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Invited Review

Forged Under the Sun: Life and Art of Extremophiles from Andean Lakes†

Virginia Helena Albarracín[1,2]*, Wolfgang Gärtner[3]* and María Eugenia Farias[1]

[1]Planta Piloto de Procesos Industriales y Microbiológicos (PROIMI), CCT, CONICET, Tucumán, Argentina
[2]Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina
[3]Max-Planck-Institute for Chemical Energy Conversion, Mülheim, Germany

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ABSTRACT

High-altitude Andean lakes (HAAL) are a treasure chest for microbiological research in South America. Their indigenous microbial communities are exposed to extremely high UV irradiation and to multiple chemical extremes (Arsenic, high salt content, alkalinity). Microbes are found both, free-living or associated into microbial mats with different degrees of mineralization and lithification, including unique modern stromatolites located at 3570 m above sea level. Characterization of these polyextremophilic microbes began only recently, employing morphological and phylogenetic methods as well as high-throughput sequencing and proteomics approach. Aside from providing a general overview on microbial communities, special attention is given to various survival strategies; HAAL's microbes present a complex system of shared genetic and physiological mechanisms (*UV-resistome*) based on UV photoreceptors and stress sensors with their corresponding response regulators, UV avoidance and protection strategies, damage tolerance and UV damage repair. Molecular information will be provided for what is, so far the most studied HAAL molecule, a CPD-Class I photolyase from *Acinetobacter* Ver3 (Laguna Verde, 4400 m). This work further proposes some strategies that make an appeal for the preservation of HAAL, a highly fragile environment that offers promising and ample research possibilities.

INTRODUCTION

Anthropomorphically, an extreme environment is one in which physical conditions are not conducive to human life (1). On that account, these environments are defined as habitats that experience steady or fluctuating exposure to one or more environmental factors, such as salinity, osmolarity, desiccation, UV radiation, barometric pressure, pH and temperature.

The high-altitude Andean lakes (HAAL; Fig. 1) at the Central Andes region in South America (2) are a paramount example of such extreme environments. With almost unexplored ecosystems, they comprise shallow lakes and wetlands spreading out at up to 6000 m altitude, in a wide range of ecosystems from the Atacama Desert to the Altiplano-Puna Plateau up to the High Andes. Being exposed to an array of severe climatic and physicochemical conditions, their indigenous microbial communities have managed to thrive in diverse niches: shallow water, sediments, microbial mats and microbialites (3–13). As HAAL microorganisms endure such extreme environmental contexts, it is not surprising that NASA has classified some of these lakes as model systems for prospecting life on other planets, a topic of utmost interest within astrobiology (7). Probably more fascinating than the window into space is the window that opens up into the early origins of life: modern stromatolites were found thriving in Lake Socompa (3570 m), which—unlike others—are located at very high altitude and exposed to hostile conditions, providing HAAL with an exceptional template for studies on early life development (6).

The high altitude and tropical latitude yields a solar irradiance at HAAL much higher than at sea level with impinging UV-B flux reaching 10 W m^{-2} in some lakes (4,5,14–16). Thus, HAAL provides natural laboratories for *in situ* exploring and monitoring of the interactions between the geophysical environment and the dynamics of microbiodiversity. Accordingly, HAAL-isolated strains display intrinsic high UV resistance (3–5,8,10,14,16–19) that render models for studying adaptive responses and mechanisms that underlie light sensing and UV resistance in environmental microbes. In fact, the availability of genomes of model polyextremophilic microbes (17,20) and several metagenomes of complex microbial communities in microbialites is providing a great opportunity to perform in-depth basic and applied research (4,6,19,21–29).

In the course of this review we will outline the biodiversity of HAAL extremophilic microbial communities, highlighting those strategies and mechanisms that explain their ability to survive in such irradiated environments. A layout of the microbes' lifestyle opens the path to potential applications in various fields of biotechnology in conjunction with photobiology. In turn, these environments require careful protection from current economic activities (*i.e.* mining) that pose a threat to the preservation of their unique biologic resources.

HIGH-ALTITUDE ANDEAN LAKES: EMPIRE OF THE SUN

The Andes extend along the western side of the continent from 11° N in northern South America to 56° S in Tierra del Fuego

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*Corresponding author emails: viralbarracin@gmail.com (Virginia Helena Albarracín) and wolfgang.gaertner@cec.mpg.de (Wolfgang Gärtner)

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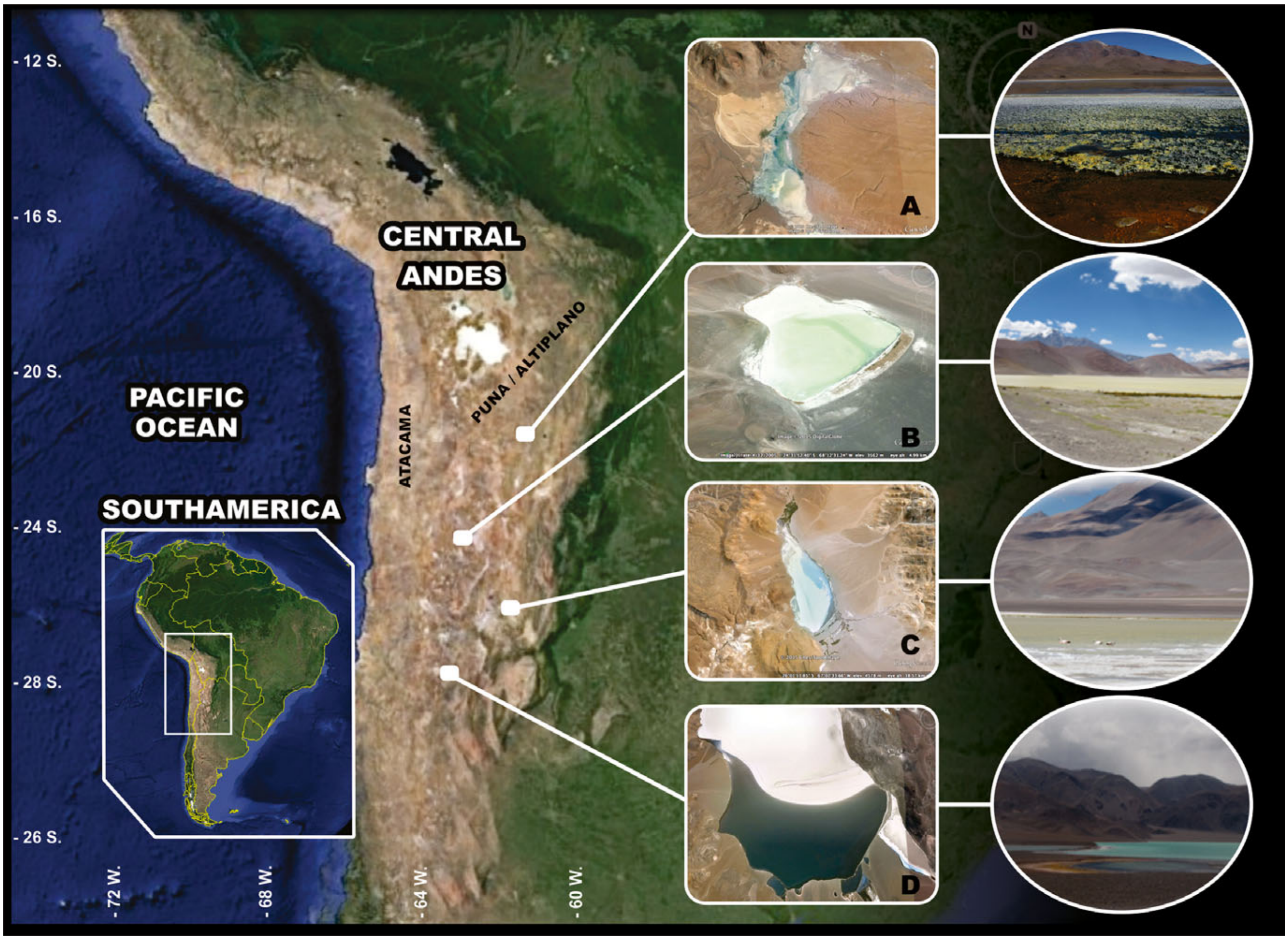

