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REVIEW

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Adaptation, Ecology, and Innovation: unraveling the secrets of endolithic life

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ABSTRACT

Endoliths, a unique subset of extremophiles, inhabit rock interiors, including microscopic pores and cracks, and demonstrate remarkable survival strategies under extreme conditions. These microorganisms thrive in challenging habitats such as the Atacama Desert, Antarctic rocks, and deep-sea basalt formations by utilizing rock matrices as natural barriers against desiccation, UV radiation, and nutrient scarcity. They are classified into cryptoendoliths, which reside in microscopic pores; chasmoendoliths, which colonize cracks; and euendoliths, which actively bore into rocks through biochemical processes. Endoliths play a vital role in carbon and sulfur cycles, contributing to essential ecosystem functions. Their ability to switch between chemoautotrophic and photoautotrophic lifestyles ensures metabolic activity under diverse conditions. Beyond their ecological significance, these organisms provide insights for astrobiology, serving as models for potential biosignatures on Mars and other celestial bodies with extreme environments. However, challenges in culturing endoliths due to their slow growth and habitat-specific requirements limit research progress. Future investigations should target deeper biospheres and polar ice sheets to uncover new microbial species. Advanced molecular tools like single-cell sequencing and CRISPR-based genome editing will help elucidate the metabolic pathways and adaptation mechanisms of endoliths. Biotechnological applications, including the use of endolith-derived enzymes for bio-mining and genetically engineered microbial strains for life-support systems in space missions, represent promising areas of innovation. Addressing these research gaps will enhance our understanding of extremophilic life and foster breakthroughs in multiple scientific fields.

KEYWORDS

Endoliths; Extremophiles; Chemoautotrophy and Photoautotrophy; Molecular Adaptation Mechanisms; Microbial Survival Strategies

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Introduction

Extremophiles are organisms that thrive in environments previously thought to be inhospitable due to extreme conditions such as intense radiation, high salinity, desiccation, or temperature extremes. A unique subset of these organisms, endoliths, inhabits the interior spaces of rocks, including microscopic pores, cracks, and fissures. By colonizing rock substrates, endoliths evade environmental stressors like desiccation and UV radiation, leveraging the rock matrix for protection. These organisms are known to survive with minimal water and nutrients, thriving in extreme habitats such as the Atacama Desert, Antarctic rocks, and deep-sea basalt formations [1].

Endoliths are classified into three groups based on their habitat niches: cryptoendoliths reside within microscopic rock pores, chasmoendoliths occupy natural cracks and fissures, and euendoliths actively bore into rocks through biochemical processes. These microorganisms exhibit diverse metabolic strategies, including chemoautotrophy, where they oxidize minerals for energy, and photoautotrophy, using the limited sunlight that penetrates rocks [2]. The study of endoliths holds significance for astrobiology, offering insights into potential extraterrestrial life. For instance, Mars and Europa present conditions analogous to terrestrial habitats where endoliths thrive, making them model organisms for studying biosignatures in extreme environments [3].

Despite advances in understanding endolith biology, several gaps remain. Challenges in culturing endoliths in the laboratory limit molecular studies on their regulatory pathways and metabolic mechanisms. Additionally, the extent of horizontal gene transfer among endoliths, which may enhance their adaptation, is still poorly understood. There is also insufficient data on their interactions with the surrounding rock environment and their role in biogeochemical cycles. This mini-review explores the biological adaptations, ecological roles, and molecular mechanisms of endoliths, focusing on their survival strategies in extreme environments [4]. The review will also highlight the potential applications of endolith research in astrobiology, biotechnology, and geological studies while addressing current knowledge gaps and proposing directions for future research.

Types of Endolithic Communities

Cryptoendoliths

Cryptoendoliths occupy microscopic pores within rocks, sheltering them from extreme environmental stressors like UV radiation and desiccation. These organisms thrive in regions such as the Antarctic Dry Valleys, where they rely on limited water and sunlight penetration. Biofilms play a crucial role by retaining moisture and protecting cells from oxidative stress. The use of minimal light enables cryptoendoliths to perform

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photosynthesis during brief favourable conditions, ensuring their survival in nutrient-deprived habitats [5].

