for the most abundant interstellar molecular PAHs from astronomical infrared emission spectra (*11*). Thus the observations are consistent with partial production of the observed deuterium enrichments by photoprocessing of free PAH molecules. Caution is warranted, however, since it is not clear how much significance to ascribe to this comparison because it is not certain that all of the carbon and hydrogen measured in IDPs and meteorite acid residues is part of the deuterium-rich carrier phase. As an example, the hydrogen content measured in these materials may include a contribution from water of hydration.

The D/H ratio in meteoritic acid residues roughly correlates with total hydrogen concentration [see figure 4 in (*26*)]. This is consistent with interstellar photolytic enrichment since larger PAHs have lower relative hydrogen concentrations and will produce smaller deuterium enrichments. The high D/H ratios in IDPs and meteorite acid residues do not correlate with the ^{13}C/^{12}C ratios in the same material (*2, 26, 34*). This is consistent with deuterium enrichments that originate from both photoprocessed interstellar PAHs and ion-molecule reactions.

Although the observed characteristics of the deuterium carrier in meteorites and IDPs are consistent with an interstellar PAH interpretation, the relation is not proven. The deuterium enrichment of the insoluble polymer seen in meteorites could also be explained by ion-molecule reactions combined with subsequent chemical processing. There are observational tests that can potentially separate the possibilities. The ion-molecule reaction scheme would predict that both the aromatic structures (regardless of size) and their cross-linking bridges should have related D/H ratios since both structures would presumably be made from the same deuterium-rich parent molecules. The PAH photodissociation model, however, does not necessarily predict that the D/H ratios in the aromatic structures will be related to the D/H ratios of their associated inter-ring links. In addition, the photoprocessing scenario would predict that above a C/H ratio of about 2 the deuterium enrichments within the aromatic structures would decrease with increasing molecular size.

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36. B. Wopenka acknowledges support by grants from the National Science Foundation (EAR 8408004) and NASA (NAG 9-55).

24 February 1987; accepted 19 May 1987

Fossil Mycorrhizae: A Case for Symbiosis

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Vesicular-arbuscular mycorrhizae are significant in the physiology and ecology of extant vascular plants, and they may also have played a major role in the origin of the vascular land flora. The case for fossil vesicular-arbuscular mycorrhizae rests upon hyphae and chlamydospore-like bodies in several Paleozoic taxa, but fossil arbuscles are unknown to date. Specimens from the Triassic of Antarctica represent the first known occurrence of arbuscles in the fossil record.

ALTHOUGH IT WAS ASSUMED FOR many years that fungi would not be significantly represented in the fossil record because of their delicacy, it is now known that fossil fungi parallel modern forms in diversity, complexity, and function. Although the development of fungal diversity early in geological time has been relatively well demonstrated, with all of the major groups of fungi being present by the Paleozoic (*1*), the biological relations between fungi and land plants have been more difficult to investigate. This difficulty has been particularly obvious when researchers have attempted to document the physiological relation in mycorrhizal associations.

Vascular plants are believed to have originated in the Late Silurian. Pirozynski and Malloch (*2*) speculated that the appearance of vascular plants was facilitated by the evolution of mycorrhizal associations. In their view, the increased efficiency in nitrogen and phosphorus uptake that resulted from a symbiotic association was necessary for the exploitation of new habitats and the development of more complex tissue systems. In support of these arguments Piro-

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Fig. 1. Several cortical cells showing branched, nonseptate hyphae. Magnification, ×495.

zynski and Malloch cited the fungi present in the structurally preserved axes of the Rhynie chert plants and suggested that they represented the first fossil evidence of endomycorrhizae.

One of the most often cited examples of fossil endomycorrhizae is *Palaeomyces*, a fungus from the Rhynie chert, which many have regarded as the earliest vesicular-arbuscular mycorrhizal (VAM) fungus. Kidston and Lang illustrated that within the axes of these early land plants, there were hyphae and a variety of vesicles and chlamydospores that resemble those formed by extant endogonaceous fungi (*3*). Similar structures have been reported for the Paleozoic (*4*). However, the most definitive morphological indicator of a VAM association, the arbuscle, to date has not been demonstrated from the fossil record. Earlier reports of fossil arbuscles actually refer to nonhyphal aggregations of cytoplasm or ergastic substances (*5*). In extant VA mycorrhizae the arbuscle is a three-dimensionally branched, bush-like structure involved in nutrient transfer (*6*). The absence of these structures in the fossil record is, perhaps, not surprising in view of their delicate and ephemeral nature. Within a brief time (4 to 15 days) the arbuscle degenerates within the host cell (*7*).

