Biosignatures and microbial fossils in endolithic microbial communities colonizing Ca-sulfate crusts in the Atacama Desert

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Abstract

Since the description of microbial communities colonizing Ca-sulfate crusts in the Atacama Desert, there has been much interest in the mechanisms that could lead to the formation and preservation of biosignatures or microbial fossils of these communities. A key to understanding physico-chemical processes of taphonomy and early diagenesis is to examine microfossils in their natural environment. In this study, we characterize organomineral traces and microbial fossils found around microbial communities present in these Ca-sulfate crusts. Through scanning electron microscopy, microanalytical (EDS) and Raman spectroscopy techniques, calcium carbonate precipitates were detected around remnants of cryptoendolithic algae beneath the crust surface. As what seems to be the final step in the organomineralization of these cryptoendolithic communities, we also observed alga

cell remains permineralized by Mg-Si-rich minerals inside gypsum crystals. Additionally, Mg-Si bearing minerals formed a web-like structure within the hypoendolithic cyanobacterial habitat via permineralization of extracellular polymeric substances. Our observations indicate that despite the extremely hyperarid environment, microenvironmental conditions may be appropriate for the formation of biosignatures and microbial fossils of extinct endolithic microbial communities. A model of the possible organomineralization processes involved is presented.

Keywords

Atacama Desert, organominerals, biosignatures, endoliths, microbial fossils, Mg-silicates

Highlights

- Mineral biosignatures of the endolithic microbial communities of Atacama's Ca-sulfate crust were characterized in their microhabitat by SEM-BSE, EDS and FT-Raman spectroscopy.
- Cryptoendolithic algae induced the precipitation of calcium carbonate within the pores of Ca-sulfate crusts.
- Magnesium silicate minerals permineralized algal cells and extracellular polymeric substances in endolithic habitats.
- Through taphonomic processes and diagenesis, organomineral traces of microbial life were generated in Atacama's Ca-sulfate crusts.
- Our data suggest organomineralization processes in this extremely hyperarid environment.

1. Introduction

Organomineralization *s. l.* (Dupraz et al., 2009) is a major focus of many investigations of life in extreme environments or studies with astrobiological implications (Brasier and Wacey, 2012; Westall et al., 2011, 2015 and articles herein). Such studies require an understanding of mechanisms of organomineral formation to distinguish between biotic and abiotic features. An attractive line of investigation in

the field of extreme arid environments is the view of these settings as terrestrial analogs to address the early habitability of Mars. Evaporite minerals such as gypsum deposits are frequent candidates for this type of investigation because their presence is consistent with possibly habitable environmental conditions on Mars (Farmer and Des Marais, 1999; Glamoclija et al., 2012; Summons et al., 2011; Szyrkiewicz et al., 2010). Similarly, highly resilient microbial communities found in extreme environments are useful model systems of evaporite-bearing Martian deposits (Gendrin et al., 2005; McLennan et al., 2005; Osterloo et al., 2008, 2010; Roach et al., 2009). Microbial communities within evaporite rocks in extreme environments were recently described as the last possible outposts for life on Mars (Dávila and Schulze-Makuch, 2016). However, on Earth's surface UV radiation hazards are not comparable to the cosmic rays and solar energy particles on Mars' surface (Hassler, 2014). This means that the implications of these different conditions for microbial survival or the preservation potential of organic biosignatures need to be taken into account.

Northern Chile's Atacama Desert is one of the driest places on Earth. According to geological and soil mineral data, this desert has experienced extreme aridity for >10–15 million years (Houston and Hartley, 2003). The Atacama Desert has thus been described as a natural laboratory to explore the limits of life and processes of decay or extinction. Conditions in some areas of the Atacama Desert are so harsh that the presence of highly selective endolithic microbial ecosystems makes these areas an excellent target for the search for traces of microbial life. While microbial activity in the Atacama's hyperarid core area is scarce (Connon et al., 2007; Crits-Christoph et al., 2013; Drees et al., 2006; Navarro-González et al., 2003; Neilson et al., 2012), several forms of endolithic microbial colonization have been detected within rocks such as: halite (De los Ríos et al., 2010; Robinson et al., 2014; Vitek et al., 2010; Wierzchos et al., 2006); Ca-sulfate crusts (Dong et al., 2007; Cámara, 2012; Vitek et al., 2013; Wierzchos et al., 2011, 2015); ignimbrites (Cámara et al., 2014; Wierzchos et al., 2013) and calcite and rhyolite (DiRuggiero et al., 2013). In addition, the undersides of quartz rocks show another form of colonization known as hypolithic (Azúa-Bustos et al., 2010; Lacap et al., 2011; Warren-Rhodes et al., 2006, 2007).

Gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) deposits are able to host endolithic photosynthetic microbial communities with microaerobic and low light requirements (Boison et al.,

2004), providing protection against ultraviolet radiation (Cockell et al., 2010; Edwards et al., 2006; Hughes and Lawley, 2003; Wierzchos et al., 2015), desiccation (Dong et al., 2007; Wierzchos et al., 2011) and extreme low temperature conditions (Friedmann, 1982; Rhind et al., 2014; Ziolkowski et al., 2013). The reporting of endolithic microbial colonization of Ca-sulfate crusts in the Atacama Desert has sparked interest in the mechanisms that could lead to the preservation of fossils or biosignatures of these communities. As far as we know, few morphological biosignature studies have examined this type of substrate (Allwood et al., 2013) despite numerous molecular biomarker studies focusing on substrates such as halite (Vitek et al., 2012, 2014a), gypsum crusts (Edwards et al., 2007; Stivaletta et al., 2010; Vitek et al., 2014b) as well as soil (Skelley et al., 2007). A current topic of interest is the description of processes of organomineralization that take place in water-limited conditions such as those in our study. The question that arises is how mineral precipitation occurs in such hyperarid conditions. In prior work describing the endolithic colonization of these Ca-sulfate crusts, we reported microclimate conditions of no rain and extremely low relative humidity (RH) values in the middle of the day (Wierzchos et al., 2011). However, the present study area in the southwestern Tarapacá region has been described as foggy (Cereceda et al., 2008a, 2008b). Surprisingly, some areas in this region have a high biodiversity of vascular plant ecosystems, depending mostly on fog oases, and epilithic lichens (Cámara, 2012; Vargas Castillo and Beck, 2012; Wierzchos et al., 2011). Such environmental conditions indicate that water condenses frequently at night on the Ca-sulfate crust surface through absorption of fog micro-droplets. Moreover, overnight relative atmospheric humidity values, often above the 85%, and relatively low temperatures (Wierzchos et al., 2011) are likely to give rise to dewfall precipitation on the Ca-sulfate crust surface. These moist conditions are appropriate for organomineralization processes inside the Ca-sulfate crust allowing for the formation of biosignatures and microfossils.

Electron microscopy has proven useful to describe endolithic microbial fossils and biosignatures in the Dry Valleys of Antarctica (Ascaso and Wierzchos, 2002, 2003; De los Ríos et al., 2005, 2014; Wierzchos and Ascaso, 2001, 2002; Wierzchos et al., 2003, 2005). In the present study, we use these same electron microscopy techniques to describe the endolithic microhabitat provided by the Ca-sulfate crusts of Atacama's

hyperarid zone. This *in situ* approach reveals endolithic communities in different stages of viability, decay and early and/or advanced permineralization in their natural environment. Based on these observations, we propose a model for the organomineralization processes that give rise to fossils and biosignatures of contemporary endolithic microbial communities in this environment.

2. Material and Methods

2.1 Study site and sampling

Samples of Ca-sulfate crusts were collected during field expeditions in April 2008, May 2009 and January 2010 from the southwest Tarapacá region, 22 km from the Pacific Ocean coast and 940 m a.s.l. (20° 43'56.0''S; 69°58'30.2''W). This region is a hyperarid zone of the Atacama Desert that experiences extremely low rainfall of about 3 mm yr⁻¹ or less (Houston, 2006a) and rain events typically occur once per decade (Houston, 2006b). Rainfall sensors installed in the sampling area registered no rainfall in 2010 and 2011. However, relative humidity (RH) probes indicated high quantities of moisture provided by fog with mean annual RH values of 47.97% (Wierzchos et al., 2011). Mean annual temperature at the sampling site was 20.34°C ± 6.38 from May 2008 to May 2009 (Wierzchos et al., 2011). In this zone, Ca-sulfate crusts composed mainly of gypsum (70-90%), anhydrite (10-30 %) and minor amounts of quartz, potassium feldspar and calcite (Wierzchos et al., 2011) were randomly spread across the ground surface (Fig. 1a). The crusts were about 5-10 cm in diameter and 0.5 to 5 cm thick (Fig. 1b). Microbial colonization of these crusts has been recently characterized by Wierzchos et al. (2011), Cámara (2012) and Vitek et al. (2013), describing endolithic microbial communities composed of free-living and lichenized algae, fungi and cyanobacteria and non-photosynthetic bacteria. Frequently in freshly fractured samples, a thin green layer or spots of colonization just beneath Ca-sulfate crust surface can be distinguished (Fig. 1c).

