

Life in (and on) the rocks

Rocks, apart from being ancient records that enlighten us about the geological history of our planet, are dynamic repositories that support life forms central to the sustenance of our biosphere. It is the latter that our discussion will be largely focused on. Life associated with rocks has been documented as early as 1914 (Diels 1914), but it was in the 1960s that Friedmann and colleagues, with their extensive studies on rock-dwellers in hot and cold desert habitats, gave shape to this modern branch of geobiology. The presence of microscopic algae and bacteria was first demonstrated within exposed rocks from hot desert environments such as the Negev and the Sinai (Friedmann and Galun 1974) by electron microscopy and laboratory cultivation methods. Subsequent studies in ortho-quartzite rocks from the Dry Valley area of Antarctica also showed morphologically similar algae (related to the genus *Gloeocapsa*) to be colonizing areas ~1.5 mm wide parallel to and ~2 mm beneath the rock surface (Friedmann and Ocampo 1976). The results from the latter caught the attention of the scientific community as NASA had been testing their Voyager mission probes on the apparently lifeless cold deserts of Antarctica with the aim of studying a habitat analogous to Mars. In 2005, Walker and colleagues, through the use of culture-independent molecular methods, discovered the microbial colonization of rocks from the extremely acidic (pH~1) Yellowstone geothermal environment. By employing universal PCR primers that targeted 16S rRNA genes from all three domains of life, the authors were able to retrieve sequences phylogenetically related to extant red alga (*Cyanidium* sp.), bacteria (α -, β -, γ -Proteobacteria; Actinobacteria; Bacteroidetes and Firmicutes) and archaea (*Euryarchaeota* and *Crenarchaeota*). The astoundingly high diversity of microbial life forms present in such extreme habitats captured the imaginations of geo(micro)biologists, astrobiologists and microbial ecologists alike. Astrobiologists imagined that if rock interiors could support the major fraction of life in the harshest of environments on earth, then the same could be applicable to other planets such as Mars, and they sensed that there was a need to extend the scope of extraterrestrial life detection missions beyond the mere analysis of top soils. Microbial ecologists wondered if rock-associated life was ubiquitous in the biogeosphere, and geo(micro)biologists hypothesized that the rock micro-habitat offered life (a) protection from intense solar radiations, temperature and desiccation and (b) a supply of nutrients, moisture and growth surfaces. Today, with two dedicated international scientific journals – *Geobiology* and *Geomicrobiology Journal* and an ever growing number of papers dealing with rock-associated microbes in microbiological research journals, the concept of ‘life in/on the rocks’ has become as hardened as the rock itself. What is apparently lacking, however, is an understanding among the general public that a ‘dumb-looking’ average rock in their gardens (on this planet and perhaps in the gardens of intelligent beings on other planets) could be home to a dynamic assortment of interesting yet diverse living organisms of inevitably microbial nature.

*Don't give up! I believe in you all.
A person's a person, no matter how small!
And you very small persons will not have to die
If you make yourselves heard! So come on, now, and TRY!
– Dr Seuss (1954) in Horton Hears a Who!*

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1. Classification of ‘rock-dwellers’

Rocks constitute an important refugium for diverse microbial life forms, and although they might appear similar superficially, variations in the local micro-environmental conditions could influence colonization by distinctly different living organisms. For all practical purposes in geobiology, such rock-dwellers have been broadly classified into endoliths, epiliths and hypoliths (figure 1) (Golubic *et al.* 1981).

- *Endoliths*: Organisms that colonize the inside of the rock matrix. Closely related in function to endoliths are euendoliths, which colonize by actively boring into rocks, *Chasmoendoliths*, which colonize cracks or fissures in rocks and *Cryptoendoliths*, which live within the interstices or structural cavities in rocks. Although such distinctions are highly tenable both in theory as well as in the actual micro-habitat, it is practically difficult for the trained microbiologist to distinguish between these.
- *Epiliths*: Organisms that colonize the exposed outer surface of rocks.
- *Hypoliths*: Organisms that colonize the underside of rocks.

