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The Earth's Oldest Colonizers

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Fungi – organisms that were the first to appear on land – still remain largely unknown. What insights have we gained into their history and evolution?

Dead man's fingers (*Xylaria polymorpha*)

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Life on Earth is incredibly diverse and abundant. To better understand this vast diversity, living organisms are classified into major categories called "kingdoms" based on key differences. Each kingdom includes organisms (taxa) that share distinct (albeit derivative) adaptive traits. Today, we recognize five kingdoms, a classification first introduced by Robert Whittaker in 1969.

Research on the fungal kingdom is relatively recent, but we know that fungi have been around for millions of years, playing a vital role in shaping terrestrial ecosystems and influencing the evolution of other organisms. Over time, scientists have worked to pinpoint the defining characteristics and genetic traits that distinguish fungi from other groups. Molecular dating techniques have shown that fungi originated in marine environments and are older than the earliest known land plants and animals.

Oak powdery mildew (*Erysiphe alphitoides*) is a fungus especially dangerous to young oak trees

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The ancestor of all fungi was likely a parasitic microalga with the ability to engulf food particles (*phagotrophy*), exhibiting both amoeboid and flagellated movement, and having chitinous cell walls. Regardless of how fungi are defined, understanding the evolutionary changes that shaped them is crucial for unraveling the complex relationships within Earth's ecosystems. Fungi are heterotrophic organisms found worldwide, displaying remarkable diversity in both their evolutionary history and ecological roles. Their hyphae form networks known as *mycelium*, which can grow in various environments, digest materials externally, and absorb and metabolize a wide range of substances, including lignin and cellulose. This adaptability enables some fungi to interact with many hosts across different environmental conditions. They also adjust exceptionally well to food sources that vary in space and time.

It's estimated that the fungal kingdom includes around 5.1 million species, which are grouped into nine major phyla: *Ascomycota*, *Basidiomycota*, *Blastocladiomycota*, *Chytridiomycota*, *Glomeromycota*, *Mucoromycota*, *Neocallimastigomycota*, *Opisthosporidia*, and *Zoopagomycota*. Compared to other fungus-like groups, such as *Corallochytrium* (*Holozoa*, *Opisthokonta*), *Hyphochytriomycetes* (*Pseudofungi*), and *Oomycetes*, fungi were the first to colonize land and have successfully maintained their ecological niches through further adaptation. The discovery of fossilized fungi in Grassy Bay in 2019, showing distinct fungal cell structures, suggests that fungi appeared 600 million years earlier than previously thought. The subkingdom *Dikarya* emerged around 500 million years ago and includes two main groups: *Ascomycota* and *Basidiomycota*, which together account for over 1.5 million species. *Dikarya* is the most diverse and extensively studied group of fungi, characterized by a unique sexual cycle in which hyphae fuse without undergoing meiosis, resulting in the formation of cells containing two independent nuclei (known as dikaryotic hyphae).

The split between *Ascomycota* and *Basidiomycota* occurred roughly 1.2 billion years ago. In contrast, molecular clock data suggests that *Oomycetes* appeared on Earth about 250 million years ago. The earliest terrestrial members of Peronosporales are thought to have emerged around 150 million years ago, long after fungi had already colonized environments similar to those preferred by plants. This indicates that fungi spent a considerable amount of time developing the traits that enabled them to establish and maintain niches in terrestrial ecosystems. Key evolutionary adaptations that allowed fungi to thrive on land include the loss of phagotrophy and flagella, which occurred alongside the development of hyphae. Instead of retaining a flexible membrane, fungal cells began to develop rigid, structurally reinforced cell walls. This change protected the cells from high turgor pressure and allowed them to fill their cytoplasm with highly concentrated substances, supporting a fast metabolic rate. The evolution of these rigid cell walls also facilitated polarized growth at the tips of branching

False turkey tail (*Stereum hirsutum*)

hyphae, which in most fungi contain organelles consisting of numerous vesicles derived from the Golgi apparatus. These vesicles carry enzymes, lipids, and polysaccharides essential for synthesizing cell membranes and walls.

Masters of Adaptation

Fungi play a crucial role in connecting different organisms and ecosystems, influencing both macroecology and the evolution of species. Fossils of *Ascomycota*, *Blastocladiomycota*, *Chytridiomycota*, and *Mucoromycota* found at the Rhynie Chert site in Scotland, which date back to the Early Devonian, are associated with the earliest known land plants. This provides strong evidence that interactions between fungi and plants have long been a key ecological force, shaping relationships between hosts, competitors, and their surrounding environments.

Moreover, fungi are found in nearly all terrestrial ecosystems, playing a wide variety of roles. They break down organic matter, recycle nutrients, and form both helpful and harmful relationships with plants and animals. Fungi use two main survival strategies: biotrophy (relying on living organisms) and necrotrophy (living off dead organic matter). These strategies place very different evolutionary pressures on fungi, which is reflected in their genomes. Fossil records show that fungi have been performing many of the same ecological roles since the Devonian period, such as heterotrophy, parasitism, and even forming mycorrhizal relationships.

