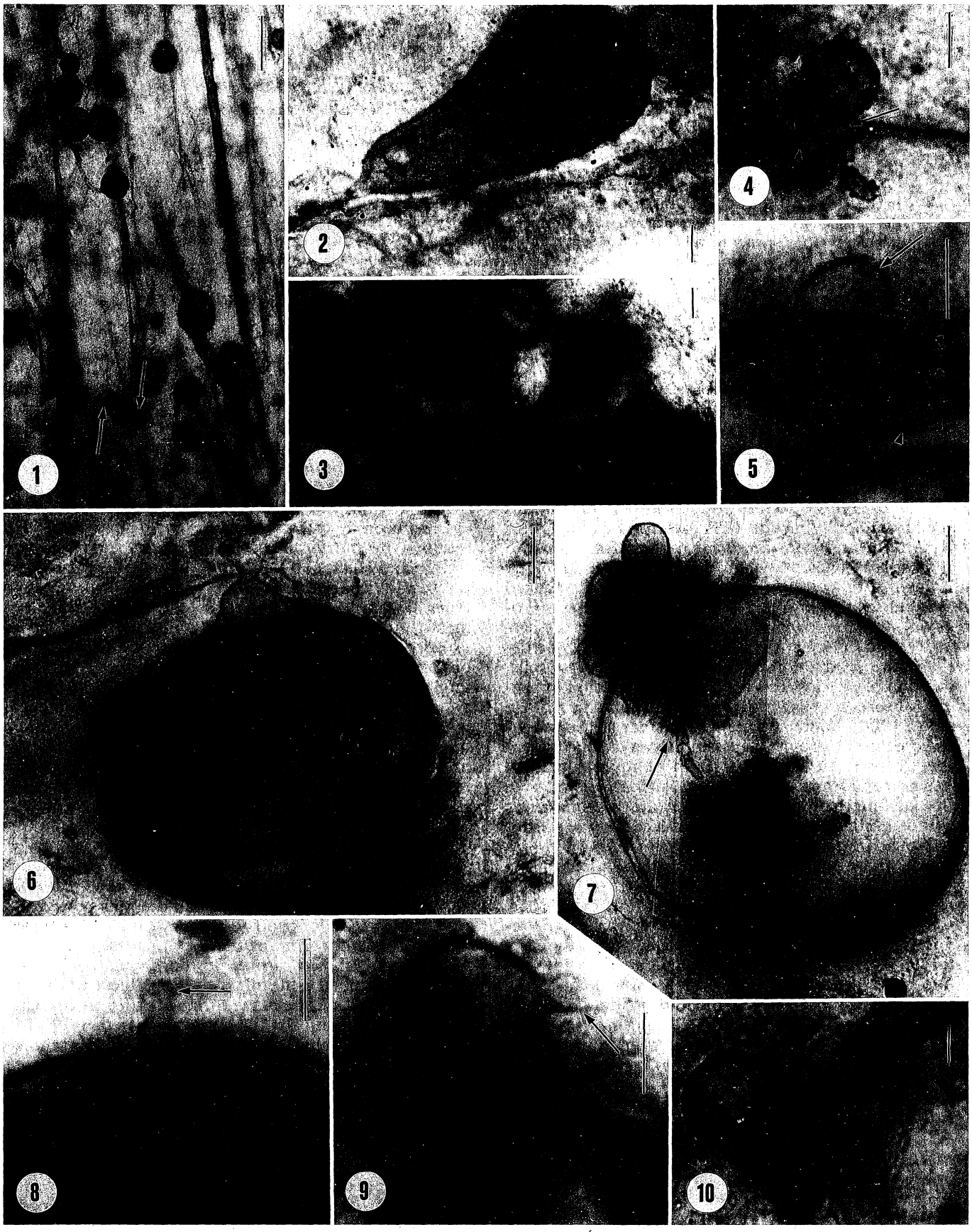
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form of terminal chlamydospores attached to delicate hyphae (Fig. 1), and thin-walled vesiclelike structures (Fig. 2). Chlamydospores are circular to slightly globose and range from 40 to 60 μm in diameter, while the thinner-walled vesicles are often larger and more irregular in shape. In other regions of the axes are large clusters of spores (Fig. 3), many not associated with hyphae.

Epibiotic mycoparasites—A number of the Rhynie chert fungal spores have epibiotic chytrid thalli attached to the outer surface (Fig. 14) (Taylor, Remy and Hass, 1992a). Some of the common mycoparasites of these fungal spores are globose-pyriform-shaped thalli (zoosporangia) that may completely invest the outer surface of the host. These holocarpic mycoparasites range from 13 to 18 μm in diameter and are delimited by a delicate discharge papilla and single rhizoid that often penetrates the spore wall. *Lyonomyces pyriformis* is the name given to similar chytrid thalli found on cells of the green alga *Palaeonitella,* also preserved in the Rhynie chert (Taylor, Hass, and Remy, 1992).

