FROM THE SOIL TO THE SKIES

When we mention mushrooms, our minds generally turn to grilled champignons for breakfast or gnomes lurking under toadstools. But the taxonomical kingdom to which they belong, the fungi, is actually vast and highly diverse: over one hundred thousand species have been described so far, and scientists estimate that the real number could be as much as fifty times greater. Some fungi have even taken a liking to aviation fuel!

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Fungi are everywhere: they are found on all continents and in vastly diverse environments, including those generally regarded as extreme or uninhabitable. One of the most extreme environments, in fact, may be the one inside aviation fuel systems. This first came to light in the late 1990s, when the cause of many airplane and boat engine failures was finally discovered to be the growth of microorganisms on the boundary between water and fuel. Further research conducted in subsequent years revealed that the main culprit is a fungus named *Amorphotheca resinae*, which can use alkanes in aviation fuel as its only source of carbon – the key element essential for the survival of organisms on Earth.

Fungi have also been detected at the ruins of the Chernobyl nuclear reactor which exploded in April 1986, spilling radiation contamination over an area of over 100,000 km^2. In early 1990s, the remains of the power plant building were found to contain *Cladosporium*, *Wangiella* and *Cryptococcus* fungi. They all have highly melanized cell walls. The research team led by Ekaterina Dadachova postulated that the fungi are not only able to survive under high ionizing radiation, but that they are likely to utilize it in their physiological processes. Under laboratory conditions, fungi with melanized cell walls are found to migrate towards sources of gamma radiation.

Melanin is a pigment found in a wide range of organisms. It is composed of polyphenol compounds with unique physicochemical properties. This means melanins perform a range of biological functions and are responsible for adaptation to extreme environmental conditions. Fungi with highly melanized cell walls have also been found in the Arctic, Antarctic and high-altitude deserts. At high altitudes, melanin content tends to be higher in specimens found on south-facing slopes because the compound protects fungi against damage caused by powerful UV radiation.

Another physiological mechanism which enables fungi to inhabit extreme environments is their incredible ability to form symbiotic relationships with other organisms. The best known such association are lichens – composite organisms comprising algae or cyanobacteria together with fungi. Researchers recently discovered that the relationship is more complex than previously believed, in that it also involves bacteria and *Basidiomycota* fungi. The ability of lichens to withstand extreme environmental conditions has been known for a long time. It was shown recently that *Peltigera aphthosa* (known as green dog lichen) can survive temperatures ranging from −70°C to +70°C and endure under anaerobic conditions. And that's not all: none of these stress factors have a significant impact on the lichen's photosynthesis. It seems likely that it is the interactions between the different organisms which are behind this ability of lichens to inhabit environments which are hostile for any of the individual components.

One characteristic enabling lichens to survive a drought is their ability to halt their physiological function until the point when conditions are favorable again. The extraordinary properties exhibited by lichens have also been tested in space. In 2005, a team of researchers from the Russian Soyuz craft placed two lichen species outside an artificial satellite for fifteen days. Once the organisms were brought back inside, they immediately resumed their life function.

In another kind of symbiotic relationship, mycorrhizae, fungi form associations with roots of a vascular host plant. Such systems were first described in the 19th century and have been the subject of extensive research since. In fact, scientists believe that it was developing symbiotic relationships with fungi which enabled plants to colonize land environments in the first place. In simple terms, in mycorrhizae the plant component shares carbon compounds it photosynthesizes, and in return it receives nitrogen and phosphorus compounds from the fungus. However, as is the case with lichen, the systems are usually far more complex. In the late 20th century, researchers identified the mycorrhiza helper bacteria (MHB). It turns out that various bacterial strains found in the rhizosphere, such as *Pseudomonas* and *Streptomyces*, can affect the expression of genes in fungi which form ectomycorrhizal relationships with trees. Similar mechanisms have also been observed in relationships between endomycorrhizal fungi and herbaceous plants. In this instance, bacteria stimulate spore maturation in *Glomeromycota*.

Research into mycorrhizae has given rise to many discoveries revealing the wide reach of interactions between fungi and bacteria. In 2010, an American team was the first to isolate endosymbiotic bacteria from the hyphae of endophytic fungi which develop