Chasmoendoliths

Chasmoendoliths reside in cracks and fissures within rocks, exploiting these natural crevices to access moisture and nutrients. These organisms are particularly adept at forming layered biofilms, which trap water and buffer against environmental fluctuations. The production of pigments serves a dual purpose: shielding them from UV radiation and scavenging reactive oxygen species (ROS). Their ability to tolerate desiccation and oxidative stress makes them highly resilient in fluctuating environments, including volcanic rocks and arid deserts [6].

Euendoliths

Euendoliths actively penetrate rock surfaces by secreting organic acids, which dissolve minerals and create micro-channels for colonization. They are often found in marine environments, such as limestone structures, where they contribute to rock weathering. Beyond rock-boring activity, some euendoliths display metabolic flexibility, switching between autotrophic and heterotrophic lifestyles in response to nutrient availability. This adaptability allows them to persist in nutrient-poor and chemically harsh environments, playing an essential role in biogeochemical processes [7].

Ecophysiology and adaptations of endoliths

Nutrient acquisition

Endoliths inhabit environments where organic nutrients are scarce, necessitating unique survival strategies. One such strategy involves adopting autotrophic lifestyles to produce essential organic molecules from inorganic sources. Chemoautotrophic endoliths harness energy by oxidizing compounds like sulfur, iron, or ammonia, which are often found in specialized environments. For instance, iron oxidation predominates in volcanic regions, while sulfur oxidation is more common in marine ecosystems. This ability enables these organisms to maintain their metabolic functions in deep subsurface environments where no sunlight is available [8].

In addition to chemoautotrophy, photoautotrophic endoliths utilize sunlight to fuel their metabolic processes. These organisms possess pigments such as chlorophylls and bacteriochlorophylls to absorb light across different wavelengths, allowing them to conduct photosynthesis efficiently. The presence of diverse pigments reduces competition among multiple phototrophic organisms sharing the same niche by enabling them to absorb various wavelengths of sunlight. Through their autotrophic pathways, both chemo- and photoautotrophic endoliths ensure survival and maintain essential metabolic activities even in resource-poor environments [9].

Energy sources

Endoliths exhibit various mechanisms for acquiring energy, allowing them to adapt to different environmental conditions:

- **Mineral Oxidation:** Chemoautotrophic endoliths derive energy from oxidizing inorganic compounds, such as sulfur, iron, or ammonia. This metabolic strategy enables survival in subsurface rocks, volcanic regions, and areas where chemical gradients are prevalent [10].
- **Sunlight Utilization:** Photoautotrophic endoliths employ chlorophylls and bacteriochlorophylls to capture solar energy. These pigments, supported by accessory pigments like carotenoids, enhance light absorption across a broader spectrum, optimizing the energy available and minimizing competition among coexisting phototrophs [11].
- **Chemical Reactions in Subsurface Environments:** In deep, dark subsurface environments, redox reactions between minerals provide the primary source of energy for endoliths. This metabolic strategy ensures survival in habitats completely devoid of sunlight or organic matter [12].

The diversity of metabolic strategies in endoliths allows them to thrive in environments ranging from sunlit rock surfaces to deep ocean crusts, underscoring their remarkable adaptability.

Survival strategies

Endoliths have evolved several mechanisms to endure environmental stressors, including desiccation, radiation, temperature extremes, and high pressure.

Desiccation Resistance

In arid regions, endoliths face extreme water scarcity. To mitigate this, they produce biofilms rich in exopolysaccharides, which act as a protective barrier. These biofilms retain moisture, shielding the microorganisms from desiccation. Some endoliths may also enter dormant states, halting metabolic activity until favourable conditions return [13] .

Radiation Tolerance

Exposure to UV and ionizing radiation is a common challenge for endoliths living in polar regions and high-altitude environments. To counteract this, they produce pigments such as carotenoids, which function as antioxidants by neutralizing reactive oxygen species formed during radiation exposure. Additionally, endoliths have developed robust DNA repair mechanisms that correct damage caused by radiation, helping to maintain cellular stability [14].

Temperature Extremes

Endoliths demonstrate the ability to survive extreme temperature fluctuations. Psychrophilic endoliths adapted to polar environments produce antifreeze proteins, which prevent the formation of ice crystals inside cells. In contrast, thermophilic endoliths inhabiting volcanic regions rely on heat shock proteins (HSPs) to stabilize enzymes and other cellular structures under high-temperature conditions. These specialized adaptations enable them to maintain metabolic functions across a wide range of temperatures [15].