The chytrid thalli illustrated in Fig. 7 fall within the same size range as *Lyonomyces* (8–12 μm); however, these mycoparasites possess a more extensive rhizoidal system that extends well into the lumen of the spore (Fig. 12). The thallus of other epibiotic chytrids develops within the spore wall of the mycohost, usually between the delicate outer layer and thicker inner component (Fig. 6). Figure 4 illustrates what we interpret as a chytrid zoospore attached to the outer surface of its mycohost, in this case a thick-walled chlamydospore. The two arrowheads mark the position of spore wall layers that have separated. Between these layers is a small bulge that is attached to an immature rhizoidal system. A more detailed view of the chytrid zoospore thallus partially penetrating the spore wall is illustrated in Fig. 10. In this specimen, however, there is no evidence of a rhizoidal system. Although the chytrid thallus develops just beneath the outer layer of the host spore wall (Figs. 5, 6), the rhizoid penetrates the thicker component of the chlamydospore (Fig. 11). Occasionally some of the small spores that are interpreted as zoospores are attached to a hypha (Figs. 9, 13). There are several interpretations as to the affinities of these spores. The hypha may represent a discharge tube of a zoosporangium. Another interpretation is that the "spore" is some type of reproductive structure such as a gametangium of some oomycete.

Comparisons—A large number of living chytrids are nutritionally mycoparasites (Sparrow, 1960). Immature thalli of *Spizellomyces* are morphologically similar to the fossil forms described in the Rhynie chert (Barr, 1984); however, the fossils differ in lacking the extensive rhizoidal system that develops in mature thalli of *Spizellomyces.* Further attesting to the similarities with *Spizellomyces* is the fact that several of the living species are reported as mycoparasites of *Gigaspora margarita* azygospores (Paulitz and Menge, 1984) and the chlamydospores of *Glomus gigantea* and *G. macrocarpus* (Ross and Ruttencutter, 1977; Daniels and Menge, 1980).

Endobiotic mycoparasites—Another example of mycoparasitism in the Rhynie chert are chlamydospores and vesicles that contain evidence of a coenocytic fungus thallus. In a few spores the thallus is delicate and irregular, with uneven constrictions along its length (Fig. 15). Because the hyphae are narrow and only a small percent of the lumen contains the parasite, we interpret these spores as containing early stages in the development of the mycoparasite thallus. In other spores, however, the thallus of the parasite develops between the outer thin layer of the chlamydospore wall and the thicker inner component (Fig. 8). These hyphae are irregular and approximately 4 μm in diameter and often show numerous, random constrictions. The flask-shaped structure extending through the spore wall in Fig. 8 may represent the discharge tube of the zoosporangium. In a few examples a portion of the thallus may also extend into the lumen of the spore (Fig. 26). It is difficult to determine whether the fungus that is present in the lumen of the spore is the same as the one that occurs between the spore wall layers (Fig. 26), or whether more than a single mycoparasite is present. In other mycohosts the entire cavity of the spore is filled with irregularly shaped aseptate hyphae (Figs. 23, 27). Typically in these spores the wall of the host is less dense and in some regions is represented by a single, delicate membrane (Fig. 23). In other regions of the spore, the wall appears thickened but less opaque (Fig. 23). The thallus of these endoparasites typically appears as irregular, beadlike segments that range from 1.5 to 15 μm in diameter (Fig. 23). Occasionally, large, pyriform-shaped thallus segments occur around the periphery of the spore wall (Fig. 27), often extending through the wall (Fig. 23). They may represent early stages in the formation of zoosporangia in this endoparasite.

Mycoparasites are also present in vesicles that sporadically occur within the matrix of the chert, and within the axes of *Aglaophyton.* Some vesicles are attached to a hypha while others are solitary in the matrix. Vesicles are up to 100 μm long and range from pyriform (Fig. 2) to tubular

