RESEARCH REVIEW

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Microorganisms in desert rocks: the edge of life on Earth

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Summary. This article reviews current knowledge on microbial communities inhabiting endolithic habitats in the arid and hyper-arid regions of our planet. In these extremely dry environments, the most common survival strategy is to colonize the interiors of rocks. This habitat provides thermal buffering, physical stability, and protection against incident UV radiation, excessive photosynthetically active radiation, and freeze–thaw events. Above all, through water retention in the rocks' network of pores and fissures, moisture is made available. Some authors have argued that dry environments pose the most extreme set of conditions faced by microorganisms. Microbial cells need to withstand the biochemical stresses created by the lack of water, along with temperature fluctuations and/or high salinity. In this review, we also address the variety of ways in which microorganisms deal with the lack of moisture in hyper-arid environments and point out the diversity of microorganisms that are able to cope with only the scarcest presence of water. Finally, we discuss the important clues to the history of life on Earth, and perhaps other places in our solar system, that have emerged from the study of extreme microbial ecosystems. [**Int Microbiol** (2012); 15(4):171-181]

Keywords: arid environments · endoliths · hyper-arid deserts · lithobiontic microorganisms · desert rocks

Introduction

Although water is essential for life, even the tiniest amount may be sufficient for the survival of some microorganisms, as long as the accompanying environmental conditions are stable over long periods. Such conditions, which may eventually become extreme, are often found in the arid environments, or so-called deserts, of our planet. The main indicator of the dryness of a desert is its aridity index (AI), defined as the ratio between mean annual rainfall and mean annual evapotranspiration. Hyper-arid and arid regions with an AI of less than 0.20 occupy some 36.2 million km², making up 20 % of the Earth's surface area (Fig. 1). However, extremely arid conditions may be found in hyper-arid areas of AI under 0.05, usually with an annual rainfall of less than 25 mm. These areas occupy around 10.0 million km² and therefore represent 7.5 % of the Earth's surface (Fig. 1). Northern and southern polar regions may also be arid or hyper-arid [46], but note that Figure 1 only shows the Dry Valleys of Antarctica as a hyper-arid zone. Mean annual temperatures are >18 °C in hot deserts and <18 °C in cold deserts, while polar deserts have cold temperatures all-year-round, with maximum temperatures below freezing (polar frost) or 0 to 10 °C (polar tundra) [45]. As examples of hyper-arid deserts, we should mention a large part of the Atacama Desert (northern Chile) and some zones of the Negev Desert (Israel).

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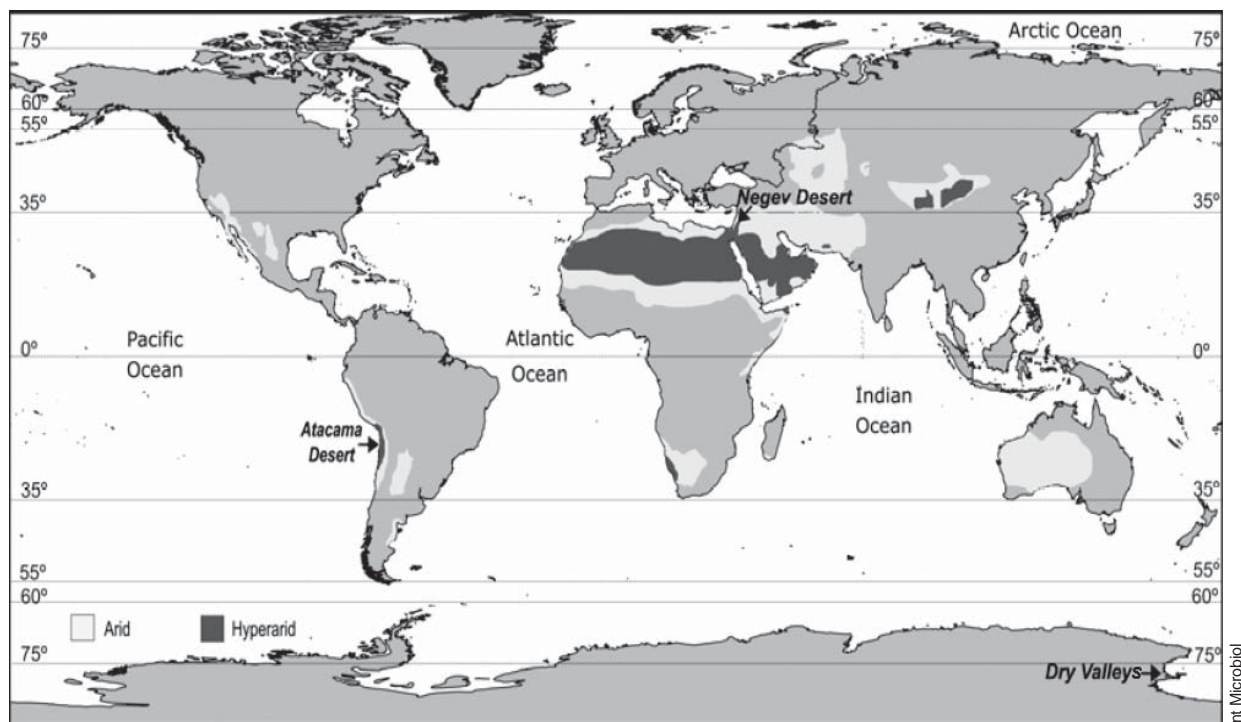E-mail: j.wierzchos@mncn.csic.es

Fig. 1. World deserts classified as arid (AI = 0.2–0.05) and hyper-arid (AI < 0.05) according to the United Nations Environment Program (UNEP). Arrows indicate the hyper-arid deserts noted in this review as the regions examined by the authors: Atacama Desert, Chile; Dry Valleys, Antarctica; Negev Desert, Israel. (AI: aridity index.)

While specialized organisms can exist in all but the most arid parts of the Earth, at some point water is too scarce to permit the full range of functions necessary to sustain viable populations of organisms, and biological adaptation to desiccation is no longer possible. We call this threshold the dry limit of life. Understanding the dry limit of life is critical to maintain the water activity envelope for life on Earth, and to consider the possibility of life elsewhere.

Lithobiontic microorganisms in arid environments

The lack of moisture that defines a desert determines the regulation of biological activity by an ephemeral availability of water. However, the disappearance of water from a cell leads to severe, often lethal, stress. Even in only moderately dry air, cell dehydration may be instantly lethal for most species [4] with a water activity limit (a_w) of 0.61. In air conditions, this corresponds to a relative humidity (RH) of 61 %. Moreover, crucial for the survival of organisms in arid environments is their ability to reversibly activate metabolism, allowing growth during the short periods when water is available and

the delay of metabolic activity during dehydration [27]. Desiccation-tolerant cells implement structural, physiological, and molecular mechanisms to survive a severe water deficit. While these mechanisms are still poorly understood, it is clear that the dryness, or aridity, of a desert is not the only condition unfavorable for life. In desert zones, besides the scarcity of water, microorganisms also need to withstand solar fluxes, including lethal UV light, high and low temperatures and their rapid fluctuations, high rates of water evaporation, prolonged periods of desiccation, oligotrophic conditions, and frequently high salinity levels such as those in evaporitic rock habitats. Even brief exposure to solar radiation can cause cell death within a few hours [9]. Despite these numerous hurdles for life, researchers have been able to detect the presence of microorganisms in all of Earth's deserts. It has thus become apparent that through a long process of evolution microbes have developed colonization strategies, with their survival in the extreme desert habitat dependent upon a delicate balance between favorable and less favorable conditions. Since any disturbance in this balance could have lethal consequences, these microhabitats generally sustain low levels of biomass [36,51].

