



Review

Life at the dry edge: Microorganisms of the Atacama Desert

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ABSTRACT

The Atacama Desert, located in northern Chile, is the driest and oldest Desert on Earth. Research aimed at the understanding of this unique habitat and its diverse microbial ecosystems begun only a few decades ago, mainly driven by NASA's astrobiology program. A milestone in these efforts was a paper published in 2003, when the Atacama was shown to be a proper model of Mars. From then on, studies have been focused to examine every possible niche suitable for microbial life in this extreme environment. Habitats as different as the underside of quartz rocks, fumaroles at the Andes Mountains, the inside of halite evaporates and caves of the Coastal Range, among others, have shown that life has found ingenious ways to adapt to extreme conditions such as low water availability, high salt concentration and intense UV radiation.

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1. Introduction

By definition a “desert” is a region that receives extremely low rains, far less than the amount required to support the growth of most plants. The majority of Earth's deserts have average annual rains (AAR) of less than 400 mm per year. This is the case of the Kalahari and Mojave Deserts, which receive 250 and 330 mm of AAR, respectively. In turn, “true deserts” receive less than 250 mm of AAR. The Gobi and the Sahara Deserts, with AAR of 194 mm and 20–100 mm, respectively, classify in this category. The special category of “hyperarid” is assigned to those deserts possessing aridity indexes lower than 0.05. This implies that their ratios between AAR and potential evapotranspiration are extremely low.

Among the latter is the Atacama Desert. Located between 17° and 27°S latitude in northern Chile, it is bordered on the east by the Andes Mountains and on the west by the Coastal Range. With AAR of less than 2 mm, in extensive areas of the Atacama even the sturdiest plants cannot grow (Fig. 1A).

As part of the NASA's Astrobiology program, McKay's group collected data (temperature, relative humidity, rains, sun irradiation and winds) that contributed to better understand the origin of the Atacama dryness [1]. The rationale was to focus on the moisture sources and their role in creating suitable environments for photosynthetic microorganisms. They found that during a four-year period, the average air temperature had been 16.5 °C, with recorded extremes of −6 °C and 38 °C. Annual average sunlight

was about 336 Wm^{−2} and winds averaged a few meters per second. Strikingly, during the measured period only one rain event was recorded. This event, of only 2.3 mm, led the authors to suggest that it may have corresponded to a rainout of a heavy fog. Dews were frequently recorded following nights of high relative humidity, but they did not contribute much to the moisture of the soil surface. They also concluded that groundwater did not contribute to surface moisture. Additional work by Houston and Hartley contributed to classify the Atacama as a hyperarid desert [2]. These authors proposed that the west slope of the central Andes exhibits a pronounced rain shadow effect, causing a core zone of hyper-aridity which extends from 15 to 30 °S, at elevations from sea level up to 3500 m. They also suggested that the initial onset of hyper-aridity most likely developed progressively with the uplift of the Andes as these mountains reached elevations between 1000 and 2000 m above sea level, coupled with the intensification of a cold, upwelling Peruvian Current about 10–15 million years ago.

The Atacama has been proposed to be the oldest desert on Earth. Based on palaeomagnetic data, Hartley et al. found no significant latitudinal movement since the late Jurassic, 150 million years ago [3]. This property, along with the location of the Atacama within the dry subtropical climate belt and the presence offshore of a cold, upwelling current dating from at least the early Cenozoic, resulted in conditions promoting climatic stability and the development of this arid desert.

For a long time it was thought that regions of the Atacama could not uphold any type of life forms. However, recent culture-independent methods (metagenomics, transcriptomics, in situ hybridization, etc.) have improved the sensitivity for life detection.