2.2 Scanning electron microscopy

To examine cross sections, samples of Ca-sulfate crust were prepared according to a described method (Ascaso and Wierzchos, 1994) with recent modifications by Wierzchos et al. (2011). For the backscattered electron mode of scanning electron

microscopy (SEM-BSE), crust pieces with endolithic colonization were fixed in 3% glutaraldehyde, postfixed in 1% osmium tetroxide solution, and dehydrated in a graded ethanol series and finally embedded in LR-White resin. To detect the presence of organic remains of decayed cells, some of the samples were stained with a saturated uranyl acetate solution in 70% ethanol during dehydration according to the SEM-BSE sample preparation protocol. As uranyl acetate stains organic matter (Silva et al., 1968; Terzakis, 1968), its SEM-BSE visualization, supported by qualitative energy dispersive X-ray spectroscopy (EDS), indicated the existence of remains of organic components in the areas showing mineral precipitates. Blocks of resin-embedded rock samples were then polished, carbon coated, and viewed with a Zeiss DMS 960 SEM microscope equipped with an EDS Link-ISI microanalytical system (Oxford). This system was used for elemental qualitative and semiquantitative analyses of minerals

2.3 FT-Raman analysis

The mineralogy of the parent material and calcium-enriched precipitate was examined by FT-Raman spectroscopy in spot laser beam mode using a Thermo Scientific DXR Raman microscope. Samples previously embedded in LR-White resin for SEM-BSE observation were polished to remove the carbon coating and then excited using a 532 nm laser beam of laser power 0.7 mW and 1 μm of spatial resolution. Raman spectra were obtained using x50 and x100 objectives. To improve the signal-to-noise ratios of recorded spectra, 5 exposures of 10 seconds and accumulation stacks of 1 to 20 of spectra were used. Raman spot analyses were performed on the sample zones previously examined by SEM-BSE+EDS for correlative spectroscopy (Raman + EDS). Prior to Raman spectroscopy, the carbon coating was removed by mild polishing with a suspension of diamond grains (diameter 0.25 μm). After this, spot confocal Raman analyses were performed focusing the laser just below the mineral surface. Several analytical spots were recorded for each zone; in the Results we provide the most representative Raman spectrum.

3. Results

In the study area, Ca-sulfate crusts showed abundant endolithic colonization yet scarce epilithic forms, as described in Wierzbos et al. (2011) and Cámara (2012). On some crusts, lichen thalli colonized the surface, while inside coexisted different types of microorganisms appearing as a green band or spots in cross-section (Fig. 1c). Almost all the large pores a few millimeters beneath the crust surface were colonized by cryptoendolithic microbial communities (arrows in Fig. 2a). A detailed view of these cavities revealed complexes of algal cells and fungal hyphae (Figs. 2b and 2c). Abundant fungal colonization was apparent in some cryptoendolithic zones penetrating the gypsum crystals (Fig. 2d and Supplementary Data (SD)1). Within the hypoendolithic habitat, on the underside of the Ca-sulfate crusts, bacterial communities were detected (arrows in Fig. 2e). At higher magnification, hypoendolithic aggregates showed mineral deposits within the matrix of extracellular polymeric substances (arrows in Fig. 2f and marked areas in SD2) around both living and decaying cyanobacterial cells (arrows in SD2). EDS point microanalysis of these mineral precipitates (asterisk in SD2) indicated the presence of elements such as Mg, Si and Al (spectra in SD2).