The inhospitable conditions of extreme deserts have induced or obliged microbial life to search out the microhabitats
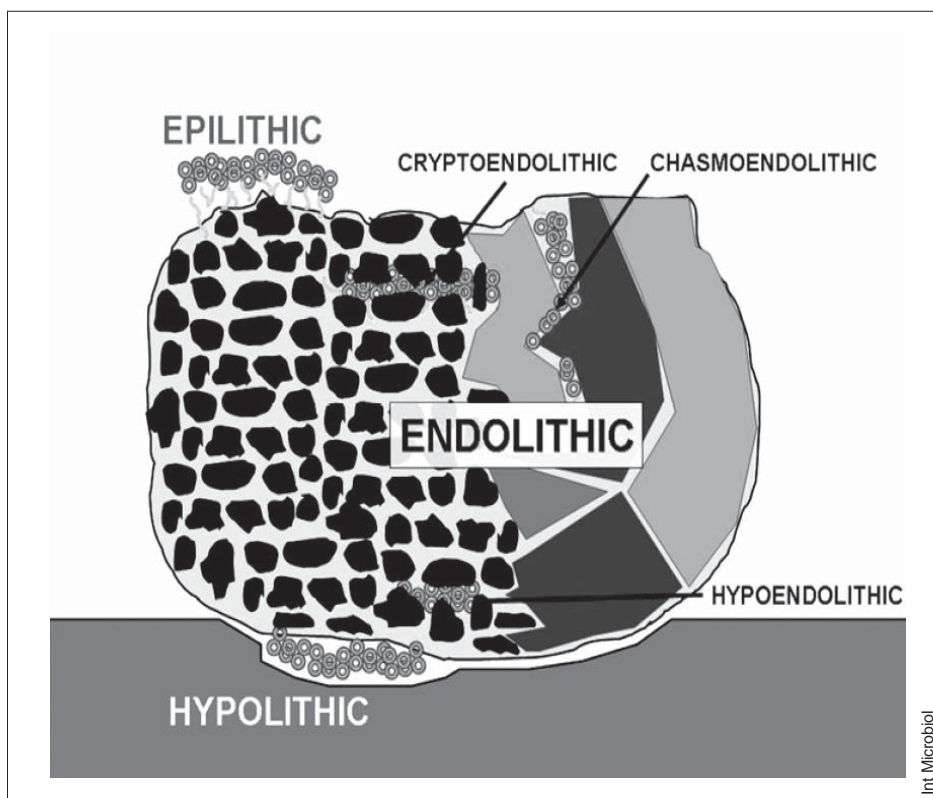
Fig. 2. The diagram indicates the possible lithobiontic habitats of microorganisms. epilithic (rock surface); hypolithic (rock underside in contact with the soil); endolithic (the main habitats of hyper-arid deserts, and further divided into cryptoendolithic, chasmoendolithic and hypoendolithic).

most suitable for life. One of these microhabitats consists of the pores and fissures inside rocks. Thus, in hyper-arid deserts, life is essentially present in the form of microorganisms that take refuge in such endolithic habitats. Beginning with the pioneering studies of Imre E. Friedmann and Rosali Ocampo [e.g., 22] on the endolithic microorganisms of the Antarctic Dry Valleys, it has been established that endolithic habitats normally offer microorganisms better moisture conditions than the outside environment, and that these habitats protect them from high UV radiation and wind and temperature fluctuations, while still allowing the passage of light needed for photosynthesis. In addition, the mineral deposits found in association with endolithic microorganisms create a relatively isolated, closed environment that efficiently recycles nutrients.

The bioreceptivity, or susceptibility, of rocks to endolithic colonization is thought to mainly depend on the physical and chemical properties of the rock substrate [25], including the rock's mineral composition, its permeability, the presence of chemical compounds, the structure and distribution of pores, and other factors such as water retention capacity, pH, and exposure to climate and nutrient sources [10,11,28,32,41]. Lithobiontic microorganisms can grow on the rock surface (epilithic growth), rock underside (hypolithic growth), or inside the rock (endolithic growth) (Fig. 2). According to

Golubic and Nienow [24,40], the endolithic habitat can be subdivided into: (i) cryptoendolithic, consisting of natural pore spaces within the rock that are usually indirectly connected to the rock surface; (ii) chasmoendolithic, consisting of fissures and cracks also connected to the rock surface, and (iii) the recently defined hypoendolithic habitat [58], in which pore spaces are not in contact with the soil but occur on the underside of the rock and make contact with the underlying soil.