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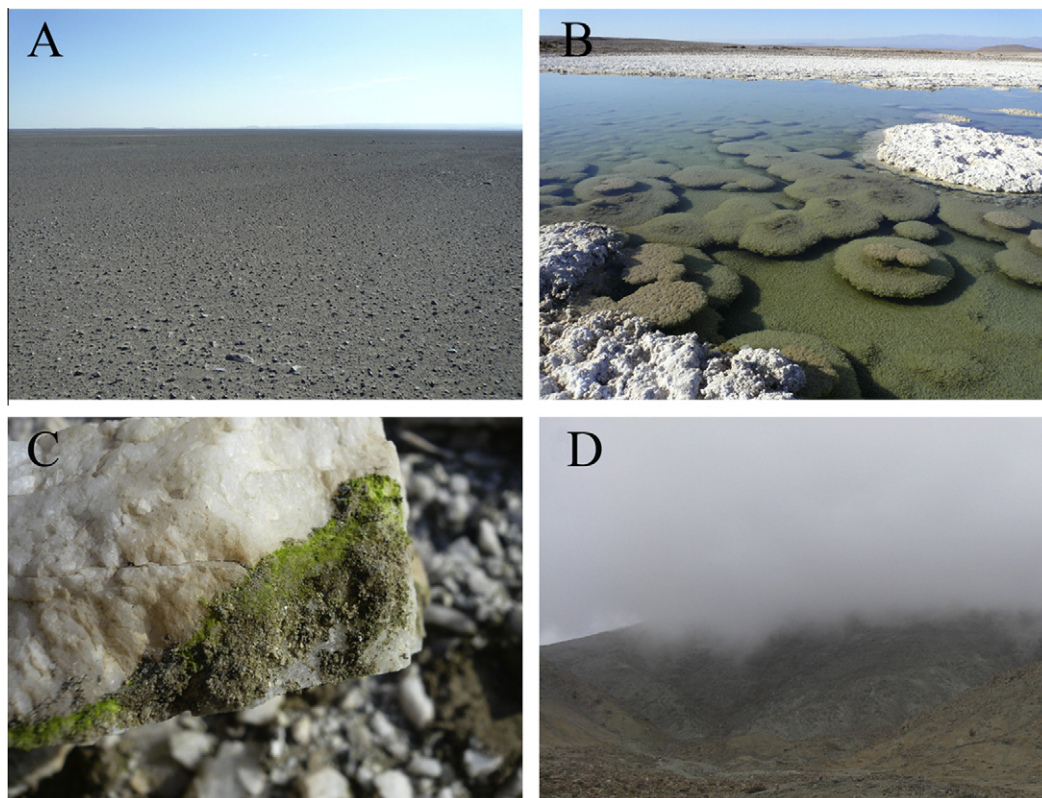


Fig. 1. Some microbial habitats at the Atacama Desert. (A) Soils in the hyperarid; (B) Stromatolites at the Llamara Salar; (C) Hypolithic communities under quartz stones; (D) Fogs advancing over the hills of the Coastal Range, which seem to be the main, if not the sole source of water for hypolithic communities under quartzes in these hills.

Thus, microorganisms have been found even in the driest areas of this desert, which makes scientists wonder about the true limit of water availability needed to sustain life as we know it. In this review, we summarize the efforts devoted to the characterization of microbial life in the Atacama Desert. For previous reviews on the subject, see Gómez-Silva et al. [4] and Gómez-Silva [5].