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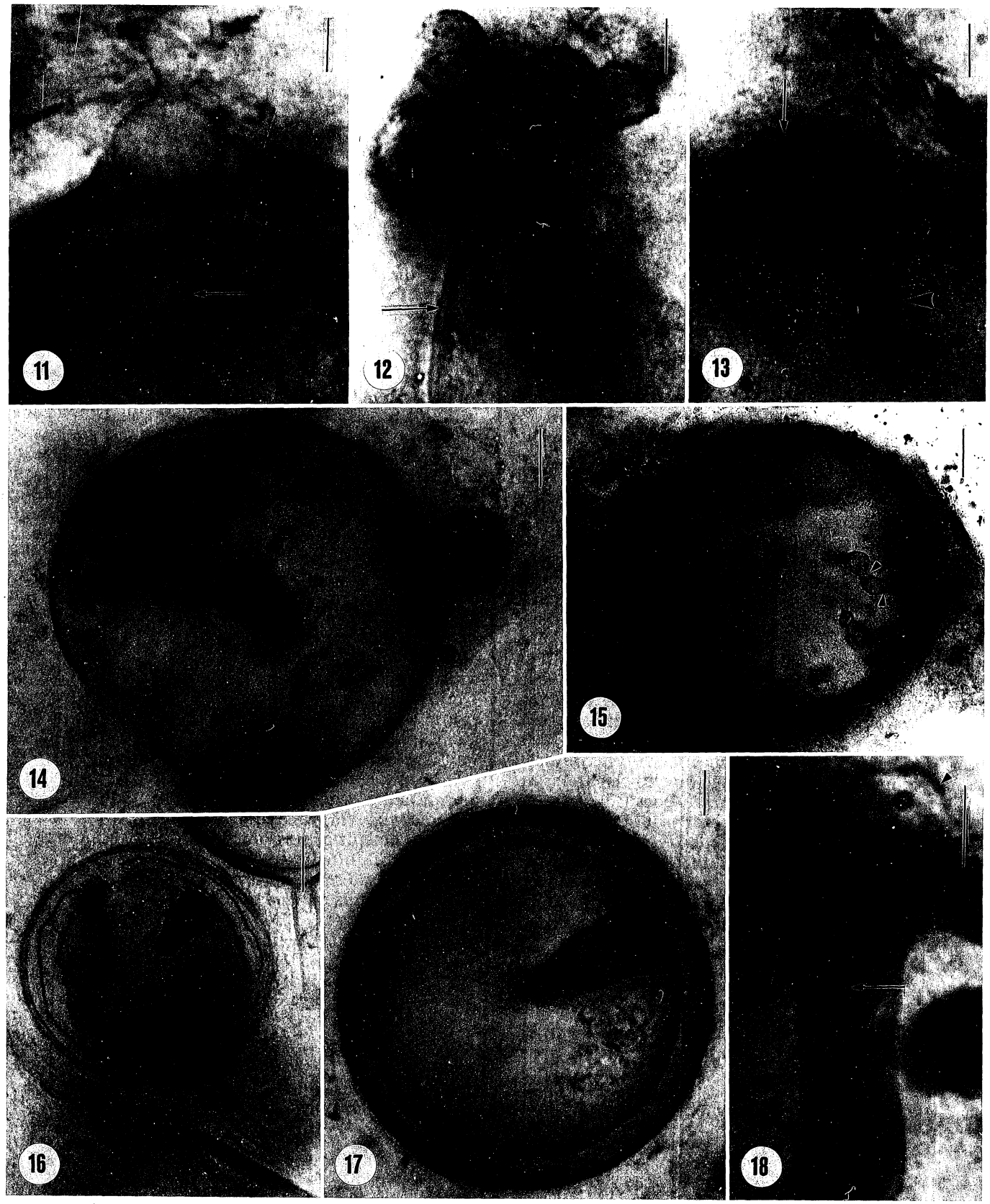
Figs. 1–10. Devonian mycoparasites. Bars = 5 μm unless otherwise indicated. **1.** Longitudinal section of *Aglaophyton major* axis showing numerous chlamydospores attached to hyphae. Arrows indicate two epibiotic chytrid mycoparasites. Bar = 100 μm. ×200. Slide No. P 1589. **2.** Thin-walled vesicle packed with hyphae. Bar = 10 μm. ×700. Slide No. P 1589. **3.** Cluster of spores in *Aglaophyton* axes. Note that many contain callosities. Bar = 100 μm. ×150. Slide No. P 1598. **4.** Zoospore resting on spore wall showing bulbous rhizoid (arrow). Arrowheads indicate layers of the spore wall that have separated. ×2,000. Slide No. P 1698. **5.** Layers of the mycohost spore wall that have separated (arrowheads) with probable chytrid zoospore (arrow) and bulbous rhizoid between layers. ×3,000. Slide No. P 2761. **6.** Chlamydospore with mycoparasite thallus developing between spore wall layers. See Fig. 11 for slightly different focal plane showing rhizoid penetrating spore wall. Bar = 10 μm. ×1,000. Slide No. P 1693. **7.** Thin-walled spore with several epibiotic chytrid thalli and conspicuous rhizoid system (arrow) inside. Bar = 10 μm. ×1,000. Slide No. P 1698. **8.** Mycoparasite coenocytic thallus developed between chlamydospore layers. Arrow indicates probable discharge papilla. ×3,000. Slide No. P 2755. **9.** Possible zoospore or gametangium. Arrow indicates hyphal attachment. ×3,000. Slide No. P 1689. **10.** Epibiotic chytrid thallus with inflated rhizoidal system between spore wall layers. ×1,500. Slide No. P 2760.