Hypolithic colonization

When desert conditions become drier, epilithic microbial life decays and "transfers" to the hypolithic habitat. Hypolithic colonization can be viewed as a stress avoidance strategy whereby the overlying mineral substrate provides protection from incident UV radiation, freeze–thaw events, and excessive photosynthetically active radiation (PAR), as well as thermal buffering and physical stability, while enhancing moisture availability from the surrounding soil [7]. For example, for Mojave Desert hypolithic cyanobacteria maximum photosynthesis rates at low light levels are 200–400 μmol m^{-2} s^{-1}, with lower rates measured at higher light intensities [50].
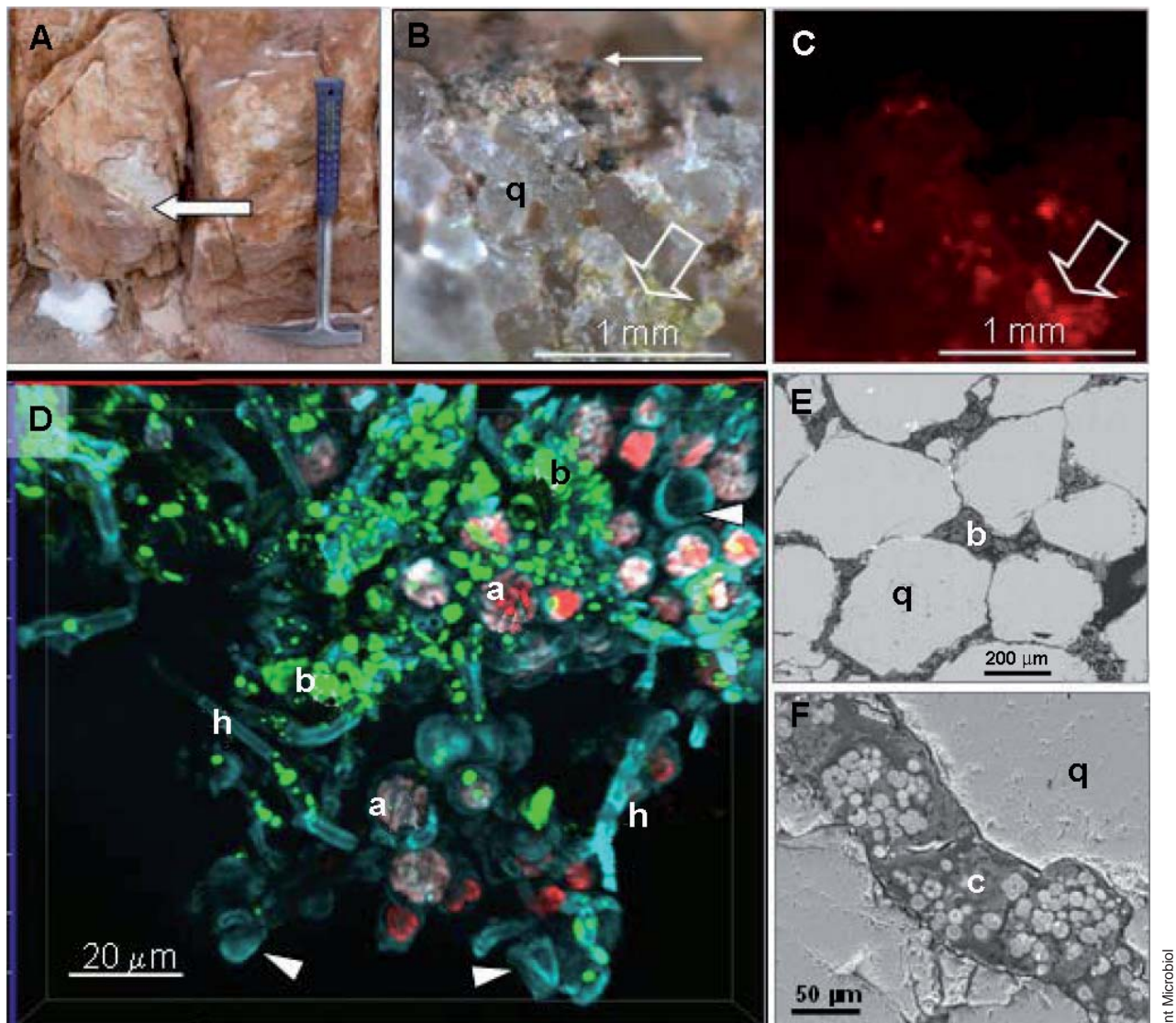
Fig. 3. Endolithic communities found within the sandstones of the University Valle (Dry Valleys, Antarctica). (**A**) Sandstone showing disaggregation of the rock surface due to the physical actions of endolithic microorganisms (the arrow points to a zone of cryptoendolithic colonization). (**B**) Closer view of an endolithic microbial community (open arrow) appearing at a depth of 2 mm from the rock surface (long arrow indicates the rock surface); (**q**) quartz grains. (**C**) Same area as in image (A), visualized by epifluorescence microscopy and showing autofluorescence emitted by phototrophic microorganisms (red signal). (**D**) *In situ* 3-D reconstruction of the microbial community appearing in (B), visualized by epifluorescence microscopy operated in structural illumination microscopy (SIM) mode, where: (**a**) algae (red signal); (**h**) hyphae (blue signal); (**b**) heterotrophic bacteria (green signal due to SYBR Green staining); the arrow heads point to decayed algal remains. (**E**,**F**) *In situ* scanning electron microscopy in backscattered electron mode (SEM-BSE) images of: (**b**) cryptoendolithic, and (**c**) chasmoendolithic associations of algae and hyphae in pores and fissures between quartz grains (**q**).

In the McMurdo Dry Valleys of Antarctica and the Atacama Desert of Chile, unicellular cyanobacteria (frequently species of the genus *Chroococcidiopsis* sp.) take refuge along with filamentous forms, fungi, green algae, and sometimes even diatom algae [12,37,53]. The rock substrate of these hot and cold deserts frequently comprises semitransparent quartz rocks [3,7,33,50,53]. However, hypolithic colonization on the underside of opaque rocks has been also reported, including in the Arctic and Antarctic polar deserts [8]. Indeed, hypolithic microbial colonization is widely present in almost all arid environments. In the Mojave Desert of the southwestern USA, hypolithic colonization covers almost 100 % of the quartz rocks [40]. Despite the importance of hypolithic habitats in arid environments, these are not a main focus of this review.

Endolithic colonization

In some zones of the hyper-arid desert, epilithic and hypolithic habitats are insufficiently "secure" and life takes refuge in the rock interior (Fig. 2). The endolithic environment is extreme and most likely arises from seeding by a relatively small reservoir (metacommunity) of microorganisms highly adapted to this environment [52]. In such endolithic habitats, chasmo- and cryptoendolithic colonization are the predominant modes. Fissures and cracks connected to the surface of rocks form chasmoendolithic habitats. Symbiotic associations of chasmoendolithic lichen have been observed in the fissures and cracks of granites (Fig. 3c) [16], as have chasmoendolithic colonies of cyanobacteria in granites in different zones of the Antarctic Dry Valleys [17].

Cryptoendolithic microorganisms live in the spaces created by pores in rocks. Since microorganisms occupy spaces beneath the rock surface, rocks composed only of translucent grains become colonized by cryptoendolithic phototrophs accompanied by heterotrophs. Cryptoendolithic communities are macroscopically recognizable as a tinted band in the rock interior at a depth of a few millimeters below the surface. Cryptoendoliths have been found in sandstone rocks, granites and meteorized basalts, gneisses, limestones, marbles, porous volcanic rocks, gypsum crusts, and halite. Figure 3 provides examples from the Dry Valleys of the cryptoendolithic colonization of porous sandstones composed of quartz grains (Fig. 3A–F).

Cryptoendolithic communities are perhaps the clearest example of how a biotype is able to avoid climate extremes. These communities were described for the first time in 1976, within porous sandstones of the Dry Valleys region [22], The Dry Valleys, one of Antarctica's largest ice-free areas, are characterized by their extremely cold temperatures and extreme aridity. Their surface mineral soils are extremely dry, with a mass water content typically below 2 %, which is equivalent to the water contents of many of the world's hottest deserts [6]. Precipitation is low, generally <100 mm/yr water equivalents, and always in the form of snow, much of which sublimes before reaching the soils. One of the most outstanding features of cryptoendolithic associations is their complexity and diversity. The most abundant is the community dominated by cryptoendolithic lichens [20], sometimes accompanied by colonies of melanized fungi and heterotrophic bacteria [14]. Black fungi also have been isolated as members of lichen-dominated cryptoendolithic communities [49]. Also present in the cryptoendolithic sandstone habitat are colonies of cyanobacteria of different genera, such as *Chroococcidiopsis* and *Gloeocapsa,* along with free-living algae [23,47].

The connected pore network and translucent properties of the lithic substrate are sufficient for endolithic colonization of an extremely dry environment. Thus, small mixed communities of phototrophic cyanobacteria, heterotrophic bacteria, and fungi have been described in the Antarctic Peninsula, within translucent gypsum crusts [29]. The cryptoendolithic colonization of gypsum crusts by cyanobacteria and non-photosynthetic bacteria has been also described in arid desert areas in Jordan, Tunisia, and the Mojave and Atacama Deserts [19]. An abundance of diverse cryptoendolithic colonizations was recently found within crusts composed of gypsum and anhydrite in the hyper-arid core of the Atacama Desert [58]. This ecosystem contains associations of algae and fungi as well as non-lichenized algae, melanized fungi, cyanobacteria, and non-photosynthetic bacteria. In some of these crusts, novel observations have been made of the colonization of hypoendolithic habitats by associations of algae and fungi (Fig. 4A,B). However, in the same desert, there are areas of extreme aridity where gypsum crusts lack apparent signs of any colonization, nor is there any evidence of hypolithic colonization [53]. While after several years of research, this zone of the Atacama Desert, called Yungay, was considered an absolute limit for photosynthetic life [39,53], later studies conducted in this area generated surprising results regarding the microbial ecology of extreme and hyper-arid environments.