2. The early stages: laying the groundwork for the Vikings

Studies on the microbiology of the Atacama Desert in modern times have been intrinsically tied to the nascent field of Astrobiology, as it will become evident below. One of the first descriptions of microorganisms in this desert was published in 1966 by Cameron et al. [6]. Working by that time at the Jet Propulsion Laboratory (JPL) and commissioned by NASA, they approached the Atacama as a way to obtain basic information on terrestrial desert environments and its microbiota. This program was undertaken in order to develop and test the life detection instruments that were to be taken to Mars ten years later by the Viking Mission. Thus, samples were collected near Uribe (apparently the name of this location is misspelled in the manuscript and most probably refers to the Uribe train station located about 15 km south east of Antofagasta), where soils were physicochemically characterized. Using trypticase soy agar plates, aerobic and anaerobic bacteria, fungi and algae were barely detected. However, growth obtained in dilution tubes of thioglycollate medium indicated the presence of 10^6 – 10^7 microorganisms per gram of soil. Subsequently, making use of an array of different growth media, a higher abundance of bacterial and *Streptomyces* colonies were additionally detected. Also commissioned by JPL and NASA, W.B. Bollen further worked on these isolates, identifying *Bacillus subtilis atterrimus*, *Bacillus brevis*, *Bacillus cereus* and *Micrococcus caseolyticus* [7].

With the ambiguous results obtained by the life detection experiments conducted by the Viking Landers in 1976 [8], the interest in the Atacama Desert greatly diminished. During the 1980's there were no reports in the literature, whereas in the 1990's an interesting new location in it was described, the Llamara Salar [9]. Located about 120 km north east of Iquique, this site contains scattered small ponds of neutral brines of the NaCl type. In them, precipitation of calcite and gypsum creates unique stromatolite-like structures (Fig. 1B), whereas progressive evaporation causes the precipitation of halites. A report describing the geochemical characteristics of the Llamara Salar would soon follow [10], along with studies from other groups dealing with its microbiology (see below).

In the year 2000, with the conceptual background of the Atacama Desert as a potential Mars model, Dose et al. reported on the ability of bacteria from other environments to survive when placed on the soil surface [11]. Spores of *B. subtilis*, cells of *Deinococcus radiodurans* and conidia of *Aspergillus niger*, *Aspergillus versicolor* and *Aspergillus ochraceus* were placed at two locations near the town of San Pedro de Atacama for up to 15 months. *B. subtilis* spores and *Aspergillus niger* conidia outlived the other species, with survival rates ($\sim 15\%$ and $\sim 30\%$) slightly lower than those of laboratory controls. Cellular monolayers of the dry spores and conidia were also exposed to full sun light, solar UV-B radiation killing even the most tolerant microorganisms within a few hours. Even *D. radiodurans* did not survive this treatment. It may be stated that the work of Dose et al. was pioneer in highlighting the severity of the conditions imposed by the Atacama to the development of life.

In the meantime, other groups were interested in finding potential sources of water required for microbial growth. Thus, Cereceda et al. studied the origin and behavior of fogs in the Coastal Range and inland locations of the Atacama [12,13]. By analyzing the data

collected by the GOES satellite, they described the pattern of formation of the stratocumuli cloud over the sea, its approach to the coastline, the entrance of fog by corridors through the coastal range and the presence of radiation fog inland. By using standard fog collectors installed at six different sites along the Coastal Range, collection rates in the range of 0.9 (February and March)–7.8 l m⁻² day⁻¹ (July and October) were obtained. Fogs were found to move onshore into the continent with different intensities depending on season and time of day, with the maximum spatial extent occurring during winter and at night. They also found that fogs were very frequent in the coastal cliffs, with water fluxes in the order of 7 l m⁻² day⁻¹. Fogs events were much less frequent 12 km inland, with collection rates below 1 l m⁻² day⁻¹.

3. Blazing the trail (2003–2005)

In 2003, the group led by Chris McKay published a report that constitutes a milestone in the field of microbial life of the Atacama Desert [14]. These scientists repeated the same experiments conducted by the Viking Landers in Mars, but this time with samples taken at the Yungay area, about 80 km south east of the city of Antofagasta. Strikingly, the results were the same as those obtained in Mars, namely, active decomposition of organic species in these soils by non-biological processes. In addition, they found that samples from this region had trace levels of organic compounds and extremely low levels of culturable bacteria. Two soil surface samples were tested for DNA and, noticeably, none was recovered. This work definitely validated the Atacama Desert as a Mars analog and also as an unparalleled place to pursue studies on the dry limit for life.