2. Factors affecting ‘life in/on the rocks’

2.1 Water and nutrients

Water or water availability is central to the survival of all extant living organisms on our planet. Water retention achieved by pore-space hydration protects endolithic communities from desiccation (Nienow and Friedmann 1993). Compatible solutes such as trehalose and sucrose, which possess water-retention properties, have been widely detected in endolithic microorganisms (Friedmann *et al.* 1993; Wynn-Williams *et al.* 1999). Endoliths are known to be able to resist repeated cycles of desiccation and wetting and apparently resume their metabolic activities within minutes of rehydration (Bell 1993). Hot desert environments are thought to be among the most extreme for endoliths in terms of water availability (Friedmann and Ocampo-Friedmann 1984). Endolithic organisms in such deserts could be largely dependent on water derived from condensation of dew (Kidron 2000). Rocks are generally

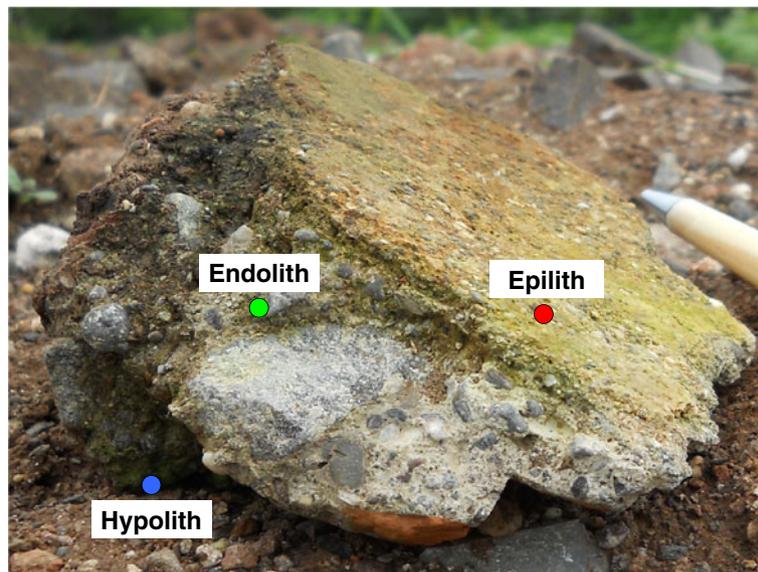


Figure 1. Main categories of ‘rock-dwelling’ life.

oligotrophic environments with limited availability of nutrients, but endoliths extract some nutrients from their host rocks as demonstrated previously in laboratory cultivation studies where addition of rock extracts to the cultivation media improved the growth of endolithic microbes (Siebert *et al.* 1996). Atmospheric deposition from precipitation and dust are likely to enrich the nutrient pool in the rock micro-habitat (Nienow and Friedmann 1993).

2.2 Temperature

Many psychrophilic (cold-loving) endoliths, exhibiting optimal growth in the range of 0–20°C, have been isolated from cold deserts such as Antarctica (Siebert *et al.* 1996). Endoliths in such environments rely on solar radiation to raise the local temperatures to ambient levels for carrying out photosynthesis. In hot desert environments, temperature could be an important limiting factor for endolithic growth, as temperatures in excess of 50°C can vaporize all the available water. Cooler early morning or late evening hours may be preferred by such endolithic communities for their metabolic activities as host rocks could absorb water formed by condensation of dew.

2.3 UV radiation and light

Ultraviolet radiation coupled with desiccation could arrest the growth and proliferation of epilithic communities in extremely dry deserts (Quesada *et al.* 1999; Cockell *et al.* 2008). In such environments, hypoliths and endoliths are better adapted to tolerate UV radiation by virtue of their strategic location and production of UV-screening compounds such as scytonemin and carotenoids (Cockell *et al.* 2003). Light in the photosynthetically active region (PAR) is required by phototrophs associated with rocks (Nienow *et al.* 1988). The depth of penetration of PAR could, in turn, be dependent on rock colour, mineralogy and structure (Walker and Pace 2007a). Endolithic phototrophs typically occupy a vertical block of a few millimeters that starts within ~1 cm beneath the exposed rock surface. However, evidence on the relationship between depth of colonization and light penetration is not very conclusive (Matthes *et al.* 2001).