In the study by Wierzchos et al. [57], the presence of photosynthetic microbial life was detected in an environment as harsh as the interior of evaporite rocks composed of sodium chloride (halite), at a site that is possibly the driest in the world (Fig. 4C–E). Molecular biology analyses of these endolithic communities revealed that cyanobacteria are the dominant microorganisms and that they are accompanied by heterotrophic bacteria and archaea [18]. The ribosomal RNA gene sequence of these microorganisms indicates that in most cases they are as yet undescribed but are closely related to microbial forms inhabiting other hypersaline environments. These endolithic communities have been detected 3–7 mm below the surface of the halites of Yungay, distributed in the pores and inner fractures of the rocks. The halites of other hyper-arid sites of the Atacama Desert (Salar Llamara and Salar Grande) are colonized as well [18], but in a more dispersed manner and even in deep subsurface zones [26,44].

Hence, not only evaporite rocks in the hyper-arid environment of the Atacama Desert serve as a refuge for endolithic microbial life. Besides halites, it has recently
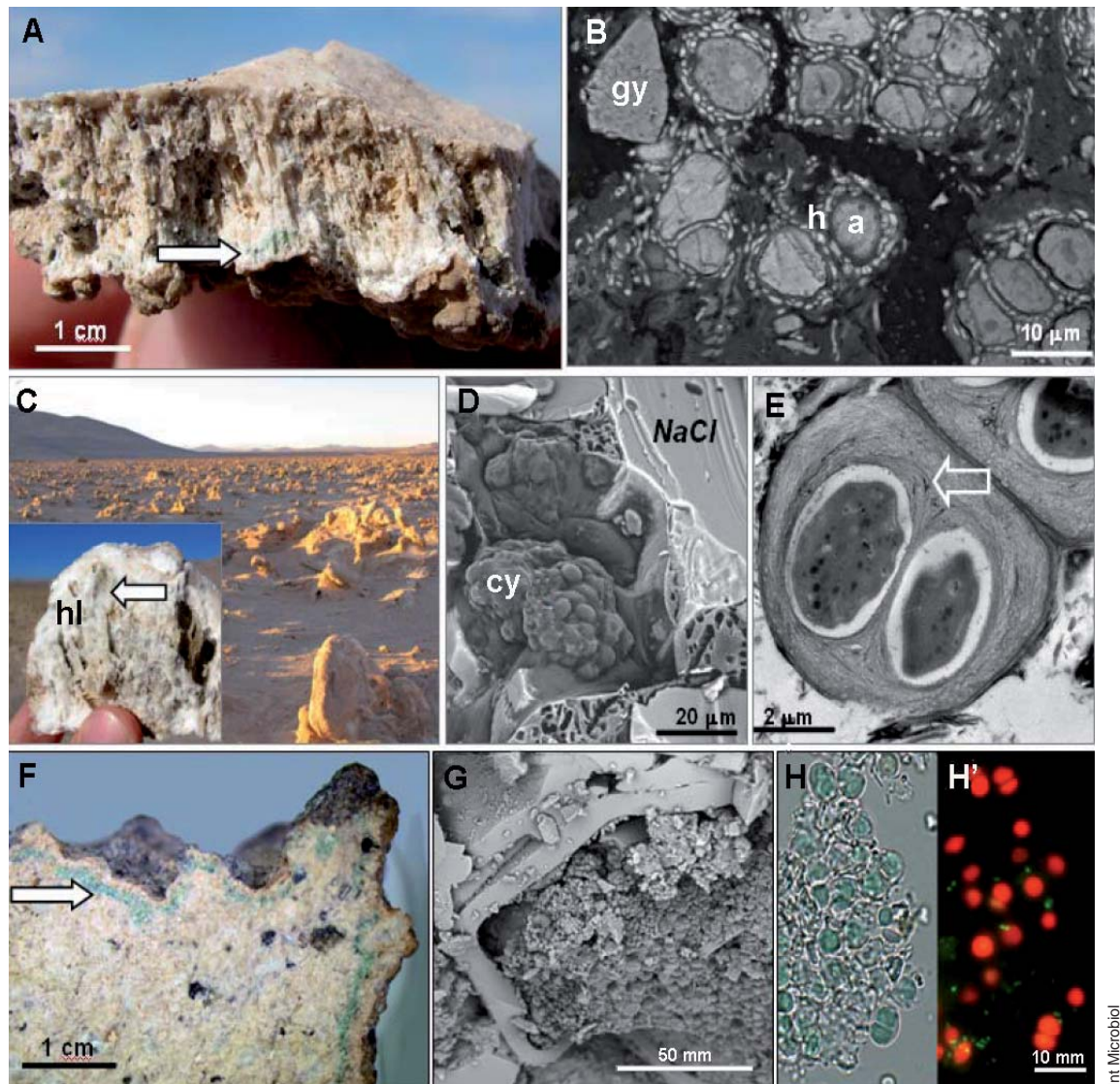
Fig. 4. Endolithic communities found within lithic habitats in the Atacama Desert (Chile); (**A,B**) Hypoendolithic communities within gypsum crusts (the arrow indicates the fractured gypsum crust showing a green colonization zone) and *in situ* SEM-BSE (scanning electron microscopy in backscattered electron mode) image of an association of algae (**a**) and fungal hyphae (**h**), among gypsum crystals (**gy**). (**C–E**) Cryptoendolithic communities within halite (NaCl) rocks: (**C**) landscape of the Yungay zone showing halite deposits and a fractured piece of halite (**hl**) bearing a greyish colonization zone indicated by the arrow; (**D**) *in situ* LT-SEM (low temperature SEM) micrograph showing cyanobacteria (**cy**) living among halite crystals; (**E**) TEM image showing cyanobacterial cells embedded in a thick extracellular polymeric substances (EPS) layer (open arrow). (**F–H**) Cryptoendolithic communities within volcanic (ignimbrite) rock: (**F**) stereoscopic microscopy view of ignimbrite revealing a green layer of endolithic microorganisms beneath the rock surface (arrow); (**G**) LT-SEM image of a bottle-shaped pore close to the ignimbrite surface totally filled with microorganisms; (**H**) bright-field image of cyanobacterial cells extracted from the cryptoendolithic community; (**H'**) fluorescence microscopy image of the same aggregate revealing cyanobacterial aggregates (red autofluorescence) and associated heterotrophic bacteria (SYBR Green stained DNA structures).

been discovered that volcanic rocks, specifically, the weakly-welded rhyolitic ignimbrites, harbor within large viable cryptoendolithic communities of cyanobacteria and heterotrophic bacteria [59] (Fig. 4F–H). In these rocks, endolithic aggregates colonize vesicle pores and spaces between glass shards to an average depth of 1–2 mm beneath the ignimbrite surface. As with other porous rock substrates, the ignimbrite habitat helps to retain moisture after a wetting event, in addition to absorbing harmful UV radiation and attenuating the PAR fraction of light. Maximum penetration

of cryptoendolithic microorganisms in the ignimbrite fabric is likely a compromise between these factors and the maximum penetration of photosynthetic light. In colonized ignimbrite the main source of liquid water is sporadic rainfall events such that <100 h of photosynthetic activity is possible over a year [59]. Hence, ignimbrite endoliths in this region rank amongst the microorganisms best adapted to withstand long periods of desiccation, and they are able to resume metabolic activity shortly after a wetting event. The dominance in the community structure of *Chroococcidiopsis* sp., a cyanobacterium well known for its desiccation tolerance, supports this claim. This is the first known example of an endolithic microbial community colonizing rocks of volcanic origin in an extremely dry environment.

