PERSPECTIVES: EVOLUTION

Terrestrial Life—Fungal from the Start?

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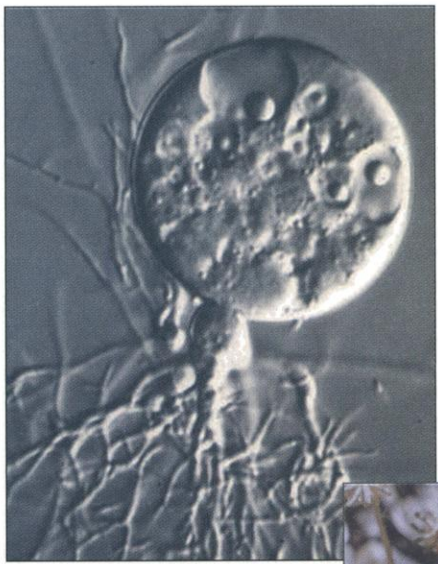
Early terrestrial environments were poor in nutrients and subject to desiccation; habitats were poorly shaded and thus fully exposed to the bright light of day. In 1975, Pirozynski and Malloch (*1*) proposed that mutually beneficial (mutualistic) symbiosis of fungi and plants assisted in the original invasion of plants into these harsh terrestrial environments. Others had previously suggested a mutualistic origin for land plants, but Pirozynski and Malloch's hypothesis was more fully developed than those of earlier workers. Advances in fungal systematics have outdated some of the evolutionary speculation in (*1*), but the basic premise that symbiotic relationships between so-called arbuscular mycorrhizal (AM) fungi and the roots of higher plants were essential in the move of plants to land continues to be accepted. Mycorrhizae are symbiotic associations between many different types of fungi and plant roots. The vast majority of plants are mycorrhizal, and they, including those associated with AM fungi, usually benefit from enhanced uptake of minerals and water.

The report by Redecker *et al.* on page 1920 of this issue (*2*) comes close to confirming this 25-year-old premise. Before this report, the earliest record of an AM fungus, in association with vascular plants, came from the 400-million-year-old Rhynie Chert (*3*). The 460-million-year-old Ordovician fungus reported in (*2*) (see the figure on the next page) was not discovered in association with plant remains, but its unique morphology strongly suggests that it was a member of the Glomales, a group in which all extant taxa are AM fungi.

In addition to the unique morphology, there is circumstantial evidence that the fossil represents an AM fungus. Dispersed microfossil evidence indicates a contemporaneous presence of bryophyte-like plants at some Ordovician sites. Bryophytes are a small group of plants comprising mosses, liverworts, and hornworts and are believed to be among the earliest plants on Earth (see the figure above). Some extant bryophytes are associated with glomalean fungi (*4*). Furthermore, it has been shown that when certain bryophytes are infected experimentally with AM fungi, they form mycorrhiza-like associations. Using calibration points from the fossil record, estimated divergence times based on ribosomal DNA sequences are consistent with the existence of a lineage of Glomales in the Ordovician Period. The results reported by Redecker *et al.* indicate that the most derived fungal (Ascomycota-Basidiomycota) lineage diverged at 600 million years ago (Ma), as suggested by Berbee and Taylor (*5*). By comparison, the origin of plants has been conservatively placed at 600 Ma; the divergence of metazoans (animals) and fungi from a close common ancestor has been placed at 965 Ma, ±140 Ma, but a later date has also been proposed on the basis of protein data and revised calibration points (*5*).



Descendants of early fungi and plants. (Top) Chytrids such as *Chytridium confervae* were the first group of fungi to split from other fungi after the fungus-animal split about 900 Ma. Chytrids are known from the Rhynie Chert 400 Ma. The fungus has a diameter of around 40 micrometers. **(Right)** Stalked starlike structures lift the female sex organs of the dioecious liverwort Marchantia from the surface of the liverwort thallus. Liverworts are nonvascular plants, and fossils of similar plants have been found in Ordovician deposits. The stalks are about 5 centimeters high.