Figure 1. Geographical location of HAAL. Satellite images and typical landscapes of representative HAAL: (A) Laguna Vilama, (B) Laguna Diamante. (C) Laguna Socompa. (D) Laguna Verde.

southern island (30). Leaving Asia aside, they form the highest mountain range with over 100 peaks above the 6000 m, including the highest active volcanoes on Earth. Specifically, the Central Andes extend through Argentine, Chilean, Bolivian and Peruvian territories encompassing diverse orographic and climatic territories such as the high volcanic plateau called as Altiplano/Puna (above 3000 m), the Atacama Desert (mean altitude of 2200 m) and the Western Andean flank between *ca* 18°S and 27°S (4000–6000 m) (Fig. 1). The most prominent climatological feature in this area is the impairing aridity (31–33). In fact, the Atacama area is considered hyperarid with a mean annual precipitation value of 1 mm per year while the High Andes and Puna present arid to semiarid conditions (7,33–39). In spite of the scarce precipitation regime, wetlands (shallow lakes, peatbogs and salt flats) are widespread in these altitudes (40), which, for this review, will be herein referred to as high-altitude Andean lakes (HAAL).

Environmental conditions are adverse in all HAAL; indigenous microbial communities are challenged by different combinations of extreme chemical concentrations and physical stress in each particular niche—in some cases including high values of alkalinity (41–43). As these lakes are endorheic basins, seasonal contraction and expansion of their water levels increases the amount of minerals from geochemical and volcanic origin yielding high concentrations of arsenic and dissolved salts (44–49). Moreover, volcanic activity and hydrothermal vents are common inputs in the Andean wetland systems modifying both the flow of nutrients as well as water temperature (6,50–52).

UV radiation is defined as three subtypes, namely UV-A (320–400 nm), UV-B (280–320 nm) and UV-C (100–280 nm). UV-A accounts for about 95% of the total UV energy that reaches the Earth's surface, the remaining 5% being UV-B. UV-C is totally absorbed by stratospheric gases, failing to reach the troposphere (53). During the last decades, ozone depletion caused solar UV-B irradiance to significantly increase at mid and high latitudes, but in the Southern Hemisphere, the expansion of the Antarctic ozone hole and the climate changing phenomena stressed this situation (40,54–56). UV-B causes formation of different types of photoproducts on DNA or affects indirectly cell macromolecules by triggering oxidative damage, whereas UV-A acts indirectly by producing photooxidizing compounds and reactive oxygen species. Hence, biologically damaging UV data were traditionally considered as the integral between 280 and 315 nm ($UVB_{280\text{–}315\ nm}$) or in terms of the integral between 280 and 320 nm ($UVB_{280\text{–}320\ nm}$). For a better assessment of sunburn risk to solar exposure, UV irradiation is now reported using the 'sunburning', or erythemally weighted radiation (UV_{Ery}) or also the UV index (UVI), which is 40 times the UV_{Ery} (57). UV Index is categorized by the World Health Organization as low when is below 2 and extreme when is higher than 11 (http://www.who.int/uv/publications/en/GlobalUVI.pdf).

As the ozone column is naturally thinner over the tropics, and UV intensity increases with the altitude, the Puna-High Andes region is consequently exposed to an exceptionally high solar irradiation including harmful UV levels; there are numerous individual reports of climatologists (57–60) and biologists exploring the Puna-High Andes region reporting astonishing solar levels in different sampling points or climatological stations for ground measurements (7,8,41,61,62). Solar erythemal UV radiation incident on a range of tropical to high latitude regions from Argentina was ground measured by Piacentini *et al.* (60): in Marambio Base, Antartica (64.23°S, 56.78°W, 300 m) the UV_{Ery} (in $kJ\ m^{-2}$) was 0 and 2.3 in July and January, respectively, whereas in Buenos Aires (34.61°S, 58.41°W, 25 m) it was estimated as ranging between 0.8 (July) and 6.2 (January). In turn, at the Northwestern city of La Quiaca (22.11°S, 65.57°W, 3459 m) in the Puna region, the UV_{Ery} was as high as 3.6 in July and 9.5 in January. In accordance, the calculated average UVI in conditions of normal ozone and albedo conditions—at noon on December 21, 2001 (59)—reached 20 for La Quiaca and only eight for the southern Argentinean city of Ushuaia (54.9°S, 68.3°W, 14 m). These values are even higher than those detected at Lhasa (29.7°N, 91.1°E, 3648 m), Tibetan plateau, with monthly mean UVI over 16 in July (63).

Zenoff *et al.* (3) explored Laguna Pozuelos (3600 m) and Laguna Azul (4560 m) in the Argentinean Puna during the austral summer and recorded—at noon—maximal UV-B irradiance of 5.5 and 10.8 $W\ m^{-2}$, respectively, for the 300 to 325 nm range. Flores *et al.* (16) documented in Laguna Negra and Laguna Verde (4400 m) a maximum UV-B of 10.8 $W\ m^{-2}$. Cabrol *et al.* (61) claimed to record the highest UV-B irradiance values (and resulting UVI) ever noted on Earth at Laguna Blanca (4340 m) and at Licancabur Volcano (5917 m) in the Bolivian High Andes. At average ozone conditions (250 Dobson Units, DU), UV-B maximum was 1.3 $W\ m^{-2}$ in winter and 4.1 $W\ m^{-2}$ in summer. Higher values were obtained around noon between November 25, 2003, and January 25, 2004, during which dates, UV-B reached 10 and 7 $W\ m^{-2}$ at Licancabur and Laguna Blanca, respectively. In accordance, UVI events >29 were observed at Licancabur, with slightly lower UVI (up to 26.2) at one HAAL at Laguna Blanca, 10 km away. Because measurements of such a high ambient UV radiation could compromise instruments producing undesired artifacts, Mackenzie *et al.* (64) have questioned these results and have recommended recalibrating the instruments used and having additional caution in reporting such high levels of UV doses, which may otherwise undermine the understanding of important aspects of atmospheric sciences. Current efforts from an interdisciplinary team of microbiologists and climatologists to systematically established climatological stations in select HAALs are in progress. A comprehensive study of solar total and UV irradiation on-ground measurements is still missing from the HAAL area (Table 1).

POLYEXTREMOPHILES: WHEN ONE EXTREME IS NOT ENOUGH

Microorganisms that colonize extreme environments are called extremophiles, a group that includes representatives of all three domains (Bacteria, Archaea and Eukarya). They are categorized into subgroups according to the environmental specificity of their surroundings, *i.e.* psychrophilic, thermophilic, halophilic, alkalophilic and acidophilic (2). In their natural habitat, many extremophiles tolerate several extremes combined and are better termed "polyextremophiles" to denote their flexibility in the face of several concurrent stressors (21,27,65). This definition is met exactly for the HAAL microbes since they simultaneously deal with the stress produced by extraordinary UV exposure, high dissolved salts concentrations (including arsenic salts) and extreme pH values (mostly alkaline). Arsenic concentration deserves special mention here as levels can reaches 234 ppm in some lakes, a value 10 000-fold higher than the World Health Organization's standard for drinking water (10 ppb) (66). In this sense, HAAL display an outstanding source of microbial diversity furnished with remarkable strategies that allow microorganisms to survive under severe conditions.