A similar simple endolithic ecosystem within sandstone rocks was described several decades ago in the southern Negev Desert of Israel [21]. In his pioneering work, E.I. Friedmann examined the microbiota of Nubian sandstone cliffs close to Timna Park (Negev). Understanding the important role played by cyanobacteria in this habitat, Friedmann hypothesized that, owing to the crust formed, the microclimate in the rock interior could differ from the outside climate. Friedmann was the author of papers revealing the existence of microbial ecosystems inside rocks, i.e., endolithic colonization. He discovered cryptoendolithic cyanobacteria, primarily *Chroococcidiopsis* sp., and heterotrophic bacteria forming a green layer up to 2 mm thick, located less than 1 mm below the sandstone rock surface [21]. Endolithic prokaryotes seem best adapted to survive the temperature fluctuations and nearly continuous drought that characterize this extreme, hot desert habitat. They are capable of 'switching' their metabolic activities on and off in response to rapid changes in environmental conditions. According to long-term measurements in the Negev Desert, average rainfall is less than 20 mm/yr [31]; instead, fog and dew seem to be frequent and relatively abundant sources of liquid water for microbial lithobiontic colonization in this desert [34].

Main microbial colonizers of endolithic habitats

Endolithic communities from hyper-arid environments comprise microorganisms in different physiological states. Living and dead photosynthetic and non-photosynthetic microorganisms are found in the communities [15,55]. Microbial death, extinction, and fossilization are common phenomena in endolithic Antarctic communities [2,56]. Unexpectedly,

microhabitats with very different microclimate conditions and substrates host a variety of similar eukaryotic microorganisms with similar spatial relations. For example, algal and fungal associations have been observed in endolithic microhabitats in the granite rocks of maritime Antarctica [1] and the Ross Sea Coast [2]. This same association has also been detected in gypsum crusts of the hyper-arid core of the Atacama Desert [58] and in limestone at a high-altitude arid site in Tibet [62]. The authors of the latter study reported that endoliths were dominated by eukaryotic phylotypes suggestive of lichenized associations. In contrast, several studies have indicated that the endolithic communities of arid and hyperarid deserts comprise relatively simple communities dominated by cyanobacteria, with some heterotrophic components [5,15,18,19,29,57]. According to these works, Archaea and Eukaryotes may be absent or present in low abundance when endolithic communities are dominated by cyanobacteria.

Although the natural habitat of the Negev Desert is nearly always dry, experiments on *Chroococcidiopsis* sp. isolated from this hyper-arid region have shown that this cyanobacterium incorporates CO_2 only when matric water potentials are above 10 MPa (equivalent to RH > 93 %) [48]. In contrast to the simple endolithic ecosystems found in hot deserts (Atacama and Negev), a much more complex community exists within sandstone and granite rocks from the Dry Valleys (Antarctica). These ecosystems in cold deserts are frequently composed of different types of microorganisms, including endolithic lichens with eukaryotic photobionts (family Chlorophyceae), although with disorganized thalli, but they host few cyanobacteria [1,2]. Ecosystems in the Negev and Atacama are, nevertheless, simpler, with a predominance of cyanobacteria [42] and sometimes even the presence of epilithic cyanolichens (C. Ascaso, personal communication). This is because hot deserts are more hostile for endolithic microbial life. Our molecular biology and in situ microscopy approaches (SEM-BSE, TEM, FM and CLSM) to the study of endolithic ecosystems colonizing sandstone in the Negev Desert (Timna Park) have confirmed previous results in addition to revealing the presence of primary producers (*Chroococcidiopsis* sp.) living within sandstone rocks (Fig. 5).

Moisture as the key abiotic driver

The irregular system of pores and natural fissures of a rock provides an efficient protective network for microorganisms and creates a place for the absorption, condensation, and retention of water [52]. Studies conducted in both cold and hot
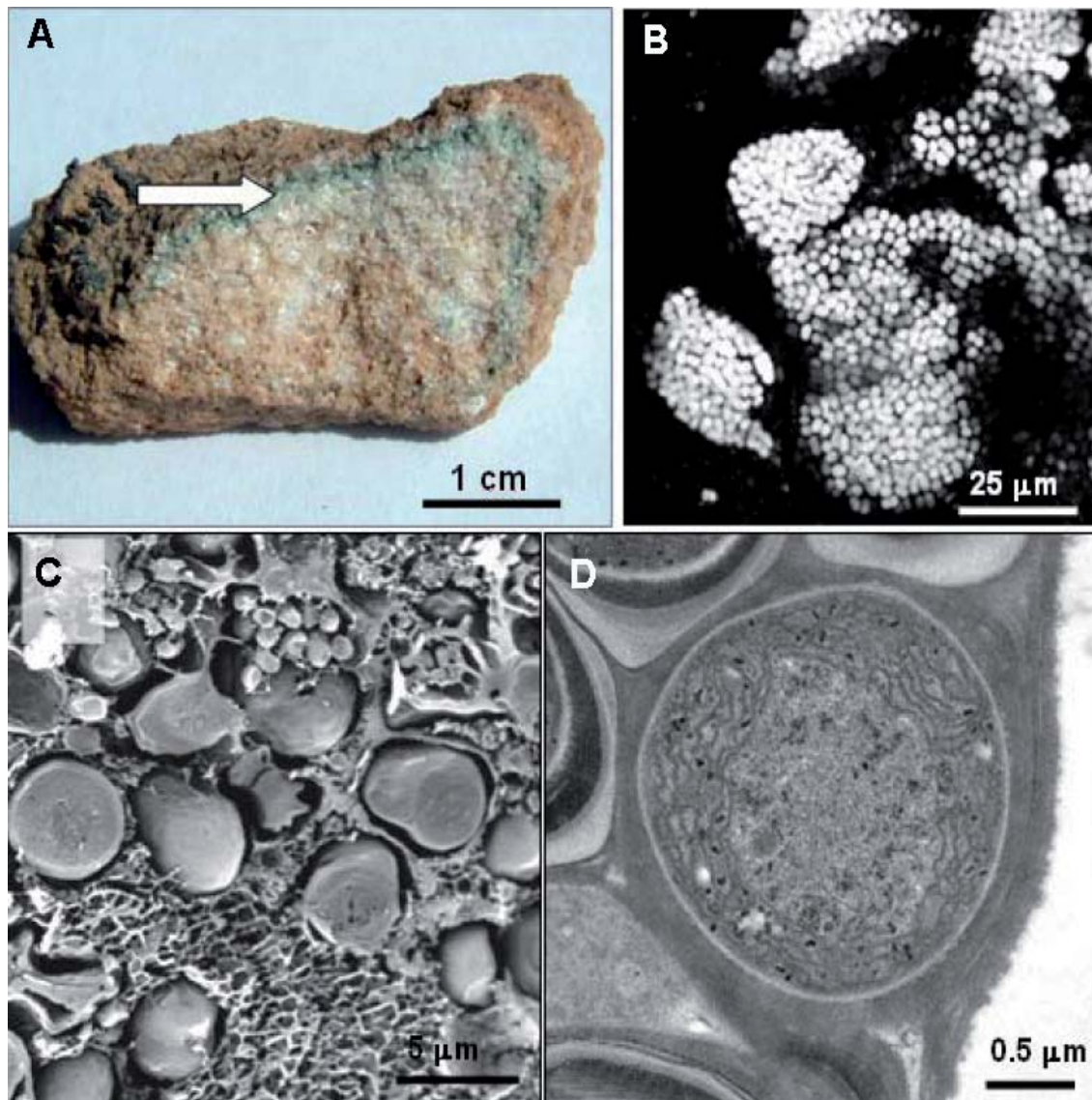
Fig. 5. Cryptoendolithic communities within sandstone from the Negev Desert (Israel). (**A**) Fractured sandstone from Timna Park, with a greenish colonization zone running parallel to the surface indicated by the arrow. (**B**) *In situ* confocal laser scanning microscopy (CLSM) image of cyanobacterial colonies forming aggregates. (**C**) *In situ* low temperature SEM (LT-SEM) showing cryofractured cyanobacteria. (**D**) Transmission electron microscopy (TEM) image of a cyanobacterial (*Chroococcidiopsis*) cell, in which thylakoids can be seen.