Within the cryptoendolithic zone, our SEM-BSE images revealed a sponge-like microfabric (Fig. 3a). This mineral precipitate bore circular pits of similar size to live algal cells. We selected the area indicated with a box in Fig. 3a containing this sponge-like mineral to generate EDS distribution maps of Mg, Si, S, and Ca, as shown in Fig. 3b. The EDS map of Ca overlapped with gypsum and the spongy structure (asterisks in Fig. 3b). A higher intensity Ca signal was detected within the spongy structure due to a higher $\text{CaK}\alpha$ signal. Mg and Si maps revealed the presence of these elements in the area of the Ca-rich precipitate (see Mg and Si maps in Fig. 3b). The SEM-BSE image in Fig. 3c shows the sponge-like precipitate in detail with much denser calcium precipitates in close proximity to these decayed algal cells. The distribution of Mg and Si follows the interior of the voids and distribution of Ca (from CaCO_3 surrounding the Mg-Si features (see EDS maps in SD3). In some areas, Ca-rich early stage precipitates appeared as individual cube-shaped crystals (arrows Fig. 3d) and in others as a compact deposit (triangles in Fig. 3e) surrounding Mg-Si rich mineral spherical structures (arrows in Fig. 3e). The CaCO_3 nature of this spongy structure was confirmed by quantitative EDS microanalysis using the Link-ISIS library standard (data not shown)

and by FT-Raman spectroscopy. This microanalytical approach was used as complementary tool to the EDS system. Micro-Raman spot analysis of the Ca-rich deposits provided spectral characteristic of the calcium carbonate (Fig. 3f). Additionally, we obtained the Raman spectrum for the surrounding gypsum (Fig. 3g). However, the amorphous nature of the Mg-silicates (arrows in Fig. 3e) meant it was not possible to obtain a FT-Raman signal. It should be noted that fungi or their remains were not observed in these carbonate precipitates. The presence of remains of organic matter in these structures was evaluated using an indirect approach. Some samples were treated with uranyl acetate during the dehydration step. This compound contrasts organic remains and generates a strong signal on the SEM-BSE images (see example in SD4). The elemental EDS maps showed an increased uranium signal in circular areas tracing the shape and size of potential algae cells (see circles in SD5).

Mg-Si-rich spherical structures were found embedded inside the gypsum matrix (asterisk in Fig. 4a). However, other Mg-Si-rich spheres appeared surrounded by calcium carbonate precipitates (black arrows in Fig. 4a). This characteristic distribution of minerals and structures was confirmed by Mg, Si, S and Ca EDS distribution maps, as shown in Fig. 4b. The EDS spot microanalysis of several sphere-like structures confirmed the presence of Mg, Si and O as major elements (top graph in Fig. 4c). The micromorphology of these Mg-Si-rich sphere-like structures was consistent with that of live algal cells of about 10 μm in diameter. When these well-defined sphere-like structures were found within the large gypsum matrix, sponge-like calcium carbonate deposits were rather infrequent.

Organominerals deposits in hypoendolithic zones differed from elsewhere described cryptoendolithic zones. Our detailed SEM-BSE study and EDS microanalysis revealed the presence of a Mg-Si-rich fibrous mineral within some of the pores and cavities close to the gypsum crust bottom. These fibrous minerals appeared around empty holes of approximately 1-2 μm in diameter and formed a web-like structure (Fig. 4d). The presence of Mg and Si, as well as O as major elements composing the fibrous mineral was confirmed by EDS spot microanalysis (bottom graph in Fig. 4c). Mg-Si-rich web-like precipitates were found only within the hypoendolithic colonization zone, whereas the interior gypsum crust was free of these deposits.

Calcium carbonate deposits were not found within the hypoendolithic bacterial communities.

4. Discussion

4.1. Moisture sources for Ca-sulfate crusts

Several lines of evidence indicate that microbial-mineral interactions in the Ca-sulfate crusts of the hyperarid zone of the Atacama Desert could lead to the formation of biosignatures and microbial fossils via organomineralization processes. This organomineralization should occur as the dissolution and precipitation of minerals in endolithic locations. The movement of ions in the surroundings in response to daily cycles in atmospheric moisture could allow for dissolution and precipitation processes inducing passive Mg-Si permineralization and the growth of calcium carbonate crystals in endolithic habitats around microbial communities. Dewfall as a main water source for endolithic microbial communities has been previously described in hyperarid zones of the Atacama Desert (DiRuggiero et al., 2013) and in the Dry Valleys of Antarctica (Büdel et al., 2008). Water infiltrating gypsum crusts as microdroplets of fog or water deposited by dewfall events is a substantial source of liquid water for living endolithic communities. Thus, in the Pacific Ocean Coastal Range of the Atacama Desert, hypolithic cyanobacteria are sustained mainly by fog (Azúa-Bustos et al., 2011). According to our proposed model, water deposited on the Ca-sulfate crust surface at night infiltrates the crust by gravity and capillary suction through intercrystalline spaces. This percolated water could remain within the crust several hours causing dissolution of gypsum and relocation of ions. In addition, day-time evaporation could induce the upward movement of water and gypsum recrystallization. Similar processes of gypsum crust deformation and upwarping have been described on a larger scale for semiarid environments (Artieda, 2013).