Figs. 11–18. Devonian mycoparasites. Bars = 5 μm unless otherwise indicated. **11.** Chytrid thallus between chlamydospore wall layers showing primary tubular rhizoid (arrow) penetrating spore wall. ×2,000. Slide No. P 1693. **12.** Several epibiotic chytrid thalli with tubular rhizoids inside spore wall (arrow). ×2,000. Slide No. P 1698. **13.** Zoospore (?) or gametangium with hyphal attachment (arrow) on spore wall. Callosity is the conical-shaped structure (arrowhead) inside of spore. ×2,000. Slide No. P. 1693. **14.** Thin-walled spore with small spores inside and chytrid thallus

(Fig. 28). Vesicles are less common in the Rhynie chert than the thick-walled chlamydospores. Although morphologically identical vesicles were described and illustrated by Kidston and Lang (1921), none showed any evidence of mycoparasitism.

Comparisons—Spores of modern vesicular-arbuscular mycorrhizae (VAM) commonly contain evidence of endomycoparasites. For example, Daniels and Menge (1980) reported spores of *Glomus fasciculatus* and *Gigaspora margarita* that contained tightly packed, sausage-shaped hyphae (Fig. 29). When these mycoparasites were cultured they were found to be *Anguillospora pseudolongissima.* Among living oomycetes, there is a close morphological correspondence with the endobiotic coenocytic hyphae of some members of the Lagenidiales, a group that is principally found in freshwater habitats (Karling, 1981).

Host response—In the foregoing examples of mycoparasitism it is unclear as to whether the Rhynie chert mycoparasites were biotrophic or necrotrophic on the chlamydospores and vesicles. In other examples, however, it is clear that the spores were alive at the time they were infected since there is a well-defined host response. Further attesting to the biotrophic nature of this interaction is the fact that the infected Rhynie chert chlamydospores are appreciably smaller than the noninfected ones, a condition that has been reported in living populations of VAM chlamydospores infected by fungal parasites (Boyetchko and Tewari, 1991). In addition, Daniels and Menge (1980) reported that VAM fungi with light-colored spores were more susceptible to attack by parasitic fungi than darker ones. It is difficult to ascertain the degree of melanization of the Rhynie chert spores and whether the thin-walled forms were naturally more susceptible to parasitism, or whether the translucent nature of the wall (Fig. 16) is the result of attack by the mycoparasites.

By far the most convincing evidence of biotrophy in the Rhynie chert chlamydospores is the presence of thickened, inwardly directed projections arising from the inner surface of the spore wall (Figs. 3, 16). These structures have been termed callosities (Swart, 1975), lignitubers (Mosse and Bowen, 1968), and papillae (Boyetchko and Tewari, 1991) in extant fungal mycohosts. Godfrey (1957) has also reported similar structures that she termed conical projections arising from the inner wall of several species of *Endogone.* Callosities represent a host response in which wall material of the spore is synthesized in response to an invading mycoparasite (Godfrey, 1957). In the fossil spores callosities may extend from a third to nearly half the way into the lumen of the spore; in a few they may traverse nearly the entire width of the spore lumen. They are generally solitary (Fig. 17), although a few may branch (Fig. 19). In transverse section they are roughly circular and range from 6 to 40 μm where they are confluent with the inner surface of the spore wall. The distal end is characteristically tapered, but in some the tip is truncated (Figs. 17, 21). In a few spores the structure of the callosity is homogeneous with the end somewhat collapsed (Fig. 25). Typically, however, they are constructed of a series of concentric, closely spaced, convex layers of varying thicknesses (Figs. 17, 19). Extending the length of each callosity is a narrow, centrally positioned (0.5–1.0 μm wide) infection canal. On the outer surface of the spore the penetration site is circular and about 10 μm in diameter (Fig. 24). Although there may be as many as 15 penetration sites on a single spore, rarely do the spores show any evidence of the endoparasite if callosities are present. When callosities are present the spore wall is generally translucent, suggesting that parasitism of the spores was completed. Figure 22 is the only example we have found in which a spore contains both a callosity and aseptate thallus of the mycoparasite. None of the vesicles contained callosities.