deserts have shown that their microbial communities are well-adapted to withstand long periods of desiccation followed by brief episodes of rehydration, and that they can resume their metabolic activity within minutes of rehydration. A study on the microbial communities of the Negev Desert showed that night-time hydration by dew activates respiration ,which continues after daybreak until metabolic inactivation caused by desiccation occurs [38]. However, those authors observed that with cyanobacteria serving as the photobiont, and some free-living cyanobacteria, some dehydrated lichens were

unable to reactivate their photosynthetic metabolism simply by their hydration under conditions of high air humidity. This was indeed the case for *Microcoleous sociatus* inhabiting the soil crust of the Negev Desert. Notwithstanding, it was noted that desiccated populations of cultures of the same organism achieve turgor and are capable of photosynthesis at a RH of 96 % [38]. To date, little is known about the photosynthetic properties of endolithic lichens. Wessels and Kappen [54] measured the photosynthetic properties of endo- and epilithic lichens on sandstone (South Africa) and correlated them with

local microclimate conditions. Lichens were found to be particularly well-adapted to the extremely varying conditions in which they occurred. In arid and semi-arid regions, water is the key environmental factor limiting photosynthesis [54,61]. In contrast, the photosynthetic properties of endolithic sandstone lichens in the cold desert of Antarctica are mainly limited by low temperatures [30].

Liquid water, with its corresponding water activity index $a_w = 1$, is essential for cell rehydration processes. However, for several decades the possibility has been considered that microorganisms are able to survive under conditions in which a_w indices are below 1 (down to 0.61), corresponding to an air RH of 61–100 %. The mechanisms used by microorganisms to survive such as low levels of a_w (or RH) are still not fully understood. Thus, RH values much below 100 % (at which there is no water condensation) may also trigger the metabolic activity of phototrophic microorganisms. For example, the cryptoendolithic lichens that inhabit sandstones of the Dry Valleys start photosynthesis at RH levels ≥70 % [42], and cultured algae (*Trebouxia* sp.) are capable of photosynthesis at a RH of 80 % [43]. However, like other prokaryotes, to carry out photosynthesis, endolithic cyanobacteria inhabiting the sandstones of the Negev Desert require a relatively high RH, in excess of 90 % [42]. It has been recently shown that a high air RH in a hyper-arid zone of the Atacama Desert induces the abundant endolithic (but also epilithic) colonization of crusts of calcium sulfate (gypsum) [58]. In contrast, a low yearly RH in another area of the Atacama results in the virtual absence of colonization of the same substrate. Thus, there is now mounting evidence that some microbial communities in arid zones absorb and retain water vapor, and not only liquid water. Nienow [40] has described an "imbibition" process whereby endolithic microorganisms in the Negev Desert are able to absorb water, causing them to swell. According to that study, 300–450 h yr^{-1} of such imbibing supports colonization by endolithic lichens, whereas below this value endolithic habits are only colonized by the fungus *Lichenothelia* sp., associated with cyanobacteria and eukaryotic algae.

In some of the hyper-arid zones of the Atacama Desert, one rainfall event can be separated from the next by several years such that scarce liquid water in the form of precipitations cannot be a source of water for microorganisms. However, high night-time RH levels along with low temperatures could give rise to dew/water vapor condensation on rock surfaces. Kidron [35] has speculated on the role played by dew in desert zones, while Büdel et al. [5] have been able to simulate the amount of water condensed on endolithically colonized granite rock surfaces in the Dry Valleys. These authors have found that the

intensity of dew and therefore the quantity of condensed water depends on the dew point, not of the air, but of the material on which the water condenses, which in turn is determined by its heat conductivity properties. As the consequence of dew/condensation and also sometimes of fog, in some hyper-arid desert zones with occasionally high RHs, it is possible to find epilithic colonizations composed mainly of lichens. In fact, epilithic lichens have been found in the more humid areas of the Negev Desert and recently in some zones of the Atacama Desert, where they colonize gypsum crusts [58]. Lichens are symbiotic associations comprising a photobiont (phototrophic microorganism) and a fungus (mycobiont) that sometimes take the form of a lichen thallus. Lichen thalli designated as heteromeric generally have a superior cortex, and their structure is conducive to maintaining a humid environment within the thallus. Consequently, the photobiont's cells may be hydrated for a sufficiently long period of time to trigger the metabolic activity of the symbionts as a water-retaining strategy.

In the case of hygroscopic minerals such as halite, a night-time rise in RH to above 75 % might lead to deliquescence, which would provide liquid water for an endolithic microbial community [13]. When the deliquescence RH is reached, water vapor condenses as a saturated aqueous solution on the surfaces of the crystals and/or the pores among the crystals. It is this water per se or its evaporation within the rock that promotes the hydration of endolithic colonies. Condensation and the build up of water inside the halites normally occur at sunrise, such that the water and light necessary for photosynthesis are simultaneously provided. However, the sporadic nature of deliquescence events makes this environment one of the most surprising and extreme for life on Earth.

Interesting data on novel water sources for endolithic life in the hyper-arid zone of the Atacama Desert have been recently reported by Wierzchos et al. [60], who have shown that halite endoliths can obtain liquid water through spontaneous capillary condensation at RHs much lower than the deliquescence RH of NaCl. This condensation could occur inside nano-pores smaller than 100 nm in a newly characterized halite phase that is intimately associated with the endolithic aggregates. This nano-porous phase helps to retain liquid water for longer periods of time by preventing its evaporation even in extremely dry air conditions. While conditions outside the halite pinnacles were shown to always be extremely dry, the pinnacle interior was found to remain wet for 5362 h yr^{-1}, with pore water brine available to endolithic microorganisms during 61 % of the year.