The study of HAAL microbial diversity was undertaken by sampling plankton, benthos, biofilms, microbial mats and microbialites as well as gut content (feces) from Andean endemic flamingos feeding on the lakes and considered microbial dispersers (3–6,13,15,16,18,41,47,51,67,68). Although most research efforts aimed at the characterization of bacterial communities, Archaea and unicellular Eukaryotes from diverse niches were also described.

Metagenomic approaches performed by Denaturing Gradient Gel Electrophoresis (DGGE), 16S rRNA gene clone libraries or 16s rDNA pyrotag sequencing indicated that prokaryotic communities from shallow water and sediment samples of HAAL are dominated by bacterial taxa of proteobacteria, bacteroidetes and firmicutes, whereas actinobacteria, cyanobacteria and spirochetes are less abundant (3,5,7–9,11,12,14,41–43,45–47,69,70). Within Archaea, halophilic Euryarchaeota (Halobacteria), non-halophilic Euryarchaeota and mesophilic Crenarchaeota were described (11,24,43,69). Regarding unicellular eukaryotes, diatoms represented the main algal group on HAAL phytoplankton; the genera *Nitzschia* and *Navicula* were the most abundant and widely distributed. Other common members of phytoplankton such as cyanobacteria, chrysophycea, euglenophyta and chlorophyceae are also found, but in lower numbers and diversity (7,71).

Aside from metagenomic approaches, culture-dependent methods yielded a large collection of polyextremophilic microbial HAAL species (4,16,18). The strains were taxonomically identified and characterized in terms of their resistance to environmental conditions such as arsenic, salt, UV and antibiotics (3–5,14,16,41,46,47), indicating that HAAL constitute an important reserve of genes and molecular mechanisms to counteract various stress factors. In the light of ongoing genomic/metagenomic projects (19,21,22,24–28,72), putative extremoenzymes and extremolytes produced by these microbes offer promising biotechnological applications that range from bioremediation and biomining to the production of important drugs.

Another aspect of the microbiological communities at HAAL is that most of them are found in the form of cooperative structures (Fig. 2); different microbial ecosystems with an increasing complexity from simple biofilms and microbial mats (Fig. 2A–C) to intricate stromatolites (Fig. 2G–I) are widespread (6,51,68). This could be viewed as a range of structures of increasing complexity resulting from interactions of microorganisms with organic products, extracellular polymers and inorganic com-

Table 1. Physical–chemical characteristics of representative HAAL in Argentina where UV-resistant microbes were isolated. These HAAL correspond to those depicted in Fig. 1.

	L. Verde	L. Diamante	L. Socompa	L. Vilama
Location	Catamarca, AR	Catamarca, AR	Salta, AR	Jujuy, AR
GPS data	27°33′S 68°38′W	26° 01′ S 67° 02′ W	24°32′S 68°12′W	22°36′S 66°55′W
Depth (cm)	10	20	10	20
Altitude (m)	4400	4570	3600	4500
pH	6.5	11 to 13	8.6 to 9	7.1
Arsenic (mg L^{-1})	0.8	115 to 230	18 to 34	11.8
Salinity (%)	5	19.4	17	11.7
Chlorophyll a (μg L^{-1})	1.04	ND	3	12.8
T (°C)	14	10 to 14	15 to 24	8.5
O_2 (μg L^{-1})	2.42	1.02	6.92	ND
Max UV-B levels (W m^{-2}) for the range 280–312 nm	10.78	ND	ND	8.94

ND, not determined.

Figure 2. Different microbialites found at the HAAL depicted at different levels of analyses: on-site, macroscopic and microscopic. 1. Halite. 2. Bacteria bind by EPS. 3. *Microcoleus* filaments. 4. Aragonite. 5. Diatomeas frustules. 6. Gaylussite crystals. 7. Archaea bind by EPS.

pounds designed to counteract hostile conditions such as UV high exposure or high salt stress.

Microbial mats are benthic communities that grow on a solid substrate (*e.g.* sand, rock or sediments) and which present a vertical stratification of functional groups of microbes embedded in an inorganic matrix with minerals such as silicates and carbonates (73–75). They often show various degrees of mineral precipitation and lithification thus forming organic sedimentary structures called microbialites (74–76). Typically, vertical stratification on mats/microbialites originates from the physical-chemical gradients (mainly governed by light conditions) and from their indigenous microbial activity (77). In phototrophic microbial mats, cyanobacteria and phototrophic eukaryotes fulfill largely the double function of harvesting light and fixing CO_2. Organic matter and extracellular polymers (EPS) formed through primary production are the basis of the food chain. In deeper layers, the mat becomes anoxic and organisms degrade the carbon reserves by fermenting and producing low-molecular organic acids and alcohols. Methanogenic and sulfate-reducing bacteria oxidize these byproducts generating methane and sulfide, which is then oxidized back to sulfate by sulfur-oxidizing bacteria (51,74,76,78,79).

In recent years, different benthonic microbial ecosystems have been reported in hypersaline HAAL in the Puna-Altiplano-Atacama area (51,68). The photosynthetic microbial mats that were first described were the ones found at the salt flat Salar de Llamará, Atacama Desert, Northern Chile (80). Their photic zone ranges from 8 to 30 mm. The association of microorganisms determined the color and pigment content of the layers. Filamentous cyanobacteria, such as *Microcoleus* sp. and *Oscillatoria* sp. were the most abundant in the top green layers, whereas in the second orange-pigmented layers, diatoms and unicellular cyanobacteria—mainly from the Cyanothece and Synechococcus groups—were predominant. In these two layers, 91 to 99% of the extracted pigments corresponded to Chlorophyll a (Chla). Further down, the deep purple layer—with lower Chla but higher BChl concentrations (44 to 61%)—was formed primarily by anoxygenic phototrophic bacteria similar to cells of the genera *Chromatium* and *Thiocapsa*. Abundant nonphotosynthetic microorganisms were found in all the mats studied, including unidentified sulfate-reducing bacteria observed as a dark deep layer below the purple one. A recent study by Rasuk *et al.* (68), also carried out in the Salar de Llamará, Chile, described a special case of lithified microbial mats as gypsum dome-shaped bioherms. These structures were found partially submerged in water, rendering two kinds of niches; in the air-exposed surface, light exposure and oxygen availability are high. In the water-submerged portion, there is lower risk of suffering desiccation, minor incidence of light, and increased nutrient availability, though conditions vary from microaerobic to anoxic. Microbial diversity and pigment distribution were different in these two systems and were also season-dependent (winter/summer). In the upper, air-exposed part, Chromatiales (Gammaproteobacteria), Rhodospirillales (Alphaproteobacteria) and Sphingobacteriales (Bacteroidetes) were the main taxa in both seasons. In contrast, the submerged portion showed predominance of Proteobacteria (Alpha and Gamma) and Verrucomicrobia in summer, but with more diverse phyla found in winter (68).

At the Salar de Atacama (Chile), microbial mats with diverse degrees of mineralization were described, and Stivaletta *et al.* (81) studied the microbial diversity from gypsum domes at Laguna de la Piedra (2341 m). The domes are actually evaporite deposits in which endolithic microbial communities developed; they host a variety of halophilic microorganisms including a single phylotype of halophilic archaea, oxytrichid ciliates, members of the candidate division TM6, Cyanobacteria, Bacteroidetes, Alpha, Beta- and Deltaproteobacteria (Stivaletta *et al.* 81). Likewise, gypsum-dominated microbialites and domes were observed at Laguna Tebenquiche (2350 m), whereas at Laguna La Brava calcium carbonate-containing mats and microbialites were detected (51). The stratification pattern was also highly dependent on the impact of strong solar irradiation; incidental UVA-B radiation measured at noon showed values as high as 57.9 W m^{-2} and 53.4 W m^{-2} at La Brava and Tebenquiche, respectively. The main phylum in La Brava microbialites comprised Proteobacteria (41.8%), Verrucomicrobia (11.8%) and unclassified Bacteria (7.6%), whereas for La Brava mat, composition was as follows: Proteobacteria (22.3%), Thermi with Deinococcales (11.8%), unclassified Bacteria (12.1%) and Spirochetes (10.4%).