These findings seem to have encouraged other groups to focus their interest in the microbiology of the Atacama Desert, since the period comprising the following two years (2004–2005) was considerably more prolific than all the previous decades. Some studies used the Atacama as a platform to test new detection methodologies, such as the sublimation of adenine to estimate bacterial cell counts in natural samples. With this technique, subsurface soil samples, among them two obtained from the Flat Top Hill site (24°S, 70°W) approximately 160 km south of Yungay, yielded levels of nucleobases expressed as *Escherichia coli* cell equivalents of 4.4×10^6 /g of soil [15]. In turn, using Raman spectra, Villar et al. examined the biomolecules produced specifically as a result of the survival strategies adopted by microorganisms. For this purpose, they analyzed biofilms from the Tatio Geysers (altitude of 4000 m) and the epilithic lichens *Acarospora cf. schleicheri* and *Xanthomendoza mendozae*, collected at altitudes of 2400 and 4500 m, respectively. The best system for the excitation of the Raman spectra with both the geological and biological materials was found to be a 785 nm laser beam coupled with a dispersive spectrometer [16]. Raman spectroscopy was also used to analyze twenty-three lichen specimens belonging to the genera *Candelariella*, *Aspicilia* and *Xanthoria* obtained at 2300–4500 meters in the east-northern tip of the desert [17]. Carotenoids and chlorophyll were found as major components in all specimens, together with a variety of protective biomolecules and accessory pigments such as usnic acid, calycin, pulvinic acid, dilactone and rhizocarpic acid.

The Mars Organic Analyzer, a capillary electrophoresis instrument for sensitive amino acid biomarker analysis developed by Skelley et al., was used to analyze three soil extracts of the Yungay region. Amino acids were detected in the range of 10–600 ppb [18]. The Mars Organic Analyzer was later employed to measure polycyclic aromatic hydrocarbons (PAHs). In samples also from the Yungay region, 9,10-diphenylanthracene, anthracene, anthanthrene, fluoranthene, perylene, and benzo[ghi]fluoranthene were found at ppm levels [19].

On the other hand, a detailed description of the microbial diversity at the Llamara Salar was also reported in this period [20]. By means of denaturing gradient gel electrophoresis (DGGE) and sequencing of 16S rRNA gene fragments, between 8 and 23 bacterial species were found. These bacterial assemblages were dominated mainly by the phylum Bacteroidetes, specifically the genera *Cytophaga*, *Flavobacterium* and *Bacteroides*.

4. A fruitful period 2006–2009

Efforts continued both to understand the physicochemical characteristics of the Atacama, as well as to uncover the microbial life dwelling in it. Regarding the former, it has long been known that Atacama soils contain large quantities of nitrates, iodates and perchlorates, the processes responsible for this situation not being fully understood [21]. Oyarzun and Oyarzun proposed that at least in the case of nitrate deposits, they might have arisen as a result of an unusual combination of massive volcanism (key for the thermal and electric fixation of large amounts of atmospheric nitrogen) and the hyper-arid conditions of the Atacama (vital for the long term stabilization and preservation of nitrate minerals) [22].

Buch et al. developed an extraction procedure coupled with chemical derivatization, followed by gas chromatography mass spectrometry [GC–MS]. Tested with samples from the Yungay area, amino and carboxylic acids were detected in the order of 1×10^{-9} – 4×10^{-11} mol per gram of soil [23]. This protocol was also applied in the same samples for quantifying purines and pyrimidines, which were found at concentrations of 0.04 nmol per gram of soil [24]. In the meantime, the Viking Lander thermal volatilization GC–MS experiments conducted to detect organics in the Martian soil were re-examined [25]. Apparently, the sensitivity of the Viking instrument may not have been sufficient to detect low levels of organics that are readily observed by permanganate oxidation. On the other hand, an instrumental platform based on GC–MS designed for “Sample Analysis at Mars” (SAM) was also tested with samples from the Atacama [26]. Using SAM, up to 10 pmol of refractive organic material in 100 mg of soil were detected. As the present article is going into press, this instrument is in its way to Mars as part of the Mars Science Laboratory rover.