Endoliths as targets for the search for life outside our planet

Life has developed strategies that have allowed organisms to survive in physically and chemically hostile environments. Extremely dry deserts are a good place to investigate the limits of life on our planet and therefore the strategies used by microorganisms to adapt to such conditions. The study of extreme microbial ecosystems can provide us with important clues to the history of life on Earth and perhaps in other places in our solar system. Deserts are important reservoirs of diversity. The strategies developed by living organisms to adapt to conditions of scarce water availability and climate change over time enrich the biota in endemic taxa that do not exist in other terrestrial ecosystems. The life and death of microorganisms and their biosignatures may bear excellent witness to past and present climate changes [2]. Scientists have long acknowledged the need to better understand the limits of life on Earth before undertaking searches for life beyond our planet: we cannot identify what we do not recognize. The existence of habitats capable of supporting abundant phototrophic and heterotrophic communities in an environment that precludes most life forms suggests that, if similar habitats were to be found on Mars, these should be considered important targets for the search for life. Indeed, chloride- and sulfate-bearing deposits have been recently discovered in many areas of Mars. In fact, the ignimbrite rocks tentatively identified in Gale Crater, the landing site of the Mars Science Laboratory (MSL) mission, might be an interesting target for its rover, *Curiosity*.

Competing interests. None declared.

References

1. Ascaso C, Wierzchos J (2002) New approaches to the study of Antarctic lithobiontic microorganisms and their inorganic traces, and their application in the detection of life in Martian rocks. Int Microbiol 5:215-222
2. Ascaso C, Wierzchos J (2003) The search for biomarkers and microbial fossils in Antarctic rock microhabitats. Geomicrobiol J 20:439-450
3. Azúa-Bustos A, González-Silva C, Mancilla RA, Salas L, Gómez-Silva B, McKay CP, Vicuña R (2011) Hypolithic cyanobacteria supported mainly by fog in the Coastal Range of the Atacama Desert. Microb Ecol 61:568-581
4. Billi D, Potts M (2002) Life and death of dried prokaryotes. Res Microbiol 153:7-12
5. Büdel B, Bendix J, Bicker FR, Allan TG (2008) Dewfall as a water source frequently activates the endolithic cyanobacterial communities in the granites of Taylor Valley, Antarctica. J Phycol 44:1415-1424
6. Cary SC, McDonald IR, Barrett JE, Cowan DA (2010) On the rocks: The microbiology of Antarctic Dry Valley soils. Nat Rev Microbiol 8:129-138
7. Chan Y, Lacap DC, Lau MCY, Ha KY, Warren-Rhodes KA, Cockell CS, Cowan DA, McKay CP, Pointing SB (2012) Hypolithic microbial communities: Between a rock and a hard place. Environ Microbiol 14:2272-2282
8. Cockell CS, Stokes MD (2006) Hypolithic colonization of opaque rocks in the Arctic and Antarctic polar desert. Arctic Antarctic Alpine Res 38:335-342
9. Cockell CS, McKay CP, Warren-Rhodes K, Horneck G (2008) Ultraviolet radiation-induced limitation to epilithic microbial growth in arid deserts—Dosimetric experiments in the hyperarid core of the Atacama Desert. J Photochem Photobiol B: Biology 90:79-87
10. Cockell CS, Olsson-Francis K, Herrera A, Meunier A (2009a) Alteration textures in terrestrial volcanic glass and the associated bacterial community. Geobiology 7:50-65
11. Cockell CS, Olsson K, Knowles F, Kelly L, Herrera A, Thorsteinsson T, Marteinsson V (2009b) Bacteria in weathered basaltic glass, Iceland. Geomicrobiol J 26:491-507
12. Cowan DA, Khan N, Pointing SB, Cary C (2010) Diverse hypolithic refuge communities in the McMurdo Dry Valleys. Antarctic Sci 22:714-720
13. Davila AF, Gomez-Silva B, de los Ríos A, Ascaso C, Olivares H, McKay CP, Wierzchos J (2008) Facilitation of endolithic microbial survival in the hyperarid core of the Atacama Desert by mineral deliquescence. J Geophys Res Biogeosci 113 G01028. DOI: 10.1029/2007JG000561
14. de la Torre JR, Goebel BM, Friedmann EI, Pace NR (2003) Microbial diversity of cryptoendolithic communities from the McMurdo Dry Valleys, Antarctica. Appl Environ Microbiol 69:3858-3867
15. de los Ríos A, Wierzchos J, Sancho LG, Ascaso C (2004) Exploring the physiological state of continental Antarctic endolithic microorganisms by microscopy. FEMS Microbiol Ecol 50:143-152
16. de los Ríos A, Wierzchos J, Sancho LG, Green TGA, Ascaso C (2005) Ecology of endolithic lichens colonizing granite in continental Antarctica. Lichenology 37:383-395
17. de los Ríos A, Grube M, Sancho LG, Ascaso C (2007) Ultrastructural and genetic characteristics of endolithic cyanobacterial biofilms colonizing Antarctic granite rocks. FEMS Microbiol Ecol 59:386-395
18. de los Ríos A, Valea S, Ascaso C, Davila A, Kastovsky J, McKay CP, Gómez-Silva B, Wierzchos J (2010) Comparative analysis of the microbial communities inhabiting halite evaporites of the Atacama Desert. Int Microbiol 13:79-89
19. Dong H, Rech JA, Jiang H, Sun H, Buck BJ (2007) Endolithic cyanobacteria in soil gypsum: occurences in Atacama (Chile), Mojave (United States), and Al-Jafr Basin (Jordan) Deserts. J Geophys Research G: Biogeosci 112 G02030. DOI: 101029/2006JG000385
20. Friedmann EI (1981) Endolithic microorganisms in the Dry Valleys of Antarctica. Antarctic J USA 16:174-175
21. Friedmann EI, Lipkin Y, Ocampo R (1967) Desert algae of the Negev (Israel). Phycologia 6:185-196
22. Friedmann EI, Ocampo R (1976) Endolithic blue green algae in the Dry Valleys: primary producers in the Antarctic desert ecosystem. Science 193:1247-1249
23. Friedmann EI, Hua M, Ocampo-Friedmann R (1988) Cryptoendolithic lichen and cyanobacterial communities of the Ross Desert, Antarctica. Polarforschung 58:251-259

24. Golubic S, Friedmann EI, Schneider J (1981) The lithobiontic ecological niche, with special reference to microorganisms. J Sediment Petrol 51:475-478

25. Guillitte O (1995) Bioreceptivity: a new concept for building ecology studies. Sci Total Environ 167:215-220

26. Gramain A, Díaz GC, Demergasso C, Lowenstein TK, McGenity TJ (2011) Archaeal diversity along a subterranean salt core from the Salar Grande (Chile). Environ Microbiol 13:2105-2121

27. Harel Y, Ohad I, Kaplan A (2004) Activation of photosynthesis and resistance to photoinhibition in cyanobacteria within biological desert crust. Plant Physiol 136:3070-3079

28. Herrera A, Cockell CS, Self S, Blaxter M, Reitner J, Thorsteinsson T, Arp G, Dröse W, Tindle AG (2009) A cryptoendolithic community in volcanic glass. Astrobiology 9:369-381

29. Hughes KA, Lawley B (2003) A novel Antarctic microbial endolithic community within gypsum crusts. Environ Microbiol 5:555-565