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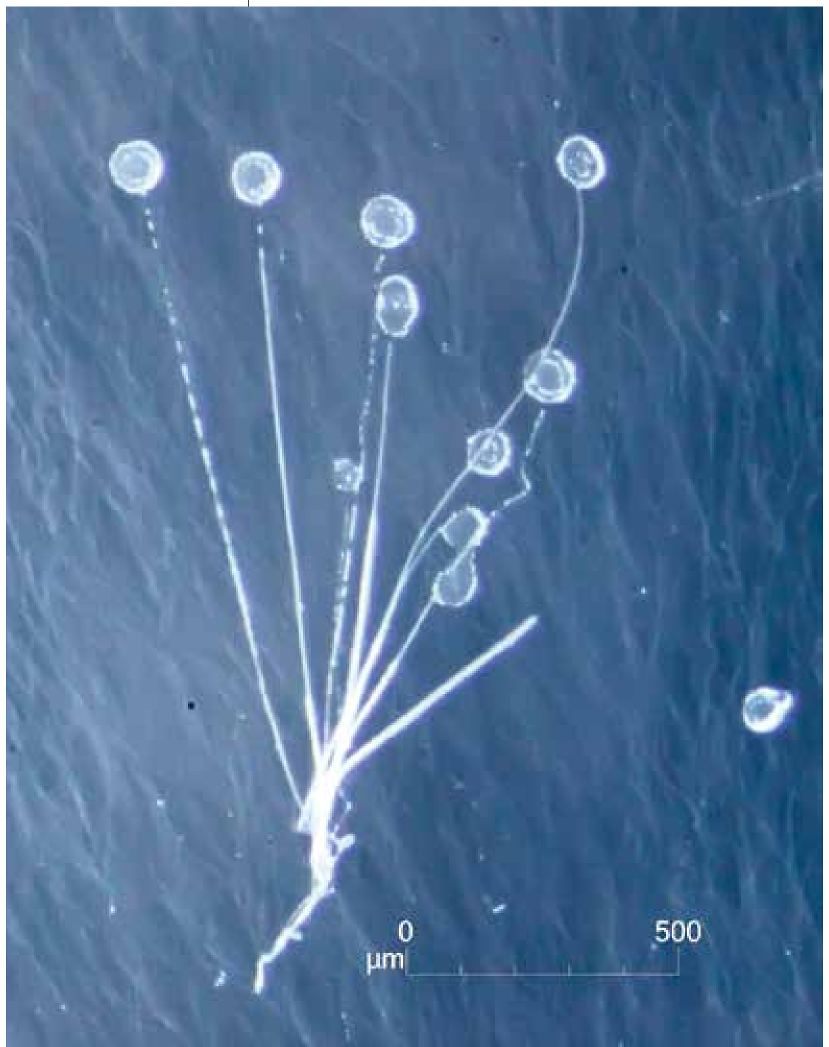

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Mortierella calciphila isolated from calcareous soil from Western Pomerania.

within plant tissues without causing any negative effects. A few years later it turned out that endosymbiotic bacteria actually stimulate endophytic fungi to secrete plant hormones regulating growth and development.

The team also later showed that bacteria found in hyphae affect the fungus's ability to utilize different sources of carbon. When endophytic fungi are stripped of their endosymbiotic bacteria, they lose the ability to use the sugar trehalose. This suggests that bacteria found within hyphae of endophytic fungi have a direct effect on the host plant's adaptive abilities. In other words, their presence or absence affects whether the plant can survive in a given ecological niche.

Research into endosymbiotic fungal bacteria reveals their effect on the host's toxicity. Hyphae of *Rhizopus microsporus*, the fungal pathogen causing rice seedling blight, contain the bacterial endosymbiont *Burkholderia rhizoxinica* which produces the toxin rhizoxin. Since *Rhizopus* were some of the first fungi to colonize land, the discovery stimulated interest in their interactions with prokaryotes. They grow as filamentous, branching hyphae that generally lack cross-walls, and they frequently enter into endosymbiosis with bacterial colonies. It is difficult to say whether they first appeared as parasites or symbionts.

Recent phylogenetic research indicates the subphylum *Mortierellomycotina* as the first fungi to have colonized land; they are mainly saprotrophic soil fungi. They are cosmopolitan organisms frequently found in environments in which nutrients are scarce. Recent research indicates that many representatives of this group enter obligatory or optional interactions with hyphae-inhabiting bacteria. The analysis of the *Mortierella elongata* genome and its bacterial endosymbiont *Mycoavidus cysteinexigens* published last year reveals that the genome of the fungal host contains a core set of primary metabolic pathways, while the endosymbiotic bacterial genome is reduced in size and function. Subsequent experiments involving removing the endosymbiont confirmed its powerful influence on the host's metabolism. The results indicate an evolutionarily-ancient interaction between fungi and bacteria.

The origins of this symbiosis likely date back to the time when fungi first started colonizing land. In comparison with aquatic environments where life first originated, early land environments were extremely unfavorable and completely lacking soil (loose material comprising mineral and organic components). Surviving on bare rocks exposed to powerful UV radiation and extreme temperatures must have been one of the greatest challenges in the history of life on Earth. It is likely that before plants and their fungal symbionts first appeared on land, they were preceded by simple consortia and symbiotic systems of fungi and bacteria. Over time, once land was covered with a layer of soil, more fungal species arose able to break down plant and animal remains, while the original pioneering organisms were slowly superseded. However, they can still be found in extreme environments such as deserts, polar regions and at high altitudes – environments where organisms which are responsible for the decay of cellulose and lignin cannot survive. We look to these extreme environments to find fungi which interact with other organisms hoping to answer many important questions on the evolutionary past of life on Earth, including how fungi first came to populate land environments.

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The research is being conducted at the Institute of Molecular Phylogenetics and Ecology. Faculty of Biology, University of Warsaw, financed as part of a National Science Centre project (Marta Wrzosek, PhD, OPUS no. 2016/23/B/NZ8/00897, and Julia Pawłowska, PhD, SONATA no. 2015/17/D/NZ8/00778 and OPUS no. 2017/25/B/NZ8/00473).