Microbialites have also been traced on the Argentinean side (6,82). These microbial systems are even more exotic than the ones in the Chilean region because they have to cope simultaneously with high concentrations of arsenic, high UV exposure and hypersalinity in the context of a volcanic setting and hydrothermal inputs that constantly affect the chemistry and temperature of the lakes. In fact, this scenario is deemed to resemble some of the conditions that prevailed anciently on Earth and Mars, rendering models for evolutionary studies.

In Laguna Socompa, a shallow hypersaline lake (115 mS cm^{-1}) located at the footsteps of the Socompa Volcano (3570 m Fig. 2, middle panel), modern stromatolites were described as columnar round dome-shaped, laminar mats (22). Here, the stromatolites were found submerged along the southern shore, near several hydrothermal inputs (26°C) and thereby protected from the direct incidence of such radiation levels during the summer. In the winter, the water level decreased and, as a consequence, top layers of the stromatolites got directly exposed to UV-A/B light. These changes affected the structure and microbial distribution of the mat: a white-pinkish crust covered the surface under nonsubmerged conditions, which changed to green-yellowish when the surface was covered by water. Below this first layer, a dark-green layer (thickness *ca* 0.5–1.5 mm) showed up, which progressively declined and disappeared at a depth of 3–5 mm. Deeper parts showed alternating layers of a light-brown (5–20 mm thick) and dark-brown (0.5–1.5 mm thick) color. The main structural constituents of the stromatolites were silica (in the form of diatomeas frustules) and calcium carbonate in the form of aragonite (Fig. 2, upper panel). The analysis of 113 255 bacterial 16S pyrotags showed a rich and strictly organized microbial community (6), in which Proteobacteria represent the most abundant phylum (34% of all sequences), with a majority of sequences related to Alpha- (15%), Delta- (13%) and Gammaproteobacteria (4%), and very few Epsilon- (0.45%) and Betaproteobacterial (0.05%) sequences. Other main phyla were Spirochetes (8%), Deinococcus-Thermus (7%), Bacteroidetes (6%), Firmicutes (5%), Cyanobacteria (3%, dominated by the genus *Microcoleus*) and Chloroflexi (1%). In addition, 1% of all sequences correspond to the 16S rRNA gene of Bacillaryophyta (diatoms) chloroplasts.

Other microbialites and microbial mats were observed and sampled in Argentinean lakes such as Laguna Diamante (4570 m, Fig. 2, bottom panel), a shallow hypersaline lake

(217 mS cm^{-1}) located inside the crater of the Galán volcano near a hydrothermal spring effluent (82). Its hypersaline water displays a high pH (9 to 11) and outstandingly high arsenic concentrations (115 to 234 mg L^{-1}). Its (unique) microbial communities suffer from these chemical constrains, but also from intense UV-A/B radiation (84 W m^{-2} in summer). At this lake, partially, submerged calcareous rocks (microbialites) were found widespread and their bottom part showed red biofilms associated with gaylussite crystals (Fig. 2, bottom panel). Metagenomic shotgun sequencing of the biofilm indicated it was formed mainly by archaea such as *Halorubrum* and *Natronomonas*. The metabolic potential of these biofilms was explored, especially for arsenic metabolism (82) and bacteriorhodopsin-like genes (N. Rascovan, unpublished).

SURVIVING THE SUN

HAAL render true "hotspots" for quantifying the amount of biologically damaging radiation that reaches the Earth surface, as well as natural laboratories for *in situ* exploring and monitoring of microbe survival and the molecular mechanisms that counterbalance intense solar UV- B irradiation (3–5,8,10,14,16–19,70). High solar irradiation challenged HAAL microbial communities (including mats) in diverse ways selecting unique UV resistance/adaptation phenotypes; Farias *et al.* (70) and Fernandez-Zenoff *et al.* (14) carried out *in situ* exposure of bacterioplankton samples from Laguna Azul and Laguna Vilama (4650 m, Jujuy, Argentina) using DGGE and demonstrated the low impact of natural solar radiation had on the microbial community structure. Among the DGGE bands sequenced after the *in situ* solar experiment, the dominant bacterial groups in these two lakes were Proteobacteria, Bacteroidetes, Actinobacteria and Firmicutes. Zenoff *et al.* (3) described the succession and survival rate of five aqueous bacterial isolates (*Acinetobacter* sp., *Nocardia* sp., *Bacillus* spp., *Staphylococcus* sp.) collected at Laguna Azul, Catamarca, Argentina (4560 m) after a long-term exposure to UV-B (Irradiance: 5 W m^{-2}; maximal dose: 600 kJ m^{-2}). In addition, Fernandez-Zenoff *et al.* (5) showed that UV resistance was consistent with the isolation source of the microorganism, *i.e.* bacteria that withstand minimal or nule UV exposure in the wild, *i.e.* the marine *Pseudomonas putida* strain 2IDINH, and *Acinetobacter johnsonii* ATCC 17909, showed the lowest values of survival under UV (Fig. 3). In contrast, bacteria from HAAL′s bacterioplankton were able to resist up to the maximal dose tested with minor reductions in their survival rates. Isolates from Chilean wetlands (*Exiguobacterium, Serratia, Shewanella, Halomonas, Aeromonas*) resisted similarly, yet to different UV wavelengths (Table 2). Microbes regarded as tolerant or resistant to UV were described in different habitats including aquatic environments, stratosphere and troposphere, soil, plant phyllosphere and even spacecraft assembly (36,83–93).

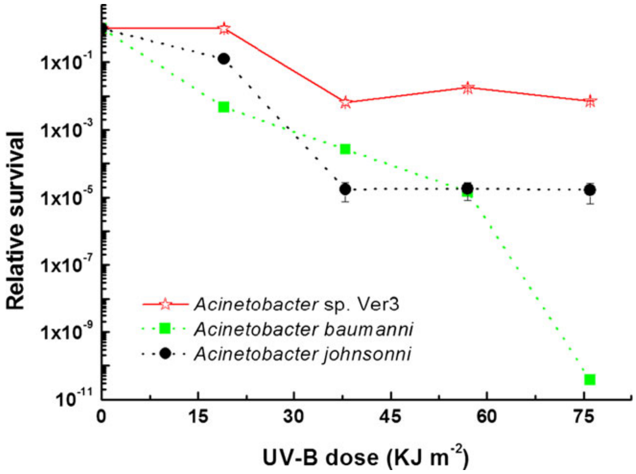

Figure 3. Relative survival of UV-B-resistant strain *Acinetobacter* sp. Ver3 isolated from Laguna Verde (4400 m), Catamarca, Argentina after exposition to different UV-B doses (0–76 kJ m^{-2}) in agar plates. The clinical isolates *A. baumanni* and *A. johnsonii* were used as sensitive controls.