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Price (*6*, p. 375) has proposed that "in the broadest sense ecology recapitulates phylogeny," so that in the progression from the earliest prokaryotic microorganisms to eukaryotic microorganisms, each group had a role in preparing Earth for successive groups of organisms. Moreover, Price helped popularize the ecological importance of microorganisms by pointing out that "Noah's ark ecologists" ignore organisms smaller than "bird food." More recently, biologists have increasingly recognized the presence and function of microorganisms in communities and ecosystems (*7*). As a result, the apparent universality of plant and fungal associations is now well recognized.

In addition to AM fungi, other fungi form a variety of mycorrhizal associations that have been distinguished and named on the basis of morphology and plant host. The annual autumn fruitings of mushrooms in temperate forests throughout the world provide spectacular evidence of such mycorrhizal associations. However, the commonest mycorrhizal fungi usually do not produce aboveground evidence of their presence (*8*).

Endophytes and lichens are two more examples of fungus-plant mutualisms. With very few exceptions, terrestrial plants all have endophytic fungi in their aboveground parts, but they too can be overlooked because they are microscopic and cause no outward signs of their presence. The role of endophytic fungi is less well known than that of mycorrhizal fungi. One group, the Clavicipitaceae, produces alkaloids in endophytic associations, primarily with grasses. Other plants have endophytic associations with a diverse assemblage of fungi (*9*). Lichen-forming fungi associated with green algae and cyanobacteria comprise thousands of species of ascomycetes (*10*). The universality of mycorrhizal, endophytic, and lichen associations with plants belies the large number of independent origins that occurred as the phototrophs and fungi invaded Earth and filled its niches.

To overlook the ubiquitous mutualistic fungi, in association with plants, can have

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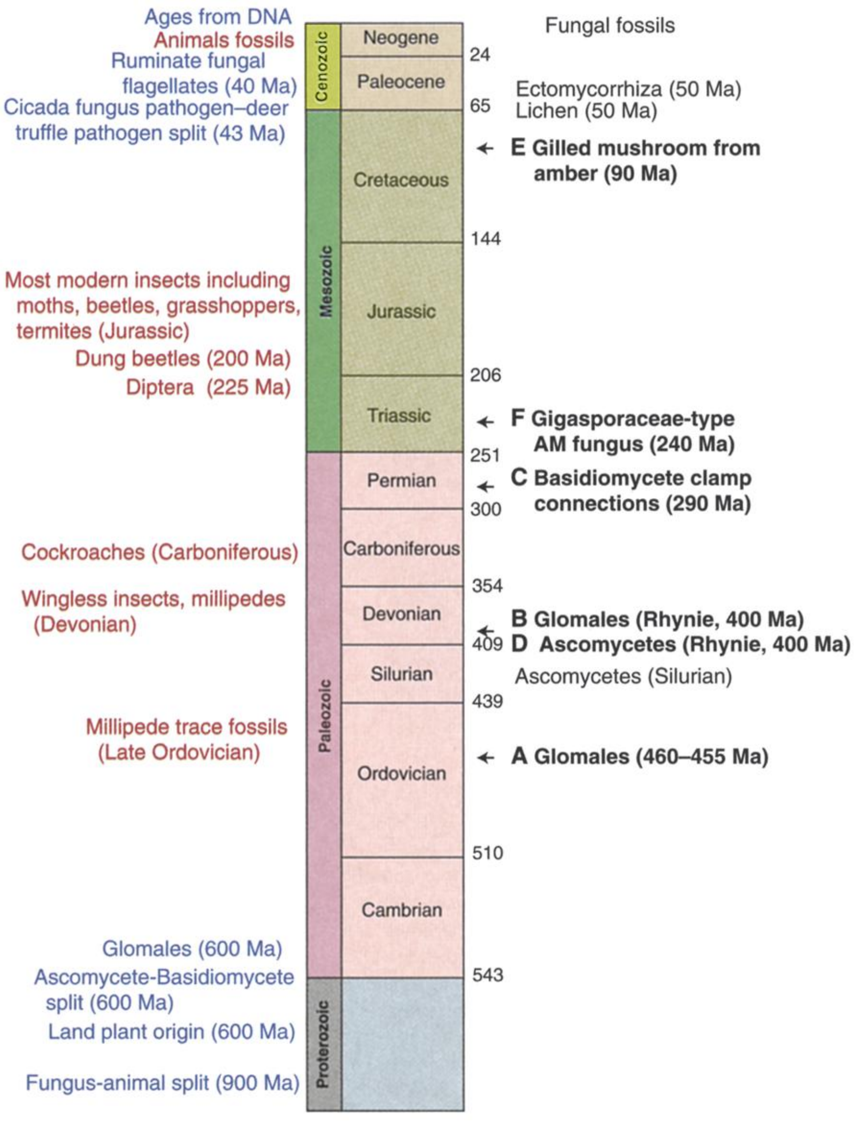
unfortunate consequences. For example, if one were unaware of endophytes, one would expect DNA extracted from the leaves of plants to be plant DNA, and a symbiotic fungus has tricked more than one systematist (*11*, *12*). Worse yet, fungi can contaminate other fungi growing with them, an even more difficult situation to detect. Sequence alignment tools and specific primers are now commonly used to prevent mistakes. It is equally important to consider the physiological effects of plant mutualists to a plant, and the consequences of mutualism are now more frequently taken into account in experimental studies (*13*).