Although *Glomus*-like chlamydospores have been reported from a number of Carboniferous coal ball localities of differing geologic ages, callosities have not been reported (Wagner and Taylor, 1982). Perhaps the absence of this host response in the Carboniferous coal swamps is a reflection of a variety of factors in the peat swamps that eliminated certain mycoparasites from the ecosystem.

Callosities, some with a penetration canal extending the entire length of the structure, have been described and illustrated in extant spores of *Glomus* sp. (Figs. 31, 32) and *G. dimorphicum* (Boyetchko and Tewari, 1991). Because these spores lacked evidence of bacteria or fungi, it was suggested that perhaps these papillae formed as a result of parasitizing amoebae (Boyetchko and Tewari, 1991). Although similar wall perforations in fungal spores and hyphae are known to be caused by amoebae and other microbes (Old and Patrick, 1976), callosities are never formed in association with these parasites. Edwards and Allen (1970) report that chemical changes occur around the penetration site and papilla when barley is infected by a race of *Erysiphe graminis,* and it may be that these biochemical alterations may include barriers that do not exist in response to penetrating soil microbes.

Nothing is known about the affinities of the mycoparasite that caused the callosities to form in the Rhynie chert chlamydospores, although in a few instances what appear to be chytrid thalli appear on the outside of the chlamydospore directly over the penetration site (Figs. 18, 20). Associated with a number of the fungal spores in the Rhynie chert are "mushroom caplike" structures (Fig. 30). The fungal spores associated with the caps often lack the hyphal attachment present in other chlamydospores, but are approximately the same size and have a wall of comparable thickness. The caplike structure is rounded on the outer surface and approximately 4.0 μm