2.4 Rates of mineralization

Production and deposition of carbonates in aquatic habitats (Schneider and Le Campion-Alsumard 1999) or iron oxides in hydrothermal vents (Emerson and Moyer 2002) may engulf and immobilize living cells, thereby posing a direct threat to endolithic life. Endoliths in such habitats may be dependent on active or passive demineralization processes (Cockell and Herrera 2008).

2.5 Predation

In the marine and other aquatic habitats, rock-associated microbes are susceptible to intense grazing by macroscopic organisms such as mollusks, sea urchins, fishes and snails (Chazottes *et al.* 1995). There is evidence of endolithic algal predation by endolithic fungi in corals (Priess *et al.* 2000). Endolithic predation by phages, although theoretically possible, has not been demonstrated in any environment so far.

3. Diversity and ecology of ‘rock-dwellers’

Rock-associated microbes have been reported from several interesting habitats across the world such as dry deserts (Friedmann and Galun 1974; Friedmann and Ocampo 1976), hot springs (Walker *et al.* 2005), sea-floor (Mason *et al.* 2007), hydrothermal vents (Daughney *et al.* 2004), tsunami deposits (Cockell *et al.* 2007), meteorite impact crater (figure 2) (Cockell *et al.* 2002, 2005), the deep subsurface (Amy *et al.* 1992; Pedersen 1997), mountains (Walker and Pace 2007b; Horath and Bachofen 2009) and cultural heritage monuments (Scheerer *et al.* 2009). Microbial colonization has been observed in igneous rocks, both crystalline and glassy (Thorseth *et al.* 1992; Villar *et al.* 2006; Herrera *et al.* 2009); sedimentary rocks such as limestones, sandstones and salts (Weber *et al.* 1996; Matthes *et al.* 2001; Wierzchos *et al.* 2006);

and metamorphic rocks such as granites and gneisses (figure 3) (Cockell *et al.* 2002; de los Ríos *et al.* 2005). Fungi, red and green algae and cyanobacteria are known to exhibit euendolithic activity (Perry 1988; Ghirardelli 2002). In extreme environments, microorganisms that bore into rocks are at a greater advantage than epilithic (surface) microbial life as the rock micro-environment offers them protection from the hostile macro-environmental conditions. The remarkable ability of such endolithic microbes to use the clement rock interior micro-environment for metabolism and growth represents an ancient evolutionary trait that is evident from microfossils dating back to the 3.4-billion-year-old Archean (Furnes *et al.* 2004).

Diverse metabolic strategies are employed by endolithic life forms to adapt to various environments, and these range from photosynthesis in the shallow subsurface (e.g. cyanobacteria thriving beneath translucent rocks) to chemolithoautotrophy in the deep subsurface (McLoughlin *et al.* 2007). The subsurface chemolithoautotrophs depend on H_2 , H_2S , S , CH_4 , CO , Fe^{2+} , or Mn^{2+} as potential electron donors, and CO_2 , Fe^{3+} , and Mn^{4+} in rocks or SO_2^{-4} and O_2 in circulating fluids as electron acceptors (McLoughlin *et al.* 2007). Endolithic microorganisms that are adapted to harsh polar environments such as the Antarctic Dry Valleys and the Canadian High Arctic commonly produce extracellular polysaccharides to avoid desiccation and to minimize the damaging effects of freeze–thaw cycles. These endoliths also actively participate in the ‘biomineralization’ of their surroundings, which results in the release and cycling of elements and nutrients essential for life (Omelon 2008). Fungal and cyanobacterial endoliths thrive by apparently releasing acids to dissolve the rock or by using calcium pumps for the sequestration of calcium ions and the subsequent dissolution of rock carbonates (Garcia-Pichel 2006).