Redecker *et al.*'s discovery of an Ordovician AM fungus affords an opportunity to draw attention to yet more fungal mutualists. Symbiotic associations between fungi and animals, although usually of more recent origin, may be as pervasive as those between fungi and plants, despite their discontinuous taxonomic distributions. There are several well-known fungal mutualists of animals, such as gilled mushrooms cultivated by ants and Old World termites, fungi carried by bark beetles and wood wasps in their ectoskeleton "pockets" to feed their young, and fungal fermenters in the gut of many mammalian herbivores. Less generally known are the vitamin-supplying fungal symbionts in the gut of aquatic insect larvae and adult marine crustaceans (*14*), yeasts that participate in sterol utilization and nitrogen recycling in gut pockets of insects such as plant hoppers (*15*), mildly parasitic ascomycetes that associate with arthropods for nutrition and dispersal (*16*), and the scale insects that sacrifice individuals as fungal food in return for fungal protection (*17*). The list can go on, and intriguing new animal-fungus associations continue to be discovered, such as the many new species of yeasts that lay unsuspected in the gut of mushroom-feeding beetles (*18*). When the animal-symbiotic fungi are better known, their distributions may seem as continuous as those of plant associates. Investigations of fossil insects may reveal additional information on their symbionts (see the figure, this page).

Renewed interest in fungal evolutionary biology has come not only from phylogenetic studies but is enhanced by the discovery of fossils such as the one discussed here. Evolutionary studies that integrate the fossil record, divergence based on DNA, and knowledge of symbiotic associations will continue to be important and will be extended to a broader range of organisms. Awareness of the symbiotic relationships is essential if we are to learn more about the fungi themselves. Perhaps a next report may include an Ordovician AM fungal fossil associated with a plant.



Fungi everywhere. Geologic time scale showing relative positions in time of fossils (A to F and ectomycorrhiza, black type) and estimates of phylogenetic splits (blue type) mentioned in Redecker *et al.* (*2*) and Berbee and Taylor (*5*). Animal fossils (red type) are known associates of several groups of symbiotic fungi, and could help in the discovery of fungal symbiont fossils (*5*, *19*). See also Selosse and Le Tacon (*7*). Information on endophytes might be obtained by investigating grasses and other plant groups. The first definite lichen fossil (50 Ma) is relatively recent. A few much earlier reports of Rhynie and even Precambrian lichens exist but are not fully accepted (*6*).

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21. I would like to thank Berbee and Taylor for allowing me to cite their paper prior to publication [see (*5*)].