Dib *et al.* (47) proved that the UV-resistant Actinobacteria, Firmicutes and Gammaproteobacteria isolated from Laguna Vilama (4650 m) and Laguna Azul displayed concomitant resistance to damaging chemical agents such as antibiotics, high salt and arsenic. UV-resistant strains of *Exiguobacterium, Bacillus, Pseudoalteromonas, Pseudomonas, Kocuria, Acinetobacter, Stenotrophomonas, Staphylococcus* and *Desemziaf* were isolated rom the bacterioplankton of two hypersaline lakes, Laguna Negra and Laguna Verde (4400 m, Catamarca, Argentina), (16) (Table 2). Most of these strains were able to grow in culture media added high salt contents (up to 10% NaCl). Ordoñez *et al.* (4) determined that after a 24 h exposure to UV-B radiation, Proteobacteria were the most resistant strains: 33.3% of betaproteobacteria, 44.4% of gammaproteobacteria, 40% of alphaproteobacteria were able to survive through the entire exposure period. UV-B resistance of the isolates was not different considering the various biotopes from which they were isolated, *e.g.* hypersaline (Laguna Vilama or Salar Grande) or oligosaline (Laguna Aparejos or Laguna Verde) environments. The most prominent HAAL UV-resistant microbes belong to Gammaproteobacteria (Table 2), *e.g. Acinetobacter johnsonni* sp. A2 from L. Azul (4400 m), *Pseudomonas* sp. V1 from L. Vilama (4650 m), *Pseudomonas* sp. MF10 from L. Pozuelos (3600 m) and *Acinetobacter* sp. Ver3 from Laguna Verde (4400 m).

The described UV-resistant phenotypes as well as the great diversity of microbial communities indicated that HAAL microbes might have developed an intricate system of adaptation to UV (3,5,6,16,22). UV resistance is a complex attribute that depends on the expression of a vast array of genes devoted to evading or repairing the damage provoked direct or indirectly by this harmful radiation. HAAL indigenous microbial community suffering from constant and intense UV irradiation may have developed a multifaceted system of shared genetic and physiological mechanisms (*UV-resistome*) (27). Following this assumption, HAAL UV-resistome would consist of some—or probably all—of the following sub-systems: (1) UV-photoreceptors or other stress sensors with their corresponding response regulators; (2) UV avoidance and protection strategies; (3) damage tolerance; and (4) UV-damage repair (27). So far, strong evidence for the last three subsystems has been identified in HAAL microbes and mats and will be discussed in the following subsections. The first subsystem hypothesis (UV-sense and response) is still largely unexplored for microbes and will be only discussed in the light of the genomic projects of some HAAL microbes (27).

Avoidance and protection

As described in the previous section, cooperative strategies are widespread and suggest that associative behavior pursues a com-

Table 2. Principal taxa of UV-resistant strains isolated and characterized from HAAL.

Phylum	Class	Family	Genus	HAAL	References
Actinobacteria	Actinobacteria	Nocardiaceae	*Nocardia* *Rhodococcus*	Laguna Azul, CA (4560 m) Laguna Vilama, JU (4600 m)	Fernandez Zenoff *et al.* (5); Fernandez-Zenoff *et al.* (14); Ordoñez *et al.* (4); Bequer-Urbano *et al.* (17)
		Dermabacteraceae	*Brachybacterium*	Laguna Vilama, JU (4600 m)	Dib *et al.* (47); Ordoñez *et al.* (4)
		Micrococccaceae	*Micrococcus* *Kocuria*	Laguna Azul, CA (4560 m) Laguna Vilama, JU (4600 m) Laguna Negra, CA (4400 m) Salina Grande, JU (3400 m)	Dib *et al.* (47); Flores *et al.* (16); Ordoñez *et al.* (4)
		Brevibacteriaceae	*Brevibacterium*	Laguna Aparejos, CA (3600 m)	Ordoñez *et al.* (4)
Firmicutes	Bacilli	Carnobacteriaceae	*Desemzia*	Laguna Verde, CA (4400 m)	Flores *et al.* (16); Ordoñez *et al.* (4)
		Bacillaceae	*Halobacillus* *Bacillus*	Laguna Azul, CA (4560 m) Laguna Vilama, JU (4600 m) Laguna Negra, CA (4400 m) Laguna Aparejos, CA (3600 m)	Fernandez Zenoff *et al.* (5); Dib *et al.* (47); Flores *et al.* (16); Ordoñez *et al.* (4)
		Staphylococcaceae	*Staphylococcus*	Laguna Azul, CA (4560 m) Laguna Verde, CA (4400 m) Laguna Aparejos, CA (3600 m)	Fernandez Zenoff *et al.* (5); Dib *et al.* (47); Flores *et al.* (16); Ordoñez *et al.* (4);
		Not assigned (Order Bacillales)	*Exiguobacterium*	Laguna Negra, CA (4400 m) Laguna Lejía, CH (4325 m) Salar de Aguas Calientes, CH (4200 m)	Flores *et al.* (16); Ordoñez *et al.* (4); Demergasso *et al.* (8)
Proteobacteria	Gammaproteobacteria	Moraxellaceae	*Acinetobacter*	Laguna Azul, CA (4560 m) Laguna Verde, CA (4400 m) Laguna Negra, CA (4400 m)	Fernandez Zenoff *et al.* (5); Dib *et al.* (47) Flores *et al.* (16); Fernandez Zenoff *et al.* (2015); Ordoñez *et al.* (4)
		Pseudomonaceae	*Pseudomonas*	Laguna Vilama, JU (4600 m) Laguna Negra, CA (4400 m) Laguna Verde, CA (4400 m) Salina Grande, JU (3400 m)	Dib *et al.* (47); Flores *et al.* (16); Ordoñez *et al.* (4)
		Pseudoalteromonaceae	*Pseudoalteromonas*	Laguna Negra, CA (4400 m)	Flores *et al.* (16); Ordoñez *et al.* (4)
		Xhantomonadaceae	*Stenotrophomonas*	Laguna Verde, CA (4400 m) Salina Grande, JU (3400 m)	Flores *et al.* (16); Ordoñez *et al.* (4)
		Vibrionaceae	*Salinivibrio*	Laguna Socompa, SA (3570 m)	Gorriti *et al.* (19)
		Halomonadaceae	*Halomonas*	Laguna Lejía, CH (4325 m) Salina Grande, JU (3400 m)	Ordoñez *et al.* (4); Demergasso *et al.* (8)
		Aeromonadaceae	*Aeromonas*	Salar de Aguas Calientes, CH (4200 m) Salina Grande, JU (3400 m)	Ordoñez *et al.* (4); Demergasso *et al.* (8)
		Enterobacteriaceae	*Enterobacter* *Serratia*	Laguna Vilama, JU (4600 m) Salar de Aguas Calientes, CH (4200 m)	Ordoñez *et al.* (4); Dib *et al.* (47); Demergasso *et al.* (8)
		Shewanellaceae	*Shewanella*	Salar de Aguas Calientes, CH (4200 m)	Demergasso *et al.* (8)
		Alteromonadaceae	*Marinobacter*	Salina Grande, JU (3400 m)	Ordoñez *et al.* (4)
	Betaproteobacteria	Comamonadaceae	*Curvibacter*	Laguna Vilama, JU (4600 m)	Ordoñez *et al.* (4)
		Burkholderiaceae	*Burkholderia*	Laguna Aparejos, CA (3600 m)	Ordoñez *et al.* (4)
	Alphaproteobacteria	Sphingomonadaceae	*Sphingomonas*	Laguna Aparejos, CA (3600 m) Laguna Negra, CA (4400 m)	Ordoñez *et al.* (4)
		Rhizobiaceae	*Agrobacterium*	Salina Grande, JU (3400 m)	
		Caulobacteraceae	*Caulobacter*	Laguna Negra, CA (4400 m)	
Bacterioidetes	Flavobacteriia	Flavobacteriaceae	*Psychroflexus*	Salina Grande, JU (3400 m)	Ordoñez *et al.* (4)

CH, Chile; CA, Catamarca; JU, Jujuy; SA, Salta. CA, JU, and SA are provinces from North-Argentina.