Cryptoendolithic cyanobacteria form a blue-green layer 0.5–5 mm below the rock surface and often comprise *Chroococcidiopsis* spp. (Büdel 1999; Büdel *et al.* 2004). Molecular analysis of exposed sandstone rocks in the McMurdo Dry Valleys of Antarctica revealed the cryptoendolithic community to be dominated by lichens, cyanobacteria belonging to the genera *Phormidium* and *Plectonema*, and bacterial members belonging to the divisions α -Proteobacteria and *Thermus-Deinococcus* (de la Torre *et al.* 2003).

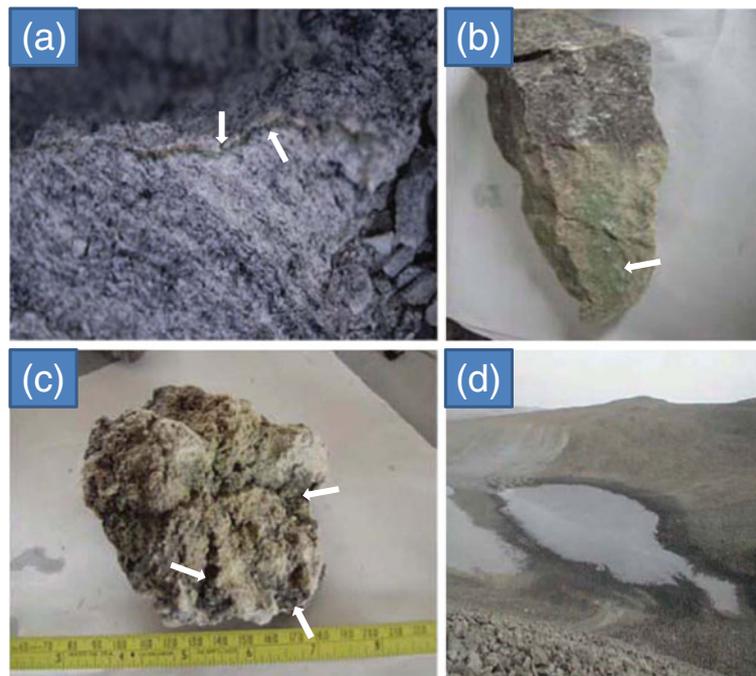


Figure 2. Rock habitats harboring microbial life in the Haughton impact structure, Devon Island, Nunavut, Canadian High Arctic (Adapted from Cockell *et al.* 2005 with modifications): (a) Endolithic colonization of shocked gneiss evident as a layer of green in the rock. (b) Hypolithic colonization of a domolite rock evident as a layer of green under the rock. (c) Colonization of the surface of shocked gneiss by *Cyanobacteria* evident as black patches in the rock. (d) Black ring around a pond that is caused by cyanobacterial epilithic colonization of adjacent rocks.

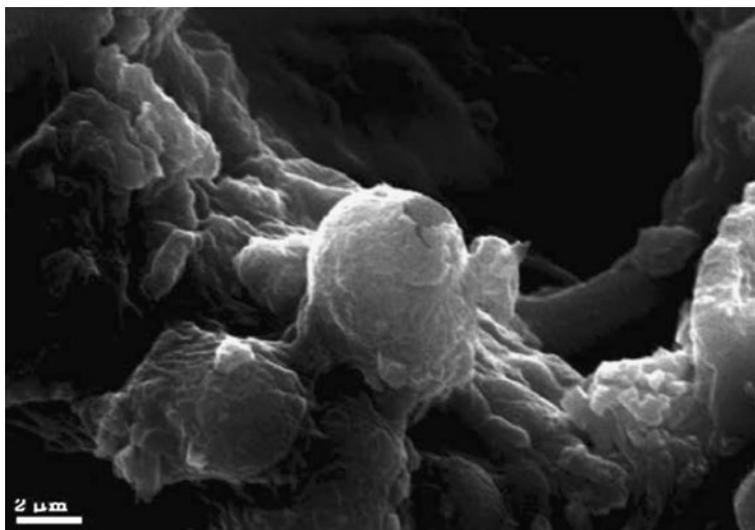


Figure 3. Scanning electron microscopy (SEM) image of a solitary *Chroococcidiopsis* growing within the fracture of a gneiss rock (Adapted from Cockell *et al.* 2002).