However, most of the findings that came up during these years were related to the microorganisms found in different niches of the Atacama and the microclimatic conditions which could explain their presence. Thus, Conley et al. isolated a variety of cultivable fungi from the hyperarid zone [27]. All fungi identified in this survey were found to be spore-forming saprobes that can be readily dispersed by wind, a likely mechanism that could account for their presence in the central areas of the desert. Accordingly, mainly ascomycetes were detected by culture-dependent methods in Yungay and other sites. With respect to prokaryotic life, DGGE profiles of soil samples taken along an east–west elevation transect through the driest areas near Yungay revealed that microbial communities from the extreme hyperarid core clustered separately from all the remaining communities [28]. For this work, soil samples were taken at depths selected to identify permanent populations rather than transient ones that could have been transported by the wind. Among others, members of the phyla Gemmatimonadetes, Actinobacteria, Planctomycetes, Proteobacteria and Chloroflexi were found. A different study of both surface and subsurface soil samples taken from the Yungay region showed members of the Actinobacteria and Proteobacteria phyla, as well as Firmicutes and TM7, the last one being a candidate division whose existence is known solely through environmental 16S rRNA sequencing. Almost all the 16S ribosomal genes cloned from these soils belonged to Actinobacteria closely related to the *Frankia* genus. Interestingly, concentrations of total organic carbon in the samples were above

the limit of detection but below the limit of quantification, with phospholipid fatty acid (PLFA) concentrations ranging from 2×10^5 – 7×10^6 cell equivalents per gram of soil [29].

Okoro et al. later focused on the diversity of the Actinobacteria, although not including samples from the hyperarid sites. Phylogenetic analysis and basic phenotypic characterization revealed that the majority of isolates belonged to members of the genera *Amycolatopsis*, *Lechevalieria* and *Streptomyces* [30]. In an analogous work, Lester et al. analyzed the microflora of surface and subsurface soil samples from the Yungay region. They found total organic contents in the range of 560–765 μg per gram of soil, whereas PLFA analysis indicated between 2×10^6 and 1×10^7 cell equivalents per gram of soil. By culturing soil extracts in water-like media and trypticase soy agar, twenty strains were isolated. Most of them were *alpha*-Proteobacteria, although Firmicutes and *beta*-Proteobacteria were also identified [31].

In oligotrophic environments, electron sources are critical to build microbial communities. Since minerals are excellent candidates for this requirement, the possibility that there might be microbial communities associated to rock varnish on stones in the hyperarid areas of Yungay was also inspected. Rock varnish is a slow-growing coating consisting of about 70% fine-grained clay and 30% iron and manganese oxides that forms on the surfaces of rocks in arid and semiarid climates. Extraction of both DNA and ATP from the samples suggested a potential participation of microorganisms in the nucleation and growth of these varnishes [32].

On the other hand, the underside of translucent stones has been demonstrated to offer an environment protected from the intense radiation typical of deserts. Sequencing 16S rRNA from samples obtained from hypolithic biofilms under quartzes showed the presence of members of the *gamma*, *alpha*, and *beta*-Proteobacteria, Actinobacteria, Gemmatimonadetes, Chloroflexi and Cyanobacteria, *Chroococcidiopsis* being the dominant among the latter [33]. This finding is not unexpected, since this genus of unicellular Cyanobacteria has been described in many dry environments. Moreover, it is known that photoautotrophic bacteria play a leading role in desert microbial consortia, since they are responsible for carbon and nitrogen input to the community. Interestingly, it was found that each quartz stone from the same area supported a number of exclusive 16S rRNA gene-defined genotypes, creating effective “islands of biodiversity” in this harsh environment. Most likely this is due to the fact that rocks that are apparently identical differ in light influx, nutrient supply and water availability beneath them.