mon benefit to HAAL's microbe survival. Microbial mats give way to the spatial compartmentalization of diverse taxonomic groups, which then produces a functional specialization of each layer (79). The first layers are oxic and responsible for light shielding, light conversion and primary production. However, at the HAAL where strong radiation hits the surface of mats the presence of natural UV-sunscreen producers like *Deinococcus radiodurans* or the related microbes (94,95) shielding photosynthetic layers seems mandatory. *Deinococcus radiodurans* belongs to the Deinococcaceae, a family of extremely radiation tolerant bacteria that comprises more than 30 species within a unique genus. Deinococci have been isolated from different environments including soil, water and air as well as feces, hot springs and irradiated food. Fourteen of the currently recognized *Deinococcus* species were isolated from arid environments, like desert soil and Antarctic rock. *Deinococcus radiodurans,* first isolated from canned meat exposed to high ionizing radiation doses—is the best characterized member within this genus. Its extreme resistance phenotype relies on a combination of different molecular mechanisms and physiological determinants (6,96–104). Its UV resistance gives its selective advantage to outcompete other microorganisms in a UV-intense, aerobic and organically rich environment (as found in the mats surface at the HAAL). Also linked to resistance is their special pigmentation, which provides a shelter against UV light for the rest of the community. Deinoxanthin is the shielding carotenoid pigment of *Deinococcus* and explains the pink appearance of Socompa stromatolites. This carotenoid is known for having a strong ability to scavenge for H_2O_2 and $^1O_2$. It also has properties for inhibiting protein oxidation *in vitro* while exerts some protective effect (20%) on plasmid DNA exposed to OH^- (99,102–104). *Deinoccocus* are more abundant in microbialites formed by calcium carbonates than in those mainly shaped by gypsum (51,68). A possible explanation for this observation is that in mats and the aragonite microbialites, bacterial communities are more exposed to UV than in gypsum domes: UV is quenched by the gypsum crust and exposure of the endoevaporitic communities is minimized. High abundance of *Deinococcus* was also reported in several high-altitude microbial systems found in Obsidian Pool siliceous mats at 2400 m in the Yellowstone National Park (105). *Deinococcus* are less common in low-latitude microbialites (76,106).

Microscopic and pigment analyses revealed that the primary producers in the first layer of the Socompa stromatolites are mainly *Microcoleus* cyanobacteria which concentrate in the first 1 mm of the mat, just below the 0.3 mm-white-pinkish Deinococci crust (D. M. Toneatti, unpublished). Thus, cyanobacteria minimize exposure to potentially harmful UV radiation while staying close to the surface to enable photosynthesis. Light measurements indicated that, with depth, both UV light and PAR attenuate steeply in the stromatolites (6). When UV pressure was removed by exposing stromatolites to artificial PAR only, or when placing them in the shadow for a few hours, stromatolite surface changed from white-pinkish to green, which is indicative of upwards migrating cyanobacteria (6). This phenomenon reverted fully when the sample was re-exposed to UV, both *in situ* at the lakes and in in-lab UV conditions. Microscopy and Chla analysis by hyperspectral imaging and HPLC revealed that reversible color changes were correlated with vertical shifts of *Microcoleus* sp. in the stromatolite. This shift also modified the net photosynthetic activity; the non-UV-exposed stromatolite increased its photosynthesis rate about 4.5- and 10-fold in terms of areal and volumetric rates, respectively, quite in accordance with the highest values recorded for benthic photosynthetic systems (107). These findings demonstrate that intense HAAL UV radiation restrains photosynthetic activity, whereas phototaxis is a clear adaptation that allows cyanobacteria to counteract this effect.

Microcoleus and other HAAL microbes can also protect themselves from the intense radiation by means of two other mechanisms: pigmentation and secretion of large quantities of extracellular polymeric substances (EPS).

EPS connect cells and admit physical compartmentalization and isolation from the surrounding environment. In this way, it promotes microbial association and has a protective role against desiccation and other stress factors (78,108). This seems to be the case for various mats at HAAL where EPS was systematically observed in microbialites samples by using scanning electron microscopy (Fig. 2). However, molecular characterization of these compounds is still pending. The synthesis of exopolysaccharides in cyanobacteria may also provide a matrix for mycosporine amino acids (MAAs) and scytonemin, as previously observed (109). Produced by aquatic organisms such as red algae, sea stars, corals, dinoflagellates and cyanobacteria, MAAs are formed by a cyclohexenone or cyclohexenimine core conjugated with the nitrogen moiety of an amino acid (85,110,111). The radiation absorption maxima for these compounds are located in the UV range $\lambda_{\max} < 400$ nm and they are supposed to act as both photoabsorbing UV-pigment and as ROS scavengers (112). Preliminary analyses of cyanobacterial mats from Laguna Socompa and Laguna Diamante revealed the presence of MAAs-like compounds (C. Medina and M. E. Farias, unpublished), with an absorption maximum of around 340 nm, thus supporting this hypothesis.

Carotenoids are known for protecting microbes from intense light damage by quenching reactive oxygen species and triplet-state photosensitizers (113). Carotenoid production significantly improved resistance of some HAAL strains (*Exiguobacterium* spp., *Staphylococcus* spp., *Stenotrophomonas* spp.) under UV-B or/and UV-A treatment (16). However, Ordoñez *et al.* (4) found no direct correlation between pigmentation and high UV-B resistance profiles in a collection of 88 HAAL bacteria. More research will be needed to unravel the role of carotenoids and other pigments in these UV-resistant microbes.

Damage tolerance

The molecular systems that allow HAAL microbes to withstand all types of damage produced by harmful UV levels deserve greater detailed discussions, as the deleterious effects are various through direct production of DNA photoproducts or indirectly, by generating reactive oxygen species (ROS), which then react and affect DNA, proteins and lipids.

Reactive oxygen species are mandatory by-products of aerobic life and their generation and degradation must be kept under delicate cellular control (114). When new ROS sources appear in the cell as a consequence of high toxic elements or UV radiation, a pro-oxidant condition called as oxidative stress settles in (115). Oxidative stress varies among bacteria affecting most cellular processes directly and indirectly and producing oxidative damage of membrane lipids, nucleic acids and proteins (114,116,117). Antioxidant strategies that depend on enzymatic scavengers are widely distributed in nature (118). Among them, catalase and peroxidases enzymes are the ones responsible for the degradation of H_2O_2 and organic peroxides, respectively. Catalases differ from peroxidases in that they do not require reductive cofactors (119); depending on the chemistry of their active site, peroxidases are classified as thiol-based peroxidases or non-thiol peroxidases (120). In turn, superoxide dismutase (SOD) is a potent scavenger, capable of converting the superoxide anion O_2^- to H_2O. There are four types of SOD, depending on their metal centers: Fe, Mn, CuZn and Ni (121).

Enzymatic scavengers were studied in UV-resistant strains *Acinetobacter* sp. Ver3, Ver5, Ver7 and N40 isolated from Laguna Verde and Laguna Negra (4400 m), respectively (116). Ver3 and Ver7 strains were the more resistant and displayed a good tolerance to the pro-oxidants H_2O_2 and methyl viologen (MV) and remarkably high catalase activity (116). Oxidative stress-related genes such as cytosolic and putative periplasmic catalases were described for Ver3 genome and their activity under UV-stress confirmed by biochemical studies and proteomic approaches (27,116). Catalases were also major components of the response to multiple stress conditions (UV-C, H_2O_2 and desiccation) of polyextremophilic *Acinetobacter* strains isolated from spacecraft assembly rooms (89,122).

Acinetobacter sp. Ver3 has several coding-genes for thiol peroxidases: *i.e.* two copies of the *ahpC* gene encoding the AhpC reductase and an *ohr* coding for a putative organic hydroperoxide-resistant protein with high identity with its homolog from *Pseudomonas aeruginosa* (71.7%) (27,123). As *ohr* mutants in other Gammaproteobacteria show normal resistance to H_2O_2 but are sensitive to t-butyl hydroperoxide and cumene hydroperoxide (124–126), we can assume a similar scenario for Ver3.