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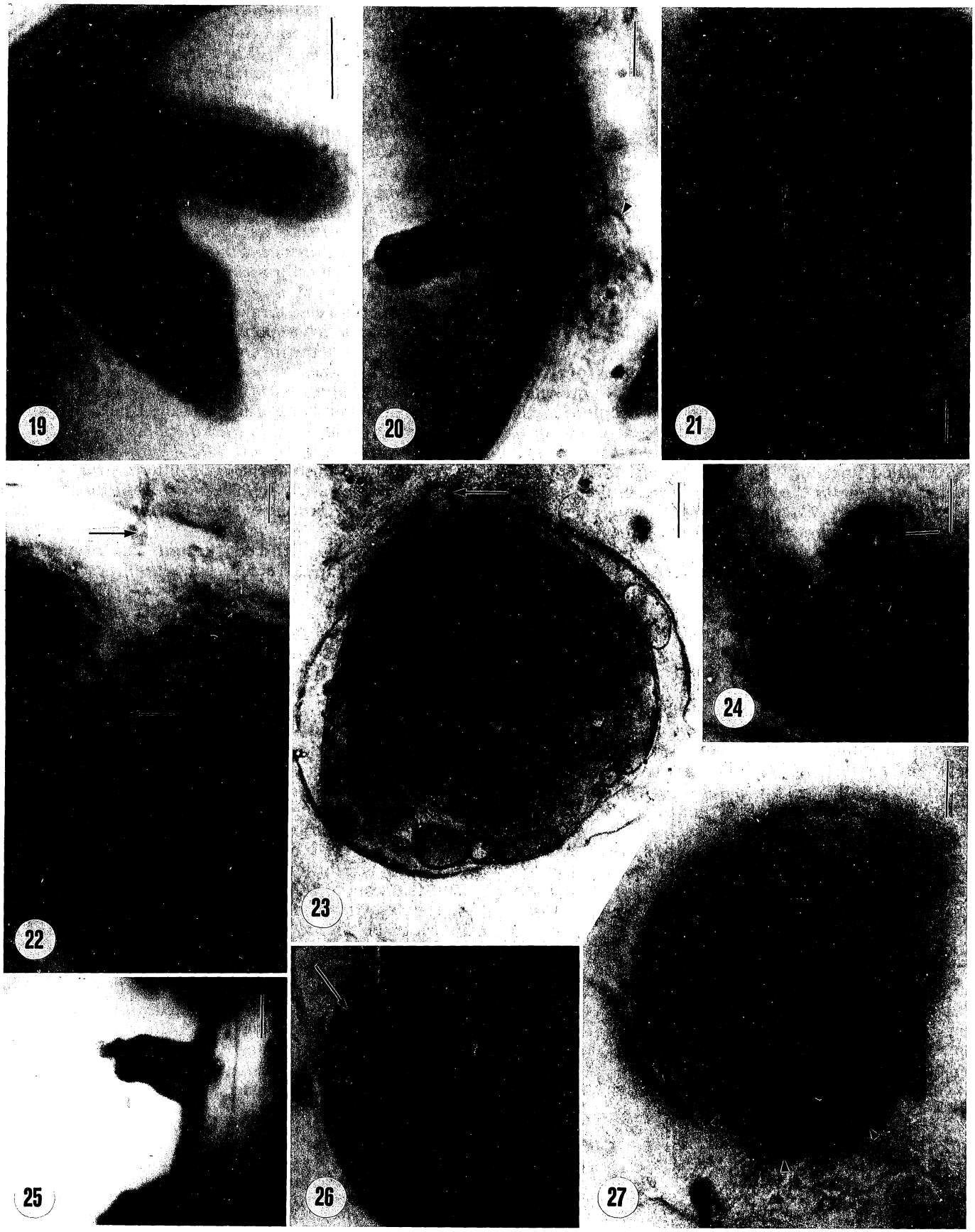
on surface. Bar = 10 μm. ×1,000. Slide No. P 1698. **15.** Thick-walled spore with loosely organized, immature (?) thallus inside. Note constrictions (arrowheads) but no septa. Bar = 20 μm. ×500. Slide No. P 1685. **16.** Chlamydospore with several callosities. Arrowhead indicates polar view of canal. Note hyphal attachment and translucent nature of wall. Bar = 10 μm. ×1,000. Slide No. P 1671. **17.** Chlamydospore with callosity. Bar = 10 μm. ×1,500. Slide No. P 2767. **18.** Detail of callosity showing penetration canal (arrow). Arrowhead indicates chytrid thallus on outer surface of spore wall. ×3,000. Slide No. P 1698.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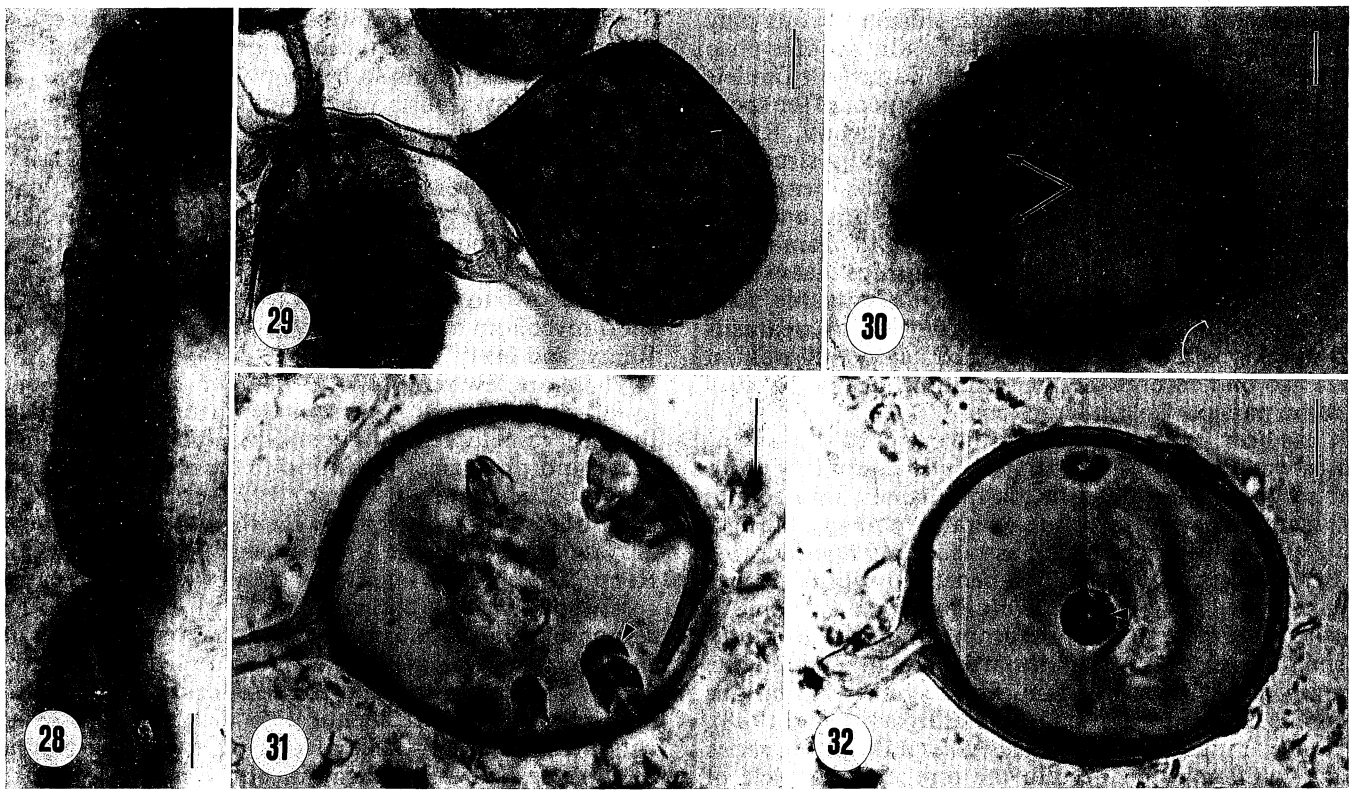