Cyanobacteria have also been found growing endolithically inside salt (NaCl) rocks in the Yungay region [34]. This colonization takes place a few millimeters beneath the rock surface, occupying spaces among salt crystals. This unlikely habitat is functional due to water vapor condensing within the pore space of the halite at relative humidity levels that otherwise hinder the occurrence of liquid water in the surrounding environment. This condensation takes place at relative humidities above 75%, which corresponds to the deliquescence point of sodium chloride [35].

Another striking example of cyanobacterial adaptation to the extreme environment of the Atacama was published by Phoenix et al. [36]. This group reported on the geomicrobiology of El Tatio geothermal field, located at 4300 m in the Andes Mountains. In this site, filamentous Cyanobacteria produce amorphous silica encasings of up to 5 μm thick, which appears to act as a protective shield against most of the UV-B and UV-A radiation, without blocking photosynthetic active radiation. A further high altitude environment in the Atacama Desert is represented by the fumaroles close to the summit of the Socompa Volcano (6,051 meters high). By analyzing 16S rRNA clone libraries from microbial mats developing in these niche, Costello et al. found photoautotroph-dominated assemblages containing members of the Acidobacteria,

Actinobacteria, Proteobacteria (*alpha*, *beta*, *gamma*, *delta*), Bacteroidetes, Cyanobacteria, and the Gemmatimonadetes. This unexpected diversity, more likely to be found in nutrient-rich wetlands than in barren soils, made the authors to suggest that fumarole-associated communities are not only buffered against cold and desiccation, but also fertilized by volcanic carbon emerging from the degassing magma [37].

The effect of UV radiation on microbial life at the Atacama has been the focus of specific analysis. Thus, based on the assumption that enzymatic repair of UV-induced damage is hindered in the absence of liquid water, Cockell et al. tested the hypothesis that UV radiation can prevent epilithic colonization [38]. By using *Chroococcidiopsis* sp. cells isolated from the Negev desert as “dosimeters” (among others), they found that monolayers of this organism were killed within one day. However, 1 mm coverings prepared with gypsum and mineral grain were sufficient to prevent measurable UV-induced damage after 8 days of exposure. A similar result was obtained by Osman et al. [39]. In this case, a monolayer of non-spore-forming bacteria (*Microbacterium schleiferi* and *Arthrobacter* sp.) survived to UV radiation in the range expected for the Martian surface, both in liquid and desiccated conditions. In these experiments, filtered-desert soil was employed.

As there are some rivers in the Atacama which are naturally rich in arsenic compounds, microbiota tolerant to this mineral has been investigated in their sediments. Of several bacterial strains isolated by Escalante et al., 55% corresponded to reducing bacteria, 4% to oxidizing bacteria and 8% presented both activities. These include members of the *gamma*-Proteobacteria: *Pantoea*, *Erwinia*, *Serratia*, *Hafnia* and *Pseudomonas*; the *alpha*-Proteobacteria *Sphingomonas* and the *beta*-Proteobacteria *Burkholderia* [40]. Arsenic tolerant bacteria at the Atacama have also been isolated from volcanic rocks [41].

Since caves offer a stable and protected environment against the harsh outside conditions, our group has focused on the characteristics and biodiversity of cave biofilms, with particular interest in phototrophic species. Thus, we reported a member of the ancient eukaryote red algae *Cyanidium* group growing at the bottom wall of a Coastal Range cave [42]. Using extremely low photon flux levels, our observations suggest that this species is a new member of a recently proposed novel monophyletic lineage of mesophilic “cave” *Cyanidium* sp., distinct from the remaining three other lineages which are all thermo-acidophilic. In a different cave near the city of Iquique, we described the first species of *Dunaliella* able to grow in a subaerial habitat [43]. This microalgae was found to proliferate onto spiderwebs attached to the walls of the entrance-twilight transition zone of the cave. This unique growth habitat suggested us that this new *Dunaliella* species takes advantage of fog condensing on the spider web silk threads to use it as a reliable source of water for photosynthesis.