DNA sequencing analysis of both natural and *in vitro* cryptoendolithic biofilms on porous sandstones from Colorado Plateau, USA, showed the major constituents to be cyanobacteria and the *Geobacteriaceae* (Kurtz *et al.* 2005). Sandstones from McKelvey Valley (Antarctica) were found to harbour a high diversity of chasmoendolithic cyanobacterial phylotypes related to diazotrophic *Chroococcidiopsis* and Nostocales (Pointing *et al.* 2009). The stringent categorization of life inhabiting rock interiors into euendoliths, chasmoendoliths and cryptoendoliths is fraught with problems as microbes belonging to any one of these categories may also qualify in the others. As seen extensively in this section, such terminologies are often interchangeably used in the literature and can sometimes lead to misleading conclusions. For all practical purposes and to avoid possible misinterpretations, we would like to advocate the use of the more general term ‘endolith’ in all studies where comprehensive experiments have not been undertaken to ascertain the categorical function of life forms associated with rock interiors.

Epilithic lichens and algae have been reported from Antarctic rocks (Hale 1987; Pizarro *et al.* 1996). Molecular analysis of epilithic biofilms on inter-tidal rocks in the Gulf of Mexico showed the presence of thick-sheathed cyanobacteria related to *Xenococcus*, *Myxosarcina* and *Chroococcidiopsis* spp. in addition to bacterial members from the divisions *Bacteroidetes*, *Actinobacteria* and *Proteobacteria* (Narváez-Zapata *et al.* 2005). Morphological and molecular analysis of differentially pigmented epilithic mats and biofilms on beach rocks in the Great Barrier Reef, Australia, demonstrated a high diversity of cyanobacterial phylotypes related to the genera *Blennothrix*, *Pseudanabanaceae*, *Chroococcidiopsis*, *Calothrix*, *Entophysalis* and *Lyngbya* (Diez *et al.* 2007). Translucent stones such as quartz, which are ubiquitous in arid environments worldwide, are considered as attractive micro-habitats for hypolithic colonization. Cyanobacterial phyla members and sometimes *Chloroflexi*, fungi and mosses are widely reported to be the dominant hypoliths across arid environments such as hot deserts (Büdel and Wessels 1991; Schlesinger *et al.* 2003; Warren-Rhodes *et al.* 2006) and cold deserts (Cockell and Stokes 2004; Cowan *et al.* 2010).

4. Potential and applications of ‘rock-dwellers’

Microbes associated with rocks play a crucial role in the biogeochemical cycling of Earth’s elements. Microbe-mediated weathering of rocks, for example, can lead to formation of soil and is an indispensable source of inorganic nutrients for plants and other higher life forms. This interesting phenomenon could potentially be exploited in ‘biomining’ operations that extract important metals from their ores. If the future prospects of human colonization and settlement of extraterrestrial planets are considered, then the