30. Kappen L, Friedmann EI (1983) Ecophysiology of lichens in the Dry Valleys of Southern Victoria Land, Antarctica. II. CO_2 gas exchange in cryptoendolithic lichens. Polar Biol 1:227-232

31. Katznelson I (1958) Rainfall in Palestine. Meterol Papers 8:37-70 (in Hebrew)

32. Kelly LC, Cockell CS, Herrera-Belaroussi A, Piceno Y, Andersen G, DeSantis T, Brodie E, Thorsteinsson T, Marteinsson V, Poly F, LeRoux X (2011) Bacterial diversity of terrestrial crystalline volcanic rocks, Iceland. Microb Ecol 62:69-79

33. Khan N, Tuffin M, Stafford W, Cary C, Lacap DC, Pointing SB, Cowan D (2011) Hypolithic microbial communities of quartz rocks from Miers Valley, McMurdo Dry Valleys, Antarctica. Polar Biol 34:1657-1668

34. Kidron GJ (1999) Altitude dependent dew and fog in the Negev Desert, Israel. Agricul Forest Meteorol 96:1-8

35. Kidron G (2000) Microclimate control upon sand microbiotic crusts, western Negev Desert, Israel. Geomorphology 36:1-18

36. Kuhlman KR, Venkat P, La Duc MT, Kuhlman GM, McKay CP (2008) Evidence of a microbial community associated with rock varnish at Yungay, Atacama Desert, Chile. J Geophys Res Biogeosci 113, G04022. DOI: 10.1029/2007JG000677

37. Lacap DC, Warren-Rhodes KA, McKay CP, Pointing SB (2011) Cyanobacteria and chloroflexi-dominated hypolithic colonization of quartz at the hyper-arid core of the Atacama Desert, Chile. Extremophiles 15:31–38

38. Lange OL, Meyer A, Büdel B (1994) Net photosynthesis activation of a desiccated cyano-bacterium without liquid water in high air humidity alone. Experiments with *Microcoleus sociatus* isolated from a desert soil crust. Functional Ecol 8:52-57

39. Navarro-González R, Rainey FA, Molina P, Bagaley DR, Hollen BJ, De La Rosa J, Small AM, Quinn RC, Grunthaner FJ, Cáceres L, Gomez-Silva B, McKay CP (2003) Mars-like soils in the Atacama Desert, Chile, and the dry limit of microbial life. Science 302:1018-1021

40. Nienow JA (2009) Extremophiles: dry environments (including cryptoendoliths). In: Encyclopedia of Microbiology. Elsevier, Oxford, pp 159-173

41. Omelon CR, Pollard WH, Grant Ferris F (2007) Inorganicb species distribution and microbial diversity within high Arctic cryptoendolithic habitats. Microb Ecol 54:740-752

42. Palmer RJ, Friedmann EI (1990) Water relations and photosynthesis in the cryptoendolithic microbial habitat of hot and cold deserts. Microb Ecol 19: 111-118

43. Palmer RJ, Friedmann EI (1990) Water relations, thallus structure and photosynthesis in Negev Desert lichens. New Phytol 116:597-603

44. Parro V, De Diego-Castilla G, Moreno-Paz M, et al. (2011) A microbial oasis in the hypersaline Atacama subsurface discovered by a life detector chip: Implications for the search for life on Mars. Astrobiology 11:969-996

45. Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrol Earth System Sci 11:1633-1644

46. Pointing SB, Belnap J (2012) Microbial colonization and controls in dryland systems. Nat Rev Microbiol 10:551-562

47. Pointing SB, Chan Y, Lacap DC, Lau MCY, Jurgens JA, Farrell RL (2009) Highly specialized microbial diversity in hyper-arid polar desert. Proc Natl Acad Sci USA 106:19964-19969

48. Potts M, Friedmann EI (1981) Effects of water stress on cryptoendolithic cyanobacteria from hot desert rocks. Arch Microbiol 130:267-271

49. Ruisi S, Barreca D, Selbmann L, Zucconi L, Onofri S (2007) Fungi in Antarctica. Rev Environ Sci Biotech 6:127-141

50. Schlesinger WH, Pippen JS, Wallenstein MD, Hofmockel KS, Klepeis DM, Mahall BE (2003) Community composition and photosynthesis by photoautotrophs under quartz pebbles, southern Mojave Desert. Ecology 84:3222-3231

51. Vestal JR (1988) Biomass of the cryptoendolithic microbiota from the Antarctic desert. Appl Environ Microbiol 54:957-959

52. Walker JJ, Pace NR (2007) Endolithic microbial ecosystems. Annu Rev Microbiol 61:331-347

53. Warren-Rhodes KA, Rhodes KL, Pointing SB, Ewing SA, Lacap DC, Gómez-Silva B, Amundson R, Friedmann EI, McKay CP (2006) Hypolithic cyanobacteria, dry limit of photosynthesis, and microbial ecology in the hyperarid Atacama Desert. Microbial Ecol 52:389-398

54. Wessels D, Kappen L (1994) Aspect, microclimate and photosynthetic activity of lichens in the northern Transvaal and Karoo, South Africa. Cryptogamic Bot 4:242-253

55. Wierzchos J, de los Ríos A, Sancho LG, Ascaso C (2004) Viability of endolithic micro-organisms in rocks from the McMurdo Dry Valleys of Antarctica established by confocal and fluorescence microscopy. J Microsc 216:57-61

56. Wierzchos J, Sancho LG, Ascaso C (2005) Biomineralization of endolithic microbes in rocks from the McMurdo Dry Valleys of Antarctica: implications for microbial fossil formation and their detection. Environ Microbiol 7:566-575

57. Wierzchos J, Ascaso C, McKay CP (2006) Endolithic cyanobacteria in halite rocks from the hyperarid core of the Atacama Desert. Astrobiology 6:415-422

58. Wierzchos J, Cámara B, de los Ríos A, Dávila AF, Sánchez Almazo IM, Artieda O, Wierzchos K, Gómez-Silva B, McKay CP, Ascaso C (2011) Microbial colonization of Ca-sulfate crusts in the hyperarid core of the Atacama Desert: implications for the search for life on Mars. Geobiology 9:44-60

59. Wierzchos J, Davila AF, Artieda O, Cámara-Gallego B, de los Ríos A, Nealson KH, Valea S, Teresa García-González M, Ascaso C (2012) Ignimbrite as a substrate for endolithic life in the hyper-arid Atacama Desert: Implications for the search for life on Mars. Icarus. DOI: 10.1016/j.icarus.2012.06.009

60. Wierzchos J, Sanchez-Almazo IM, Hajnos M, Swieboda R, Ascaso C (2012) Novel water source for endolithic life in the hyperarid core of the Atacama Desert. Biogeosciences 9:2275-2286

61. Winkler JB, Kappen L (1997) Photosynthetic capacity of endolithic lichens from South-Africa. In: Kappen L (ed) New species and novel aspects in ecology and physiology of lichens. In Honour of O. L. Lange. Bibliotheca Lichenologica Cramer J. Berlin, Stuttgart, pp 165-181

62. Wong F, Lau M, Lacap D, Aitchison J, Cowan D, Pointing S (2010) Endolithic microbial colonization of limestone in a high-altitude arid environment. Microb Ecol 59:689-699