Pressure and Isolation Resistance

Subsurface endoliths are exposed to extreme pressure and isolation. To survive, they often enter dormant states with reduced metabolic activity, a process known as oligotrophic metabolism. This strategy allows them to survive for extended periods with limited energy sources. When environmental conditions improve, they resume metabolic functions using stored energy reserves to restart growth and reproduction [16]. Table 1 explains the types of endoliths and their survival in different conditions.

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Table 1. Cotton zones in province of Punjab, Pakistan.

Type of Endolith	Habitat	Example Species	Adaptation Features	Food Sources	Life Span	Reproduction	Applications
Cryptoendoliths	Pores in desert rocks	Cyanobacteria	Moisture retention through biofilms, UV-resistant pigments	Sunlight (photoautotrophy), trace minerals	Long dormant periods	Asexual reproduction (binary fission)	Bioremediation, astrobiology research
Chasmoendoliths	Cracks and fissures in rocks	Lichen-forming fungi	Use of antifreeze proteins, oxidative stress protection	Nutrients from surrounding organic matter	Decades or more	Fragmentation or spore formation	Climate research, ecological studies
Euendoliths	Marine limestone, basaltic rock surfaces	Fungi, archaea	Secretes acids to dissolve minerals, energy from mineral oxidation	Sulfur, iron, and potassium compounds	Potentially centuries	Spore formation	Biomineralization, biogeochemical cycling
Subsurface Endoliths	Deep Earth crust (2-7 km below surface)	Thermophilic bacteria	Tolerate high pressure and temperatures, oligotrophic metabolism	Chemosynthesis (oxidizing sulfur and iron)	Extremely long lifespans	Binary fission, biofilm dispersion	Industrial enzymes, astrobiology
Endolithic Algae	Coral reefs and marine environments	Ostreobiumsp	Provides symbiotic support to coral, light absorption pigments	Photosynthesis	Indefinite under optimal conditions	Asexual and sexual reproduction	Coral reef restoration, marine ecology

Habitats of Endoliths

Terrestrial environments

Endoliths occupy extreme terrestrial habitats, including deserts, polar regions, and volcanic rocks, each posing unique environmental challenges. In deserts like the Atacama, cryptoendoliths survive prolonged aridity by retreating into dormant states during dry periods, reactivating when rare moisture events occur. The porous rock structures retain minute water amounts, supporting these microorganisms. In polar regions such as Antarctica's Dry Valleys, endoliths use brief periods of sunlight to photosynthesize while leveraging rocks for insulation against sub-zero temperatures. Volcanic rocks on Deception Island harbour thermophilic endoliths that endure chemical stress from eruptions, exploiting minerals for energy through oxidation pathways. These adaptations showcase endoliths' diverse strategies to thrive across harsh terrestrial ecosystems [17].

Subsurface and oceanic environments

Endoliths extend deep into the Earth's crust and underwater basalt formations, where they rely on chemosynthesis to sustain metabolic activities. In these subsurface environments, light is absent, and extreme pressure and isolation prevail. Endolithic microorganisms oxidize sulfur and iron from minerals, producing energy in the absence of organic nutrients. Within hydrothermal vents, where temperatures soar and minerals are abundant, endoliths form symbiotic associations with other microorganisms, contributing to nutrient cycling. These organisms also play a role in mineral weathering, altering the composition of basalt and sustaining complex ecosystems within the deep ocean [18].

Extraterrestrial implications

The survival strategies of terrestrial endoliths serve as analogs for potential life beyond Earth. For instance, Mars and icy moons like Europa display environmental conditions such as

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low temperatures, radiation exposure, and nutrient limitations similar to habitats where endoliths thrive. NASA's Perseverance rover, currently exploring Martian rock formations, aims to identify biosignatures indicative of microbial life, guided by knowledge gained from endolithic research on Earth. These studies not only assist in identifying viable extraterrestrial habitats but also help refine techniques for detecting organic molecules in future space missions [19].

Potential Applications of Endoliths Research

Astrobiology

Endoliths are essential for studying the potential for life beyond Earth due to their ability to survive in conditions analogous to extraterrestrial environments. Life would likely encounter extreme radiation, limited water, and nutrient scarcity on Mars, Europa, and other celestial bodies—similar to the conditions endoliths endure in Earth's harsh environments, such as Antarctic rocks and volcanic basalts [20].