Acinetobacter sp. Ver3 encodes two predicted SOD: a cytoplasmic FeSOD (EZQ10255) and a periplasmic Cu-ZnSOD (EZQ12222). Di Capua *et al.* (116) gave experimental proof to this outcome, as a single FeSOD band was present in cytosolic extracts of Ver3 cell cultures exposed to UV (27). FeSOD is generally essential in aerobic organisms, whereas the Cu-ZnSODs are present in the periplasm of many gram-negative bacteria, including *Escherichia coli* and *Salmonella*. The enzyme has an important role in these pathogenic organisms in the resistance to exogenously produced ROS, encountered in the course of infections (127,128). In view of such results, the utility of a periplasmic scavenger in Ver3 could be explained if the original lake where *Acinetobacter* was isolated contained harmful concentrations of external O_2^-, likely produced by algae or if Ver3 were an opportunistic pathogen, infecting members of the zooplankton or even flamingoes feeding regularly on the Andean lakes. Both subjects constitute interesting paths for future research on HAAL microbes.

Ver3's superior UV resistance phenotype is not only dependent on the presence of standard sets of genes but upon a tight, effective molecular regulation of its oxidative stress response. Homologs to the regulators OxyR, SoxR and Fur were found in the Ver3 genome; OxyR and SoxRS, activate the expression of Fur, the global repressor of ferric ion uptake in *Escherichia coli*, thus, neutralizing the formation of hydroxyl through the Fenton reaction (129). *oxyR* of Ver3 has the same genetic organization as the corresponding gene in *A. bayly* ADP1, a soil strain (130). This protein reacts to oxidative stress by triggering the expression of detoxification enzymes such as catalases and hydroperoxidases (115). Hence, a similar function may be expected of Ver3.

The differential proteome of Ver3's UV-challenged cells revealed the overexpression of a LuxR-type transcriptional regulator (EZQ11294). Such regulators are involved in Quorum Sensing (QS) and modulate the expression of virulence factors coding genes. Also, they participate in antibiotics biosynthesis, plasmid transfer, bioluminescence, motility and biofilm formation (131). In accordance, there is strong experimental evidence suggesting that UV challenge promotes cell aggregation and biofilm formation in Ver3 on synthetic surfaces (V. H. Albarracin, unpublished). On the other hand, chemotaxis protein CheY (EZQ10062) was found down regulated in Ver3 UV-challenged cells. These proteins are single-domain response regulators involved in chemotaxis (132) though for Ver3 this putative chemotaxis protein presents a CheY-like domain (Pfam PF00072) and a DNA-binding domain, which suggests a transcriptional regulatory function. Interestingly, a histidine kinase sensor (EZQ10063) was found downstream, that would insinuate a two-component signal transduction system modulated by UV. Light sensors with a function similar to plant UVR8 (133) were expected, but not found, after a BLAST search with conserved UVR8 domains in the *Acinetobacter* sp. Ver3 genome (27). Instead, Ver3 may be indirectly sensing UV light through redox changes at the cytoplasm and proteins. One protein likely for this function (EZQ10399) has two PAS domains including heme pockets, which might be involved in oxygen/redox sensing. It presents conserved domains for histidine kinase and ATPase, and in the same genomic region, a putative DNA-binding response regulator belonging also to the LuxR family (EZQ10400). Ver3 also presented a coding-sequence, PhlK (EZQ01671), highly homologous to iron-sulfur bacterial cryptochromes and photolyases (FeS-BCP). These proteins were found widespread in most available prokaryote genomes and they bear a Fe-S cluster, a FAD chromophore and 6,7-dimethyl-8-ribityllumazine (DMRL) as antenna pigment (134,135). A BLAST search with Ver3 PhlK retrieved proteins with high identity levels (>90%) in other *Acinetobacter* sp. strains. The putative FeS-BCP from Ver3 had 50.4% identity with RsCryB from *Rhodobacter sphaeroides* (136) and 49.2% identity with *Agrobacterium tumefaciens* (134,135), the only two members of this family characterized so far. RsCryB controlled the expression of genes in the photosynthetic apparatus but shows no repair activity *in vitro*. Instead, PhrB was confirmed as the first prokaryotic (6-4) photolyase. It was stated that [4Fe-4S] cluster of RsCryB can be oxidized, acting as a sensor for reactive oxygen species under photooxidative stress (136). A possible role for Ver3 PhlK on sensing photooxidative UV-induced stress for triggering DNA repair could alternatively explain Ver3 high resistance. Further research to obtain knock-out mutants on this gene will help elucidate its puzzling function.

ROS scavenging is an important strategy in the control of oxidative damage, but once ROS or direct UV has reached DNA, damage tolerance will be needed before repair systems can take action. HAAL *Acinetobacter* spp. were highly competent bypassing DNA lesions (18) as they displayed the higher UV-B resistance profiles when compared to control strains (reference strains within *Acinetobacter,* Fig. 3), however, they also showed greater photoproduct accumulation (25% more). For instance, Ver3 cells exposed to UV-B (1.2 kJ m^{-2}) gathered 400 CPDs per 10^6 bases while maintaining the viable population unchanged with respect to the nonexposed control. Under the same conditions, exposed *E. coli* cultures perished after the treatment and displayed *ca* 200 CPDs per 10^6 bases (20). The Ver3 genome encodes three operons for error-prone DNA polymerase type V coding-genes (*umuDC*), and a type IV DNA polymerase homolog suggesting dimer bypass and SOS mutagenic response (137) which will support the ability of Ver3 to withstand such high levels of damage without losing viability. Photoproduct bypass allows cells to replicate but promotes mutations; the high mutagenicity tendency of HAAL strains was reported in antibiotic-resistant strains (47), and can explain the abundant repetitive sequences in HAAL megaplasmids (28). On the other hand, strong mutation rates can be useful for adaptation and subsistence in highly UV-exposed environments with both steady and changing environmental conditions.

UV-damage repair

As a third mechanism for counteracting the detrimental effects of UV radiation, HAAL strains are proficient in repairing photoproducts produced by UV-B light. There are several mechanisms to repair DNA photodamage such as photoreactivation, excision repair, mismatch repair (MMR) or double strand break (DSB) repair. In addition, damage tolerance (dimer bypass) and SOS (save our soul) response ensure genomic integrity (138). Well-conserved enzymes called “photolyases” accomplish photorepair. These monomeric proteins (53–66 kDa) have a flavin adenine dinucleotide (FAD) as cofactor and antenna pigments such as deazaflavin, methenyltetrahydrofolate derivatives or DMRL (139). Photolyases (PLs) are considered to be among some of nature’ s initial solutions to the hazard of DNA damage produced by high UV exposure (139). Thus, studies on these photoreceptors in an environment resembling that of ancient Earth with such levels of solar exposure make this topic quite appealing.

The most common photoproduct repair by PLs is the cis-syn cyclobutane pyrimidine dimer (CPD), formed by a [2 + 2] cycloaddition of two adjacent pyrimidine bases (140). Such CPD lesions cause polymerases to stop, and eventually leads to cell death. Photolyases bind tightly to CPDs in the dark and, upon absorption of UV-A and/or blue light (320–470 nm) by semireduced FAD cofactor (FADH•−), a downhill electron transfer-driven reaction is produced. The final result is the splitting of the two C–C bonds in the CPD unit and the re-formation of the two separate pyrimidine bases (140). For HAAL strains, CPDs were more efficiently removed than 6-4PPs under light conditions indicating that a CPD-photolyase was present in these strains (18). For instance, under photorepair (PR) and dark repair (DR) treatments, *Acinetobacter* sp. Ver3 and Ver7, decreased their photoproducts in 69 and 85% (PR) and 22 and 38% (DR), respectively. In turn, *A. baumannii* displayed no significant PR or DR capabilities whereas, under PR, *A. johnsonii* achieved 31% of reduction in DNA lesions, whereas no repair was observed for control samples left in the dark. Survival and CPD removal after UV-B exposure was similarly studied in the marine bacteria *Photobacterium angustum* S14 and *Sphingopyxis alaskensis* RB2256 (141): after an UV-B exposure of 1.08 kJ m^{-2}, *ca* 120 lesions per 10^6 bases were accumulated by both strains. Subsequent recovery treatments were effective to decrease photoproducts. In the case of S14, the lesions decreased in 75 or 100% (DR 3 or 6 h, respectively) or in 100% (PR, 3 h), whereas for *S. alaskensis*, PR (85% of repair, 6 h) was significantly higher than DR (50% of repair, 18 h).