Figs. 28–32. Devonian (Figs. 28, 30) and extant (Figs. 29, 31, 32) mycoparasites. **28.** Ellipsoidal vesicles filled with hyphae. Bar = 10 μm. ×700. Slide No. P 1589. **29.** Spore of *Glomus fasciculatus* containing large sausage-shaped hyphae of *Anguillospora pseudolongissima.* Bar = 20 μm. ×400. **30.** Devonian chlamydospore with mushroom-cap structures (arrows). Bar = 5 μm. Slide No. P 1251. **31.** Chlamydospore of *Glomus* sp. with callosities (arrowhead). Bar = 40 μm. **32.** Surface view of callosity (arrowhead) in *Glomus* sp. chlamydospore. Compare with Fig. 24. Bar = 40 μm.

in diam; it measures approximately 1.5 μm in thickness. Arising from the center of the inner surface of the cap is a short, hollow tube approximately 3.5 μm long and 1.4 μm in diameter that extends out from the fungal spore. We are uncertain as to the biological affinities of these capped structures. Since they show the same refractive properties in transmitted light as other organisms in the chert, we believe them to be of biologic origin. All of the caps are located between wall layers of the fungal spores, although some look like they are depressed on the outer surface. We believe they represent some type of parasitizing organism, perhaps an endooperculate zoosporangium of a chytrid like *Nowakowskiella* (Karling, 1977). If this interpretation is accurate the lens-shaped cap would represent the collapsed zoosporangium with the hollow axis of the cap the discharge papilla. One additional possibility is that these structures represent some type of reproductive organ like a gametangium.

DISCUSSION

Although mycoparasitism appears to be widespread in nature today, the importance of this phenomenon in modern ecosystems is still poorly understood (Lumsden, 1981). The universal occurrence of this interaction does suggest, however, that fungal/plant diseases are often naturally controlled by this form of antagonism. It is also known, however, that mycoparasites negatively impact the ultimate production of chlamydospores in a population, and thus are significant in reducing the number of mycorrhizae (Ross and Ruttencutter, 1977). Such factors as nutrition, pH, temperature, humidity, water, gas exchange, and soil texture are abiotic variables that are known to affect mycoparasitism in modern environments (Lumsden, 1981). Added to this list are several intrinsic factors including the developmental stage of the host and a variety of parameters associated with host susceptibility. For example,

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Figs. 19–27. Devonian mycoparasites. Bars = 5 μm unless otherwise indicated. **19.** Irregularly shaped branched callosity. Note delicate concave lamellations. ×3,000. Slide No. P 1671. **20.** Callosity showing penetration canal in spore wall and chytrid thallus (arrowhead). Compare the structure with that in Fig. 19. ×2,000. Slide No. P 1693. **21.** Detail of truncated callosity showing penetration canal (arrow) and faint lamellae. ×1,500. Slide No. P 1698. **22.** Callosity surrounded by hyphae. Arrow indicates position of penetration canal. ×1,500. Slide No. P 1698. **23.** Spore packed with coenocytic hyphae. Arrow indicates possible discharge papilla. Note translucent nature of spore wall. Bar = 10 μm. ×1,000. Slide No. P 1695. **24.** Surface of chlamydospore showing polar view of two callosities. Arrow indicates penetration canal. Bar = 10 μm. ×500. Slide No. P 1685. **25.** Two partially formed callosities. Compare with Fig. 20. Note blunt end and absence of lamellae. Bar = 20 μm. ×400. Slide No. P 1697. **26.** Mycoparasite thallus (arrow) that has developed between spore wall layers. Note that the inside of the spore also contains evidence of a mycoparasite. ×1,500. Slide No. P 2755. **27.** Same spore as in Fig. 23 at different focal plane showing constricted hyphae. Arrowheads indicate possible zoosporangia. Bar = 10 μm. ×1,000. Slide No. P 1695.