In astrobiology, endoliths provide a model for identifying potential biosignatures, such as pigments like prodigiosin, which shield against UV radiation. These pigments could serve as molecular markers in life-detection missions. Biofilms, a protective strategy often observed in endolithic communities, are also considered promising biosignatures. These insights help refine the design of instruments for missions, such as those on Mars rovers, to detect microbial life based on analogous molecular patterns. Moreover, studying the survival mechanisms of endoliths informs researchers about what environments might be habitable beyond Earth. Their reliance on chemoautotrophy using inorganic compounds for energy provides an example of how extraterrestrial organisms might sustain themselves in nutrient-poor environments, such as subsurface rocks on Mars [21].

Biotechnology

Endoliths contribute to various fields of biotechnology through their unique metabolic capabilities. Their ability to dissolve minerals through organic acids enables bio-mining, a process used to extract valuable metals from low-grade ores, even in extreme environments where traditional mining is unfeasible. This makes them invaluable for mining operations in remote or challenging locations, including extraterrestrial surfaces in the future [22].

Endoliths also play a critical role in bioremediation, where they break down environmental pollutants such as hydrocarbons and heavy metals. Their metabolic pathways for detoxification provide solutions for cleaning industrial waste sites. Additionally, enzymes isolated from endoliths are often more stable under extreme conditions, expanding their use in industrial processes. For example, thermally stable oxidases derived from endoliths can enhance chemical reactions in high-temperature manufacturing settings. In synthetic biology, the resilience of endoliths inspires engineering microbial strains with similar traits, enhancing their utility in extreme environments. Genes encoding stress-resistant enzymes and pigments can be transferred into synthetic systems to create robust biological tools for pharmaceutical and industrial applications. This allows processes such as drug synthesis to be performed in conditions that typically degrade conventional enzymes [23].

Geological implications

Endoliths significantly impact geological processes through rock weathering and mineral precipitation. As they colonize rock surfaces, these microorganisms release organic acids that dissolve minerals, accelerating the breakdown of rocks and contributing to soil formation. This process plays a vital role in shaping ecosystems by influencing the availability of essential minerals in the environment [24] .

In addition to weathering, endoliths facilitate mineral precipitation by creating microenvironments conducive to crystallization. Through oxidation-reduction reactions, endoliths participate in key biogeochemical cycles such as the sulfur and nitrogen cycles, contributing to elemental recycling. For example, sulfur-oxidizing endoliths convert sulfides to sulfates, influencing nutrient availability and ecosystem dynamics. These microbial processes help maintain environmental stability and support the development of complex ecosystems over time. Understanding the interaction between endoliths and geological systems not only sheds light on ancient microbial ecosystems but also provides insights into past climatic changes. This research is crucial for reconstructing the history of Earth's environment and predicting how microbial communities might respond to future environmental shifts [25].

Conclusion and Future Directions

Endolithic organisms thrive in extreme conditions by adapting to minimal light, water, and nutrients. Their ability to colonize rock interiors shields them from environmental stressors such as desiccation and UV radiation. These organisms play vital roles in carbon and sulphur cycles, contributing to elemental turnover in ecosystems. The diverse metabolic pathways, including chemoautotrophy and photoautotrophy, demonstrate their ecological importance. Endoliths have promising applications in bioremediation and mineral weathering, providing insights into how life can survive under extreme environments, both on Earth and potentially on other planets.

Future studies should explore deep subsurface biospheres and polar ice sheets to uncover new microbial species and adaptive strategies. Advanced molecular approaches, such as CRISPR-based genome editing, single-cell sequencing, and transcriptomics, could further elucidate the metabolic pathways that allow endoliths to withstand environmental stress. Understanding the role of horizontal gene transfer in endolithic adaptation may offer insights into their evolutionary processes. In biotechnology, enzymes derived from endoliths that function under extreme conditions could benefit industrial applications, such as bio-mining and waste remediation. Additionally, stress-resistant genes from these organisms may inspire synthetic biology tools for space missions, aiding life-support systems in extra-terrestrial environments. Exploring these avenues will enhance both ecological understanding and technological innovation, developing future breakthroughs across multiple scientific fields.

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