4.2. Calcium carbonate precipitation

Carbonate precipitation around cryptoendolithic algae in arid environments is a novel finding of this study. Several experimental studies conducted in aquatic environments have revealed calcium carbonate precipitation around algal cells and

this process has been linked to photosynthesis (Borowitzka, 1987; McConnaughey and Falk, 1991). In an algae microsensor study, it was concluded that calcium precipitation dynamics were determined by local pH increases at the calcification micro-site and by over-saturation of calcium carbonate in the microenvironment (De Beer and Larkum, 2001). In our study, calcium carbonate precipitates were detected only in the proximity of algal cell remains, not around living communities. In the latter zone, the balance between alkalization due to photosynthetic activity and respiration induced acidification by fungi could result in pH conditions less prone for carbonate precipitation. However, we cannot rule out the presence of dispersed nanoscopic calcium carbonate crystals around living alga cells precipitated via bicarbonate photosynthesis (McConnaughey and Whelan, 1997; McConnaughey, 1998). As calcium carbonate might be dissolved by carbonic acid formed as a result of CO₂ production due to respiration by fungi, overall calcification might not be observed. These hypothetical calcium carbonate nano-crystals could form nucleation spots leading to the final precipitation of calcium carbonate in periods of water loss through evaporation, when physiological activity diminishes and algae decay. It is commonly accepted that around decayed phototrophic alga cells, the population of heterotrophic bacteria expands. Intense research efforts have focused on the bacterial precipitation of calcium carbonate polymorphs, as reviewed by González-Muñoz et al. (2010 and references herein). Moreover, even after bacterial suppression of activity, dead cells could induce calcium carbonate precipitation, as observed by Bosak and Newman (2003). This process of calcium carbonate precipitation might appear analogous to calcite biomineralization, though it differs in that it is mediated by nonliving organic matter.

Light penetration within the endolithic habitat appears to be a key factor delimiting the depth of colonization and thickness of the algal zone (Hall et al., 2008). In addition, different light intensities penetrating through various types of rocks have shown differences in photosynthetic active radiation (PAR) levels, with described effects on photosynthesis yields and thus on the dynamics of calcium carbonate precipitation (Bell, 1993; Oren et al., 1995). Given the important role played by PAR intensity on photosynthesis rates in endolithic habitats, we propose this factor might also induce the presence of calcium carbonate precipitates in the potentially “lighter”

conditions of cryptoendolithic zones and their absence in the “darker” hypoendolithic habitat. Studies conducted on other Atacama substrates have revealed the stratified distribution of photosynthetic communities (Robinson et al., 2014; Roldán et al., 2014; Wierzchos et al., 2015) and how uppermost algae show the characteristics of those inhabiting high light environments. These characteristics include orange or red secondary pigments in green algae (Wierzchos et al., 2015) and pigmented sheaths in endolithic cyanobacteria and less pigmented sheaths in hypoendolithic communities (Vitek et al., 2013, 2014b). An alternative explanation for the absence of carbonate precipitation in the hypoendolithic zone is that the production of large amounts of extracellular polymeric substances by cyanobacteria or their physiological conditions could inhibit carbonate precipitation via cation sequestering, as confirmed by several authors (Arp et al., 1999, 2012; Dupraz and Visscher, 2005; Obst et al., 2009a, 2009b; Spitzer et al., 2015). Microsensor studies have shown that under low light intensities, relatively stable, low pH values are related to constant Ca²⁺ concentrations and thus a lack of precipitation (Arp et al., 2010; Shiraishi et al., 2008a, 2008b). Above all, microsensor measurements in freshwater cyanobacterial communities have revealed light microgradients that are too low to induce CaCO₃ precipitation. Further, differences in calcium carbonate precipitation have been also described in relation to light irradiance and temperatures (Arp et al., 2001; Bissett et al., 2008a, 2008b).