Currently, the most studied photolyase from HAAL is Ver3Phr (WP035267313) from *Acinetobacter* sp. Ver3 (18,20). Based on sequence alignments and secondary structure predictions, a high sequential and secondary structural similarity was found between this novel photolyase and that from *Acinetobacter tandoii* (65% identity; WP016167485.1). Ver3Phr belonged to the Class I CPD-photolyases, placing it within the same group of the well-characterized *E. coli* photolyase (142). The strong kinship between the 3D structures of Ver3 and *E. coli* (PDB 1DNPA) becomes manifest even when they only share 41% identity (18). Ver3Phr has the typical folding motif of photolyases: an N-terminal antiparallel bundle of beta sheets enclosed by alpha helices. A proximal alpha-beta domain and a distal helical domain that binds to FAD, fully matches with the structure of the *E. coli* photolyase (EcPhr). The residues Asp105, Glu106, Lys298, Glu368 and Leu380 that interact with the antenna chromophore 5,10-methenyltetrahydrofolylpolyglutamate (MTHF) are conserved in both, EcPhr and Ver3Phr, although instead of a Cys292 (EcPhr), Ver3Phr has a Ser297. The residues Tyr225, Thr237, Ser238, Leu240, Ser241, Trp276, Arg283, Trp343, Asn346, Asp377, Asp379 and Ala382 that interact with FAD are conserved in Ver3Phr, except for Gln239 that replaces an arginine residue (Arg236) on EcPhr (18). The three tryptophans (Trp311, Trp364 and Trp387)—in close proximity to the isoalloxazine ring of FAD and involved in electron transfer (143)—are also conserved in Ver3 photolyase. This arrangement supports the putative CPD-photolyase function and agrees with Ver3 competence for repairing CPDs lesions. Moreover, Ver3Phr repair activity was confirmed when cloned in a heterologous host (20).

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

The exceptional microbiological diversity inhabiting HAAL deals with high levels of an extreme changes in salinity, temperature and UV dose. Under such pressure, extensive genotypic and physiological species diversification was observed, *e.g.* in microbial mats and especially in cooperative structures such as stromatolites where function compartmentalization admits of stricter control of fluctuating conditions and lower exposure to common extreme factors, mainly UV.

Future research directions will need to exploit next-generation sequencing technologies as essential tools for a much broader characterization of genomes of model strains and metagenomes of the most complex microbial communities. So far, eight complete genome sequences have been deposited: *Halorubrum* sp. AJ67 (CBVY01, L. Antofalla, benthonic), *Sphingomonas* sp. S17 (AFGG01), *Exiguobacterium* sp. S17 (ASXD01) and *Salinivibrio* sp. S10B (AQOE01) (L. Socompa, stromatolite), *Salinivibrio* sp. S34 (APMS01, L. Socompa, benthonic), *Salinivibrio* sp. S35 (AQOD01, L. Socompa, planktonic), *Acinetobacter* sp. Ver3 (JFYL01, L. Verde, planktonic) and *Nitrincola* sp. A-D6 (JRLB00000000, S. Ascotán, soil). In addition, four megaplasmid sequences were obtained: pLMV7 (KF577591, *Micrococcus* sp. V7, L. Vilama, planktonic), pAP13 (KF577590, *Brevibacterium* sp. Ap13, L. Aparejos, flamingo feces), pLMA1 (NC024972, *Micrococcus* sp. A1, L. Azul, planktonic), pJD12 (KR152226, *Micrococcus* sp. D12, red biofilm, L. Diamante) (19,21,22,24–28,72). Meanwhile, metagenomic shotgun sequencing is in progress. However, state-of-the-art functional genomics, proteomics and transcriptomics as well as a systems biology approach are essential to the comprehensive understanding of these microbes’ adaptation to extreme conditions, including outstandingly high UV exposure. Special attention will be given to the search and functional analysis of photoreceptors for different wavelengths such as BLUF, LOV, cryptochromes, photolyases, bacteriophytochromes, proteorhodopsins, which were preliminary detected in various genomic and metagenomic sequences available to HAAL microbial communities.

Furthermore, we emphasize the still largely unidentified biotechnological and evolutionary potential of these environments, exemplified by the two most fascinating illustrations of HAAL: NASA’s classification of some of the lakes as model systems for prospecting life on other planets, which is a topic of utmost relevance in astrobiology. A window overlooking the early origins of life accompanies this window into space: modern stromatolites thriving in Lake Socompa (3570 m) are located at very high altitude and are the most exposed to hostile conditions, providing HAAL with an exceptional template for studies on early life development.

One cannot put enough emphasis on how extremely fragile these pristine Puna-High Andes environments are. Intense grazing, adventure tourism, climate change and mining prospects are the main potential threats to biodiversity and hydrological function in this region. The vast abundance of minerals (lithium, copper, gold among others) of the Atacama-Puna Area indicates that mining enterprise will continue to expand significantly in the following years jeopardizing water cycles and compromising the indigenous microbiota among many other living forms—even humans! As a result, the scientific study of such unique landscape/environment meets a paramount social function. Accordingly, the aim of our research project is not only scientific, but has also an educative facet with an intended strong social impact. Our studies on HAAL microbial communities will bring more public attention to the biologic uniqueness and fragile nature of this environment. Research efforts are helping support an initiative intensely aimed at establishing an environmental protection program that would include in-site monitoring stations, impact assessment on microbiota as mandatory requirement for installing new mining projects and legally protected areas for this invaluable microbiodiversity treasure that must be preserved and protected for generations to come.

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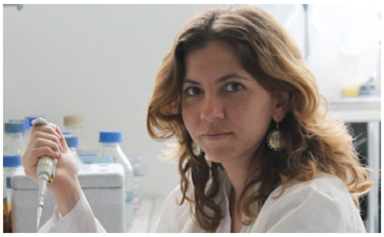
AUTHOR BIOGRAPHIES



Virginia Helena Albarracín studied Biology and Biochemistry at the University of Tucumán, Argentina. She is Head and group leader at the Center for Electron Microscopy of CONICET (Tucumán). She is a CONICET adjunct researcher at PROIMI-CONICET (Tucumán). She is Full Professor and teaches molecular biology at Univ. Tucumán. Her research topics are related with molecular photobiology of microbial extremophiles.

Wolfgang Gärtner studied Chemistry (Universities of Göttingen and Würzburg). He habilitated in 1993 and was nominated Professor adjunct (1999). He is group leader at Max-Planck-Institute for Chemical Energy Conversion (Mülheim) and teaches biochemistry at Univ. Düsseldorf. His research topics are structure–function relations in biologic photosensors.

María Eugenia Farias studied Biology at the University of Tucumán, Argentina. She is Head and group leader at the Lab of Microbial Research on Andean Lakes from PROIMI-CONICET (Tucumán). She is an independent researcher of CONICET. Her research topics are related to several aspects of the biodiversity and microbial ecology of high-altitude Andean lakes extremophiles.