The development of hyphae in early fungi is indicative of a need either to either grow over larger organisms or to increase surface area for saprotrophic (heterotrophic) living. The ability of fungi to secrete digestive enzymes, coupled with the presence of numerous vesicles at the tips of their hyphae, constitutes a crucial adaptation that facilitates both saprotrophic and parasitic lifestyles. This means that early fungi breached the cell structures of single-celled eukaryotes to access nutrients. Another key evolutionary trait was the shift to external digestion of complex chemical compounds, paired with the active transport of processed nutrients into the cell.

The main adaptive factors include stress, disturbances, competition, and combinations thereof. Fungi are constantly transforming the organic resources they grow in and feed on. Once fungi reach the material they want to decompose, their competitive strength determines whether they will successfully colonize and how long they can hold onto that territory. It's no surprise that fungi have evolved into various trophic groups able to survive in different environments. Today, human activity – such as the use of fungicides – can impact how quickly fungi adapt to new conditions. The selective pressure from fungicides means that only the strongest and most resistant populations survive. Fungi are among the most important saprotrophs due to their ability to break down dead organic matter into simple compounds that plants can easily absorb. Soil and decaying wood in forests are teeming with saprotrophic fungi, which continuously use and break down organic compounds.

In terrestrial ecosystems, organic matter is not evenly spread out in time or space. It can range from tiny fragments, like bud scales, to massive tree trunks. The ability to break down lignin – the tough compound in wood – evolved only once in Earth's history, within the *Agaricomycetes* class, around 290 million

Brown rot

years ago. The first clear fossil evidence of white rot fungi, which can decompose lignin, dates back to about 260 million years ago. During the Carboniferous period, organisms lacked the ability to break down lignin, which led to the accumulation of most of the world's coal deposits and a reduction in atmospheric CO_2 levels. This unique ability to break down lignin, which is linked to the development of complex fruiting bodies, played a major role in the evolutionary and ecological success of *Agaricomycetes*. Fungi that break down wood but cannot decompose lignin are known as brown rot fungi. However, this distinction is not entirely clear-cut, as some species are capable of partially degrading lignin.

Fungi colonizing a tree

Interspecies interactions

Symbiosis is the name for any mutually beneficial relationship between two or more organisms. One of the longest and closest such relationships in the biosphere exists between fungi and terrestrial plants. It's believed that the colonization of land by eukaryotes was made possible by a symbiosis between photosynthetic organisms (phototrophs) and fungi. Endotrophism, a less understood fungal niche, is known for its remarkable biodiversity. Fossils of *Glomeromycota* provide some of the earliest direct evidence of terrestrial fungi. Additionally, several *Dikarya* taxa include root-dwelling endotrophic species, showing that roots quickly became a crucial niche for fungi. Fossil evidence from the Rhynie Chert site confirms that mycorrhizal associations existed as far back as 400 million years ago, underscoring the importance of plant-fungi interactions in the successful colonization of land by plants.

These early mycorrhizal relationships are often called "paramycorrhizae" because the plants involved did not yet have true roots. The way fungi colonized plant organs at that time resembles the processes seen in modern liverworts. Endotrophs are fungi that live inside plant tissues without causing harm. Unlike mycorrhizal fungi, endotrophs have received less scientific attention, so there are still no precise estimates of their abundance, ecological role, or diversity. It is thought that endotrophic fungi protect plants from pathogenic fungi by triggering the plants' defense mechanisms and competing for the same niches. By producing secondary metabolites, these fungi can help plants defend against herbivores or even boost their growth.

Some fungi act as parasites on other organisms, including insects, nematodes, and even other fungi. Parasitoid fungi are rare in nature, making them less likely to be preserved in the fossil record. However, fungi are capable of attacking and digesting almost any living structure, including other fungi. The ability to inhabit and parasitize other fungi emerged early in their evolution. Fossils of mycoparasitic fungi have been found in some of the oldest confirmed fungal fossils from the Early Devonian, about 410 million years ago. From an evolutionary standpoint, mycoparasites may facilitate horizontal gene transfer (HGT), either by directly transferring DNA to their hosts or by breaking down the host's cell wall, removing the barrier to acquiring DNA from other species.

Research continues

Fungi are a key element in the evolution of life on Earth. Today, there is a growing awareness of their presence and the crucial roles they play in ecosystems, leading to increased efforts to protect many fungal species. Fungi have long been used in medicine, and more recently, in scientific research. In fact, the first complete genome of a eukaryote to be sequenced, published in 1996, was that of a fungus (*Saccharomyces cerevisiae*), a breakthrough that revolutionized science. However, many fungal taxa remain unknown due to the challenges of identification. Despite this, rapid advances in research methods and tools are allowing scientists to gain a deeper understanding of these often overlooked, sometimes invisible organisms.

This expanding knowledge can not only aid in the conservation of fungi but also help apply them to other scientific inquiries, including questions about related organisms. This is particularly important in the context of climate change, where shifting CO_2 levels and rising temperatures are progressing at an alarming rate. The study of fungi may offer insights into how ecosystems respond to these changes and how we can better manage and protect them. ■

Further reading:

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