application of ‘biomining’ for extraction of useful elements or for creation of soil would be highly rewarding (Cockell 2010). The deliberate introduction of rock-dwelling microorganisms may aid in the terraforming or the transformation of the atmosphere and surface of an entire planet to make it habitable for humans (Birch 1992). The widely reported rock-dwelling primitive cyanobacterium, *Chroococidiopsis*, has been proposed as a suitable ‘pioneer’ organism for terraforming planets such as Mars (Friedmann and Ocampo-Friedmann 1995). On a related note, the theory of ‘lithopanspermia’ interestingly postulates the natural seeding of planetary bodies across the universe with endolithic life forms present on rocks that are expelled into space from life-harboring planets upon asteroid impact (Melosh 1988). The rock records of ancient microfossils help us in answering important questions as to when and where cellular life first appeared on our planet. Further, the analysis of such ‘biomarkers’ or ‘biosignatures’ could have important implications for our search for life on other planetary bodies (Cockell 2010). Endolithic or ‘rock-boring’ microbes, for example, can create tubular microcavities (TMCs) by the dissolution of rock substrate and these can be differentiated from abiotically formed microtunnels by morphologic and petrographic analysis (McLoughlin *et al.* 2010). A negative aspect of the endolithic way of life is its widespread role in the deterioration and discoloration of monuments and buildings (Scheerer *et al.* 2009). This often presents a major challenge to the preservation of cultural heritage. Since rocks contribute to soil formation, they could also ‘seed’ soils with microbial life. The presence of pathogenic microorganisms in soils is a well-established fact and the international transport/shipment of soil is therefore regulated across many countries. Since no study so far has demonstrated any direct link between rock-based microorganisms and human/animal/plant infections, the transport/shipment of rocks do not currently come under the purview of such regulations across the vast majority of countries. Although the possibility for a rock to disseminate pathogenic microorganisms is extremely low, we would like to invite the wider scientific community to debate on any such likely scenarios and its potential impact on human/animal/plant health.

5. Future directions

Information on some important facets of endolithic life is still very sparse. The mechanisms by which microorganisms bore into rocks, their *in situ* rates of metabolic activity and cell division, their actual sources of carbon and energy and their gross contribution towards global biogeochemical cycling of nutrients are yet to be fully understood. The various limiting factors that affect life in/on the rocks have not been properly elucidated, especially the role of phages, if any, in regulating the endolithic community abundance and structure. Of particular interest would also be information as to whether microorganisms exhibit preferences for the colonization of any specific rock types. Exhaustive studies are needed to unlock the secrets of endolithic life within the deep subsurface. Analysis of the distribution, identity and activity of microbes in such extreme micro-habitats would require the development of sensitive techniques that shed light on the extremely low growth and metabolic rates of endoliths. It seems plausible that bacterial cell divisions within rock interiors could occur in time scales close to geological, and therefore, the methods currently available with us are not sufficient for deciphering the physiology of such endolithic life forms. The use of new high-throughput sequencing technologies in combination with metagenomics strategies will greatly enhance our search for novel enzymes or biomolecules from extremophilic endoliths. The emerging revolution in DNA sequencing needs to be adequately exploited so as to get deeper insights into the identity of endolithic microbial communities that mediate Earth’s elemental cycles. For improving efficiency and feasibility of ‘biomining’ operations, major advances need to be made with respect to the exploitation of specific endolithic microbes. To address important questions in astrobiology with respect to habitability of extreme planetary environments, it is crucial to understand microbial colonization of rocks in diverse extreme habitats on Earth. In our laboratories, efforts are currently underway to unravel the endolithic way of life in saline and alkaline environments (pH ~10) such as the Lonar crater lake.

6. Conclusions

The prospect of ‘life in/on the rocks’ offers us exciting opportunities to redefine our understanding of life and its limits. Rock micro-habitats teeming with a host of interesting microorganisms are potentially ‘seed banks’ of life on our planet (and perhaps other planetary bodies). The marriage between Earth and life

sciences would be cemented only with increased interdisciplinary and collaborative efforts between geologists and biologists. Importantly, there is also the need for our society in general to appreciate the rock as an abode of life. From a commonly held viewpoint, trees enjoy cult status as ‘a giver of life’. Although rocks themselves are abiotic, their life-supporting value needs to be recognized on similar lines even if they are not accorded equal status. Common phrases in the English vocabulary such as ‘dumb as a rock’ and ‘dumb as a box of rocks’ tend to cultivate confounded popular opinion to the contrary. Recently, the *Transformers 3* movie crew grabbed a few tabloid headlines with their accusations of ex-colleague Megan Fox being ‘as dumb as a rock’. We do not know about Megan Fox, but what we certainly would like to argue is that a rock does not deserve this dubious distinction. Despite its dumb appearance, a rock may still represent life’s important frontier on Earth and perhaps elsewhere in the universe.

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