4.3. *Mg-silicate precipitation*

Mg-Si-rich precipitates of biological origin have been described in several modern lacustrine microbialites (Arp et al., 2003; Benzerara et al., 2010; Bontognali et al., 2010; Pacton et al. 2012; Souza-Egipsy et al., 2005), and evaporitic environments (Jones, 2010; Lveill et al., 2000; Lveill et al., 2002a, 2002b). Mg silicates associated with the cell walls of acidophilic algae have been also described in riverbed sediments in extremely acidic conditions (Souza-Egipsy et al., 2010). Experimental studies have shown that silicification associated with Mg-complexation is also related to the presence of extracellular polymeric substances and bacterial or archaeal cells (Inisto et al., 2015; Orange et al., 2009). In environmental and morphological terms, the Mg-Si precipitates found in the present study may be akin to kerolite (Mg₃Si₄O₁₀[OH]₂·nH₂O), described as a poorly crystalline, fine-grained precipitate found in gypsum deposits on

the walls of Hawaiian caves (Léveillé et al., 2000, 2002a,2002b). However, we were unable to resolve the mineral composition of these Mg-Si precipitates by XRD or FT-Raman spectroscopy given the small amounts detected within the bulk gypsum of our samples. Hence, different formation processes of this authigenic Mg silicate could take place in Atacama's endolithic habitat.

Experimental results have indicated that the neoformation of Mg-rich silicates from solution may often begin with rapid nucleation (Tosca and Masterson, 2014). Subsequent dehydration will lead to progressive layer stacking and could occur in response to wetting/drying cycles, prolonged exposure to high salinity solutions, or burial and heating. Environmental gel dehydration has been proposed as a main driver of the formation of kerolite, a Mg-silicate precipitate associated with microbial mats in speleothems observed in basalt rock caves in Hawaii (Léveillé et al., 2000, 2002a,2002b). The porous structure and microenvironmental conditions of Atacama's Ca-sulfate crusts could locally favor some of these processes.

Biologically-mediated clay mineral authigenesis may be driven by the binding of silica and metal ions through interactions with cell wall polymers or extracellular polymeric substances (Beveridge et al., 1983; Ferris et al., 1987; Fortin et al., 1998; Konhauser and Urrutia, 1999; Urrutia and Beveridge, 1993, 1994). Metal binding may inhibit autolytic activity within an organism after death (Ferris et al., 1988) enhancing its post-mortem morphological preservation (Konhauser et al., 1994). Mg cations seem to be particularly attracted to cell walls and sheaths as seen in other studies (Souza-Egipsy et al., 2005, 2010). In effect, these structures are especially adept at binding metal ions and nucleating phyllosilicates (Ueshima et al., 2004). Our findings suggest that extracellular polymeric substances around cryptoendolithic algae and hypoendolithic cyanobacteria form a nucleating matrix for minerals that is well preserved in Atacama's gypsum crusts. According to the model proposed below, amorphous and hydrous silica precursor phases probably formed first within the endolithic habitat, and later diagenesis, dehydration and re-organization would give rise to more crystalline phases. Experimental studies have shown that the presence of silica favors the rapid stabilization of extracellular polymeric substances and organic membranes providing physical protection against degradation (Orange et al., 2012). The results of other studies have indicated that the first steps of permineralization or

encrustation of cells conditions their chemical and morphological preservation potential during fossilization (Li et al., 2013, 2014; Orange et al., 2014; Yee et al., 2003). In other cases, depending on the type of cell wall, only extracellular polymeric substances were preserved and archaea cells were lysed (Orange et al., 2009), although characteristic organic components were still identifiable after one year of experimental silicification (Orange et al., 2012). Commencing with the precipitation of amorphous nanospheres of silica, silicification is associated with internal or external organic components. This has been described as a rapid process whereby these organic components act as passive surfaces for mineral nucleation (Toporski et al., 2002). In contrast, in an experimental study, it was shown that the binding of metal cations such as Fe (III) to cell wall components was essential for successful silicification and preservation of the cell wall of a thermophilic microorganism (Orange et al., 2011).

Recent NanoSIMS element mapping studies have revealed patterns consistent with microbial communities present in old sediments (Wacey, 2010) and in living domical and conical microbialites (Wacey et al., 2010). Nano-scale chemical maps of a suite of elements (C, O, Mg, N, Si and S) have been successfully matched to specific morphological features such as trichomes, sheaths and extracellular polymeric substances in living microbialites. In contrast, older microbialites showed poorly preserved microfossils that were highlighted by enrichment in nitrogen and sulfur (Wacey et al., 2010). It has been suggested that organic matter from decaying microorganisms and their decomposition may accelerate the formation of new biominerals leading to the formation of microbial biomarkers and/or their fossils (Boyce et al., 2001; Leo and Barghoorn, 1976; Westall, 1999; Wierzchos and Ascaso, 2002). Similar postmortem organomineralization and microbial fossil formation processes have been described for endolithic communities inhabiting Antarctica's McMurdo Dry Valleys (Wierzchos et al., 2004, 2005).