5. Progress keeps on (2010–2012)

Presently, research on the microbiology of the Atacama Desert exhibits more vigor than ever before, with the hyperarid region around Yungay concentrating most of the efforts. As shown recently, surface organic carbon in this area varies from 2 to 73 μg per gram of soil, and there seems to be no relation between organic content and the geomorphology of the sites [44]. The microbiology in soils from one of these sites was analyzed by Fletcher et al. using different methodologies. The number of bacteria determined by real-time quantitative PCR was several orders of magnitude lower than that determined by PLFA and adenine content, as well as by SYBR-green microscopy [45]. It is possible that the latter methods may be overestimating bacterial concentrations owing to lifeless intact organisms which would stain positive in microscopy and preserve both adenine and PLFA.

Also from hyperarid soils, three bacteria belonging to the genus *Lechevalieria* [46] and two from the genus *Streptomyces* [47,48] have been described. From one of the latter species, compounds with antibacterial activity of the ansamycin-type polyketides have been isolated [49]. By drilling into the subsurface soils, Parro et al. discovered at 2 m of depth a hypersaline microbial habitat with halite, nitrate and perchlorate containing salts [50]. Using a Life Detector Chip containing 300 antibodies, they detected bacteria, archaea and other biological material such as DNA and exopolysaccharides. Among others, members of the *alpha*, *beta*, *gamma* and *epsilon*-Proteobacteria, Actinobacteria, Firmicutes, Acidobacteria, Deinococcus, Bacteroidetes and Euryarchaeota were identified. In a related work, Neilson and colleagues used 454 pyrotag analyses at sites in the hyperarid–arid margin, nearer to the Andes Mountains. Their analyses revealed communities with high abundance of novel Actinobacteria and Chloroflexi, but low levels of Acidobacteria and Proteobacteria [51].

Habitats other than soils are also under inspection to broaden our understanding about life under limited water availability. Thus, Wierzbos and colleagues are studying halite colonization in the Yungay and Salar Grande regions. A cyanobacteria closely related to the *Halotheca* genus was found as the sole colonizing phototroph in this niche [52]. 16S rDNA gene sequences of the accompanying heterotrophic bacteria and archaea indicated their similarity to microorganisms found in hypersaline environments, such as the Bacteroidetes *Salinibacter*, the Euryarchaeota *Halococcus* and *Natronobacterium*. Using Raman spectroscopy, they reported spectral signatures revealing the presence of the UV-protective biomolecule scytonemin, as well as the light-harvesting pigments chlorophyll and carotenoids involved in photosynthetic activity [53]. The same group is also studying the microbial colonization of Ca-sulfate crusts at the Yungay region, which constitute the habitat of lithobiontic micro-organisms, like epilithic lichens, endolithic free-living algae, fungal hyphae, cyanobacteria and other bacteria [54]. They have proposed a new category of endolithic colonization, the “hypoendoliths”, to denote colonization of the undermost layer of the crusts. Similar to halites, the colonization of gypsum crusts seems to be controlled by the existing moisture regime. The potential of these hygroscopic salts for harboring life on Mars has also been speculated [55].

As mentioned before, the underside of translucent quartz rocks in the hyperarid desert has shown to provide another micro environment suitable for microbial life. In this peculiar niche, microorganisms are not only protected against excess UV radiation, but phototrophs manage to get sufficient light for primary production (Fig. 1 C). As part of our own research, we determined that in the Coastal Range of the Atacama, colonization rates can reach up to 80% of the quartz rocks [56]. Colonization rates in this area, where fog represents the main regular source of moisture (Fig. 1D), are significantly higher than those reported inland at the same latitude. In this case, cyanobacteria – among them *Chroococcidiopsis* (Fig. 2) –, are in complex associations with archaea and heterotrophic bacteria [56]. We have proposed that the development of these hypolithic communities probably rely on a positive feedback between fog availability and the higher thermal conductivity of the quartz rocks. This association results in lower daytime temperatures at the quartz–soil interface microenvironment, favoring water condensation and microbial colonization.

