

Black Fungi Research: Out-of-This-World Implications

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Black fungi are an ecological group of melanized fungi specialized in extremotolerance and assumed to be among the most stress-resistant eukaryotes on Earth. Multi-omics studies have provided significant evidence that they have a peculiar response to stress that differs considerably from that of common mesophilic hyphomycetes. Survival strategies displayed by these organisms have situated them as attractive models for astrobiology and, in general, for studies directed towards the definition of the actual limits for life. Moreover, the ascertained aptitude of black fungi for degradation of hazardous volatile pollutants and for plastic breakdown suggests prospective application of several species.

Keywords: astrobiology ; astromycology ; biodegradation ; bioremediation ; black fungi ; black yeasts ; ex-tremophiles ; extremozymes ; plastic degradation ; rock-inhabiting fungi

Extremophiles occupy environmental niches on the planet that exhibit extremes in physical or chemical conditions. Extreme environments, as considered from the human viewpoint, include myriad niches, habitats, and ecosystems on Earth's surface and subsurface ranging from deserts to ice sheets ^[1]. Other examples of extreme environments encompass synthetic habitats that originated as a result of human intervention; these include acid mine waters, sewage and industrial effluents generated by constant discharge of pollutants and toxic waste into the environment ^[2], and also nuclear reactors, found to harbor microbial life ^[3].

Extremophiles can be separated into two categories: extremotolerant organisms, which can endure extreme values though growing optimally at "normal" conditions, and extremophilic organisms, which are highly adapted for metabolically and biochemically operating under particular environmental extremes ^[4].

Extremophiles include members of all three domains of life viz. Bacteria, Archaea, and Eukarya; however, most known extremophiles are microbes. Prokaryotes were for a long time considered the sole colonizers of habitats previously deemed as inhospitable for life. Species belonging to the kingdom Archaea and Bacteria were found to be able to adapt to a variety of extreme settings, including temperature (from 122 °C of hydrothermal vents, i.e., the archaea *Methanopyrus kandleri*, to frozen sea water at -20 °C, i.e., *Psychrobacter cryopegellain*), pH (from extreme acid, i.e., the archaea *Picrophilusoshimae* and *Picrophilustorridus* can grow at pH 0.06, to extreme basic conditions, i.e., pH 12.8, *Halomonas campisalis*), high pressure, high metal concentrations, and xerophilic conditions ^[5]. Some species, such as the bacterium *Deinococcus radiodurans* and the archaea *Halobacterium salinarum*, are known as polyextremophiles based on their aptitude to survive multiple stresses, including ionizing radiation ^[6].

Besides bacteria and archaea, molecular ecology studies additionally brought to light a wide diversity of eukaryotes in different extreme environments, revealing how these organisms are not less adaptable than prokaryotes ^{[7][8]}. Protists and the microscopic invertebrate tardigrade are examples of impressive polyextremophiles, however, among eukaryotes, fungi are considered the most versatile and ecologically successful phylogenetic lineage ^[4]. Whether alone or as lichens, fungi have a great capacity to adapt to a wide range of harsh conditions and are among the most skilled microorganisms to grow in conditions of decreased water availability ^[9]. Species that thrive in dry ecosystems—where water can be limited due to a low relative humidity, high concentration of solutes or because it is in the form of ice—such as the ascomycete filamentous fungus *Xeromyces bisporus*, have an absolute requirement for lowered water activity in order to grow ^[9]; others such as *Hortaea werneckii*, thrive in hypersaline waters and can grow in nearly saturated salt solution ^[10]. Similarly, distinctive morpho and physiological features help fungal extremophiles to adapt to extreme cold regions, acidic or deep-sea habitats, and heavily polluted waters ^[11].

The fascinating lifestyle of extremophiles has fueled much research to understand the mechanisms that enable these organisms to push the limits for life. Advances in molecular biology techniques and the availability of high-throughput DNA sequencing as well as of omics approaches, have contributed to uncovering a hidden abundance of microbial diversity and to revealing the evolution of novel physiologies and biochemistry under extreme conditions. By providing ground-breaking discoveries, the study of extremophiles has stretched the known physical and chemical limits for life and radically changed the understanding toward the conditions under which life can be sustained ^[12]. Extremophiles have therefore

become promising models to further our understanding of the molecular basis of survival and the functional evolution of stress adaptation. Because extremophiles, in particular the hyperthermophiles, are thought to lie close to the nature and behavior of primordial life on the surface of the Earth ^[13], they are also unique models for astrobiology and exobiology studies exploring the origins of life and the possible existence of life on other planets ^[14].

Not only are microbial extremophiles of ecological importance, but they also represent a valuable resource for the exploitation of novel biotechnological processes and biomolecules. Proteins, enzymes (extremozymes), and bioactive compounds obtainable from extremophiles are of great interest to biotechnology as they offer advantages over their counterparts from less tolerant organisms in terms of stability and activity (e.g., resistance to proteolysis and recalcitrance to denaturation) ^[15]. Enzymes produced by thermophiles—e.g., the heat-resistant TaqDNA polymerase from the bacterium *Thermus aquaticus*—and psychrophiles for instance have received particular attention for their commercial value and multiple industrial uses ^{[16][17]}. Myriad applications can be envisioned for enzymes that are stable at extreme values of several physicochemical parameters, including their use for biodegradation and bioremediation purposes in man-made extreme habitats. Hence, it is not hard to imagine that in the future, microbial extremophiles could play a key role in aiding the achievement of the targets of sustainability and bio-based economy ^[18].

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