4.4. Model of biosignature and microbial fossil formation in endolithic microbial communities

The model we propose for biosignature and microbial fossil formation by endolithic microbial communities in Ca-sulfate crust environments involves three main steps but with differences between cryptoendolithic algae and hypoendolithic

412 cyanobacteria communities (Fig. 5). According to this model the moisture regime
413 inside the crust due to night-time fog and dewfall events promotes the lithic
414 colonization of Ca-sulfate crusts. However, low values of diurnal relative humidity
415 followed by temperature increases leads to rapid water evaporation from the Ca-
416 sulfate crust thus impairing metabolic activity, inducing solute saturation and finally
417 mineral precipitation.

418 As a first step, when the algae cells are photosynthetically active, daily changes
419 in pH could prevent abundant calcium carbonate encrustation. However, slight
420 changes in microclimate conditions may substantially affect the delicate hydrological
421 balance within the endolithic habitat leading to the death of microorganisms.
422 Subsequently, prompt calcium carbonate precipitation could lead to the encrustation
423 of algae cells remains. According to our SEM-BSE observations, we consider this
424 process as post mortem algae precipitation, as large amounts of calcium carbonate
425 precipitates were not detected in close proximity to well-structured potentially live
426 algal cells. At this stage, the cell walls of alga cell remains would favor encrustation and
427 the formation of the sponge-like calcium carbonate structure. However, calcium
428 carbonate precipitation was not observed around hypoendolithic cyanobacteria
429 communities. It is likely that extracellular polymeric substances or low PAR intensities
430 in the present hypoendolithic environments prevent carbonate precipitation.

431 In a second step, nucleation of larger calcium carbonate starts close to the algal
432 cell walls and radiates towards the exterior. Then a gel-like Mg-silicate permineralizes
433 the organic remains of cryptoendolithic alga cells and extracellular polymeric
434 substances around the hypoendolithic cyanobacterial communities. We view this as a
435 passive postmortem process associated with algae and cyanobacteria and propose
436 that decayed microorganisms undergo aided diffusion of mineral elements along a
437 concentration gradient, leading to fossilization through substitution of organic
438 substances with inorganic components.

439 Finally, continuous recrystallization of gypsum crystals within the Ca-sulfate
440 crust obliterates the spaces between calcium carbonate precipitates and Mg-silicates.
441 As a consequence, calcium carbonate precipitates are dispersed and reduced in
442 amount while Mg-Si-rich organominerals are preserved among the gypsum crystals in
443 cryptoendolithic zones and form alga cell-like microfossils. In hypoendolithic zones of

the crust, the Mg-Si-rich web-like structures are less prone to burial by new gypsum crystals.

5. Conclusions

The hyperarid Atacama Desert and its recently discovered endolithic microbial ecosystems is a good model for investigating early diagenesis processes associated with the deposition of organominerals and microbial fossil formation within today's endolithic communities. Through an *in situ* approach, we were able to detect the permineralization of microbial cells and their extracellular polymeric substances. Calcium carbonate sponge-like material and Mg-silicate structures formed within endolithic microbial habitats emerged as possible biosignatures of extinct microbial life. Nevertheless, the occasional wet-dry cycles of the Ca-sulfate crust that favor organomineralization processes, will also likely induce gypsum recrystallization and damage some of the early formed calcium carbonate biosignatures. In the light of our findings, these Ca-sulfate crusts of the Atacama Desert could be a good terrestrial analog of the gypsum-rich dunes found on Mars.

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Figure captions

Figure 1. a) Sampling site in the Atacama Desert showing fragmented Ca-sulfate crusts covering the soil. **b)** Detailed appearance of a crust in the field. **c)** Cross-section of a crust with a green layer of cryptoendolithic microbial communities (arrow).

Figure 2. SEM-BSE micrographs of Ca-sulfate crust cross-sections. **a)** Pores bearing cryptoendolithic microbial communities (arrows) beneath the crust surface. **b)** Algae surrounded by fungi among gypsum crystals (Gy). **c)** Detailed images of algae (A) and fungi (F) present in the pore spaces. **d)** Large pore colonized by cryptoendolithic fungi. **e)** Hypoendolithic microbial habitat at the bottom of the gypsum (Gy) crust (arrows). **f)** Detailed view of hypoendolithic cyanobacterial communities associated with mineral deposits (arrows) and surrounded by extracellular polymeric substances.