In turn, Lacap et al. determined the colonization rates of quartzes of the Yungay region [57]. In addition to the common green hypolithic colonization mostly dominated by cyanobacteria (*Chroococcidiopsis* and *Nostoc*), they also found a novel red hypolithic mainly composed by a taxonomically diverse group of Chloroflexi. Heterotrophic bacteria, common to both hypoliths types, were affiliated to desiccation-tolerant species within the Actinobacteria and Deinococcus phyla. *Alpha*-Proteobacterial

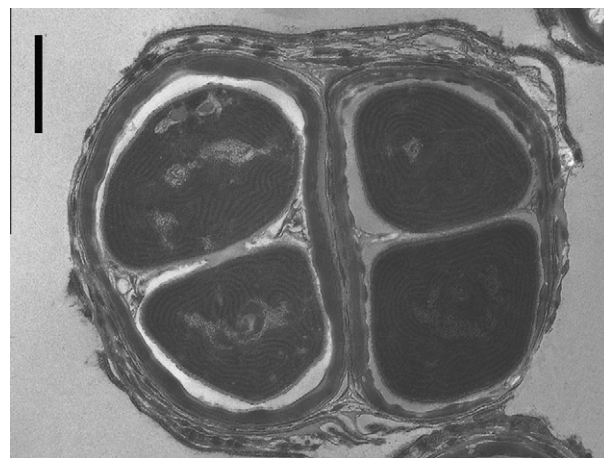


Fig. 2. Transmission electron micrograph of an ultrathin section of *Chroococcidiopsis* sp. AAB1 isolated from a hypolithic biofilm growing under quartz rocks in the Atacama Desert. Note the characteristic multi-layered electron-dense envelope of capsular polysaccharide (grey) surrounding the tetrad of cells. Scale bar: 1.0 μ m.

phylotypes that affiliated with nitrogen-fixing taxa were only found in green hypoliths, whereas Gemmatimonadetes phylotypes occurred only on red hypoliths.

6. Future directions

There is little doubt that studies on the Atacama Desert are becoming increasingly appealing for understanding the physiological adaptations of microorganisms to extreme environmental conditions, such as a very low relative humidity, high salt concentrations (among them arsenates), high UV radiation, etc. At the moment we are beginning to understand how these microorganisms optimize their access to water and use it for their physiological requirements. It is evident that most of them are living in close contact to mineral soils and rocks such as quartz, halites and gypsum. In the case of mineral soils, solid matter may account for as little as fifty percent, the rest corresponding to space occupied by gases and water [58]. It is not clear how much of this mineral containing water is accessible for microbial life. But for certain, studies at the Atacama Desert have shown that life can be sustained with extremely low water availability.

Most reports published to date are understandably descriptive. Some deal with the physicochemical and climatic characteristics of the various habitats. Others present evidence for the identification of a new species or the composition of a microbial community. Thus, the next logical step is to reinforce the use of metagenomics plus a combination of other “omic” techniques to understand adaptations to extreme conditions at the molecular level. Moreover, a systems biology approach will have to be employed to study the relationships among the components of individual microbial communities. With this information at hand, researchers in the field will be in a position to address more holistic questions. For example: What is the minimum amount of water required for microbial life in this environment, where it comes from and in which form is useful? Did the microorganisms of the Atacama already evolved to be less dependent on water or are they just adapted to it? How does evolution proceed in an extreme environment such as this? Undoubtedly, responding to these questions will not only lead us to a better knowledge regarding life under extreme environments, but will also provide us with a more solid ground to speculate about the habitability of other planets.

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