Structurally preserved plant remains from the Early to Middle Triassic of Antarctica have yielded a wealth of fungal remains. Among these are well-preserved VA mycorrhizae consisting of nonseptate hyphae (Fig. 1), chlamydospores (Fig. 2), and arbuscles (Fig. 3). In these infected roots, nonseptate hyphae (which generally range from 3.5 to 5.4 μm in diameter, with extremes of 2.5 to 7.2 μm) are most conspicuous in the central cortical region and show the characteristic loops of extant VAM fungi. Terminal hyphal swellings resembling the chlamydospores and vesicles of extant endogonaceous fungi are also common. The most important component of the VAM fungus, the arbuscle, is also preserved in these roots. It consists of a highly branched structure that nearly fills the lumen of the cortical cell (Fig. 3). These structures are morphologically identical to their modern counterparts, although most modern arbuscles terminate in branches 0.5 to 1.0 μm in diameter, while the smallest branches in the fossil are approximately 1.8 μm wide. However, Gorbunova illustrated arbuscles of comparable size in the extant cycad *Encephalartos* (*8*), and observations of VA mycorrhizae on several hundred plant species in the Pacific Northwest indicate a range of arbuscle variation that encompasses that of the fossil arbuscles.

The exact origins of VAM of a completely modern morphology and presumably modern physiology are unclear. Although information about the morphology of hyphae and chlamydospores may be used to relate fossil forms to extant endogonaceous fungi, these structures do not necessarily demonstrate a symbiotic association. However, there is no reason to assume that the earliest mycorrhizal fungi possessed an arbuscle comparable in structure to those seen today. At present, fungi from the Paleozoic provide no information regarding the nature and evolution of the arbuscle. It is possible that hyphae and chlamydospores may have remained relatively unchanged since the Devonian, whereas modern arbuscular morphology may have evolved at a later time, perhaps as recently as the Triassic. We might speculate that the finely divided, arbuscle characteristic of most extant VA mycorrhizae had its origin in a more coarsely divided, hypha-like structure similar to the arbuscle in the Triassic roots of Antarctica. Furthermore, the existence of this fossil arbuscle raises the possibility that the exchange of nutrients in the earliest symbiotic land plants was accomplished through even simpler, less modified hyphae. Selective pressure toward a more efficient organ of exchange may have then resulted in the finely divided arbuscle of today.

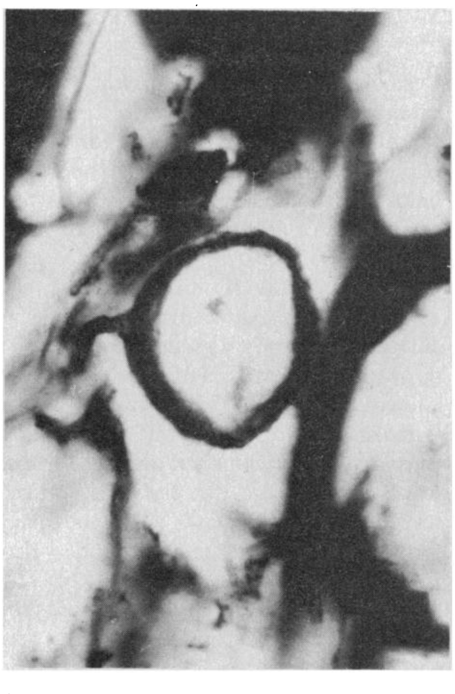

Fig. 2. Terminal chlamydospore. Magnification, ×835.

Fig. 3. Highly branched arbuscle (arrow) in cortical cell of mycorrhizal root. Magnification, ×390.

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9. We appreciate the support provided by the National Science Foundation (BSR-8516323) for this work.

9 January 1987; accepted 10 April 1987