Elad, Barak, and Chet (1983) reported that lectins play an important role in the recognition and binding of hyphae between the mycoparasite and its mycohost, while Daniels and Menge (1980) suggest the melanin content of the spore wall is related to susceptibility. More recently, Rghei, Castle, and Manocha (1992) have identified a structural feature in the form of fimbriae (cell surface filaments) that are used as a recognition factor between host and mycoparasite. At the present time the ability to characterize the complex mycoparasitic interrelationships that existed in fossil ecosystems is probably an unobtainable goal. Nevertheless, the fact that several forms of mycoparasitism were apparently well established nearly 400 million years ago underscores the long-standing genetic stability of some parasite/host interactions.

It has been hypothesized that the origin of some symbioses was the result of a parasite/host interrelationship that secondarily evolved into a mutualistic interaction. The fact that natural selection operates to reduce the negative effects from a parasitic association while favoring positive effects in the shift to a beneficial symbiosis, has been regarded as a source of evolutionary innovation. An excellent example of the shift from parasitism to mutualism involves certain grasses that contain the endophytic, ascomycetous fungus *Claviceps* which synthesizes various alkaloids that in turn discourage herbivory (Clay, 1988). In this example, mutualism has evolved through a series of coevolutionary changes in the reproductive cycle of both the host and fungus.

The shift from parasitism to mutualism has also been suggested as the basis for the initial colonization of the land by a parasitized charophycean alga (Church, 1921; Pirozynski and Malloch, 1975). According to this scenario, during the early phases of terrestrialization, endobiotic fungi were necessary for land plants to survive in a substrate deficient in several nutrients, particularly phosphorus. Precisely how and when this mutualism evolved continues to remain a more difficult problem to resolve (Pirozynski and Dalpé, 1989; Taylor and White, 1989). At least one line of evidence challenges the validity of this hypothetical mutualism. In a study of several grassland species, evidence was presented that suggests that VAM infection may not be beneficial for plant nutrition (Sanders and Fitter, 1992). Fungi parasitizing early land plants have also been suggested as the selective pressure responsible for inducing lignification, and thus providing the impetus for the evolution of specialized conducting cells in land plants (Lewis, 1991). Although exactly when these fungal/plant interactions became established remains unknown, the fact that more than 90% of all terrestrial plants are associated with some form of mycorrhizal fungus underscores the long-standing symbiotic relationships between terrestrial plants and fungi.

The importance of parasitism as an evolutionary mechanism has also been commented on by Atsatt (1991), who hypothesizes that the digestive and absorptive mode of nutrition found in seeds, pollen, and embryo tissues indicates that fungal genes must have been incorporated early in the terrestrial plant genome. Whether this nutritional mode is a manifestation of convergent evolution, or represents transfer of genetic material by a single symbiotic event (Atsatt, 1988), or through the horizontal transfer of genes (Pirozynski, 1988), is not known. In spite of these uncertainties, however, the fact that mycoparasitism has been in existence at least as far back as the Lower Devonian adds some support to the scenario that this type of symbiosis was established early in the terrestrial biota, and may have played a pivotal role in land plant colonization and seed plant evolution. It is not possible at the present time to unequivocally identify the fossil mycoparasites that are present in the Rhynie chert; however, chytrids are the most common internal mycoparasites in VAM chlamydospores today, and this group is now known to have been well represented in the Rhynie chert mycoflora more than 400 million years ago (Taylor, Remy, and Hass, 1992a).

There are few reports of a documented host response in fossil plants. One of these is the disruption of cells of the megagametophyte in a Pennsylvanian seed by a fungus that is morphologically identical to the modern oomycete *Albugo* (Stidd and Cosentino, 1975). Another host response is seen in the green alga *Palaeonitella,* a charophyte also reported from the Rhynie chert (Taylor, Hass, and Remy, 1992). Here internodal cells of the alga show excessive hypertrophy as a result of fungal attack. This host response is identical to that seen in modern charophytes that have been parasitized by certain chytrids (Karling, 1928). The callosities reported in this study document a host response that is identical to that found in extant chlamydospores. We believe it is not only surprising that the host responses are identical between modern organisms and their ancient counterparts in the Rhynie chert, but that there appears to be some level of specificity between the host and parasitizing fungus in both cases. These examples of a host response not only demonstrate the early appearance of certain aquatic fungi in the terrestrial ecosystem, but also illustrate that the antiquity of the complex genetic basis for parasite/host interrelationships was well established at several biological levels early in the colonization of the earth. These mycoparasitic interactions point to the establishment of symbiotic associations that obviously were in existence long before fungi invaded the land.

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