Figure 3. a) SEM-BSE image of a gypsum crust showing pores filled with sponge-like Ca-rich precipitates (arrows). **b)** EDS distribution maps of S, Ca, Mg and Si for the boxed area in Fig. 3a; asterisks point to the Ca-rich mineral. **c)** SEM-BSE image of the sponge-like structure of the calcium carbonate precipitates in the boxed area in Fig. 3a among large gypsum (Gy) crystals; boxed area of EDS maps shown in SD3. **d)** SEM-BSE image showing early stages of Ca-rich precipitates around decaying alga cells; arrows point to small crystals. **e)** Detailed image of Ca-rich crystals (triangles) surrounding Mg-Si rich minerals shaped like alga cells (arrows). **f)** Raman spectrum for calcium carbonate obtained from the spongy mineral precipitates. **g)** Raman spectrum from gypsum crystals.

Figure 4. a) SEM-BSE image of spherical Mg-Si rich mineral inclusions (asterisk) surrounded by gypsum (Gy) crystals and by calcium carbonate deposits (arrows); asterisk also indicates the point of EDS microanalysis, the results of which are shown at the top of Fig. 4c. **b)** EDS distribution maps of Mg, Si, S and Ca for the area shown in Fig. 4a. Zone of calcium carbonate traces is marked with an asterisk. **c)** Top graph is the

EDS spectrum obtained for the Mg-Si-rich inclusion (asterisk in Fig. 4a); bottom graph is the EDS spectrum obtained for the Mg-Si-rich web-like structure (asterisk in Fig. 4d). **d)** SEM-BSE image showing the web-like structure of the Mg-Si-rich minerals adopting a similar position to the extracellular polymeric substances observed in the hypoendolithic zone.

Figure 5. Diagram showing endolithic habitats in the Ca-sulfate crusts and the steps of our model of biosignature and microbial fossil formation. **A)** Cryptoendolithic and hypoendolithic microbial communities sustained by water from fog and dewfall. **B)** Precipitation of calcium carbonate and Mg-silicate permineralization of decaying alga on cell interiors and on extracellular polymeric substances. **C.** Occasional dew favors the dissolution and recrystallization of gypsum crystals displacing carbonate deposits.

Notes just below A, B and C in Figure 5:

A. Endolithic colonization of Ca-sulfate crust (*A*, algae; *F*, fungi; *Cy*, cyanobacteria; *EPS*, extracellular polymeric substances).

B. CaCO_3 precipitation around alga remains and Mg-Si permineralization of algae and decayed cyanobacterial EPS.

C. $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ recrystallization around Mg-Si rich organominerals revealing traces of alga microfossils. Mg-Si precipitates bearing micromorphs.

Legends to supplementary data

Supplementary data 1. EDS spectrum of the area marked by an asterisk in the right-hand SEM-BSE image. Arrows point to hyphae penetrating the gypsum microcrystals. Scale bar = 20 μm .

Supplementary data 2. EDS spectrum of the area marked by an asterisk in the right-hand SEM-BSE image. Hypoendolithic cyanobacterial communities (arrows) appear embedded in extracellular polymeric substances, which in some zones (dashed line) show the presence of precipitates of high Mg, Si and low Al and Ca contents. Stars indicate large gypsum grains. Scale bar = 20 μm .

Supplementary data 3. EDS mapping of the area marked with a square in figure 3c. Areas of Ca-rich precipitates showed the presence of amorphous Mg-Si rich material outlining the voids in the sponge-like material. Scale bar = 20 μm .

Supplementary data 4. SEM-BSE image of a sample treated with saturated uranyl acetate during the dehydration step. Areas of uranium show more contrast. There is a slight displacement from the mapped area in Figure SD6 due to differences in the working distance used for microanalytical analysis. Scale bar = 20 μm .

Supplementary data 5. EDS maps of the area shown in SD4. From left to right, BSE signal image (BSE), EDS $K\alpha$ signals for magnesium (MgKa), silica (SiKa), sulfur (SKa), uranium (UKa) and calcium (CaKa). White circles indicate areas with structures rich in uranium corresponding to the remains of organic material embedded in the Ca-rich mineral. White rectangles indicate areas of structures rich in Mg+Si and almost no U signal. Scale bar = 20 μm .