Morphological Biosignatures in Gypsum: Diverse Formation Processes of Messinian (~6.0 Ma) Gypsum Stromatolites

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Abstract

The ~5.3–6.0 million-year-old evaporitic gypsum deposits of Cyprus and Crete contain a variety of stromatolites that formed during the Messinian salinity crisis. We recognize four stromatolite morphotypes, including domical, conical, columnar, and flat-laminated structures. Observations of morphological and textural variations among the different morphotypes reveal significant diversity and complexity in the nature of interactions between microorganisms, gypsum deposition, and gypsum crystal growth. Nonbiological processes (detrimental gypsum deposition, in situ crust precipitation, syntaxial crystal growth, subsurface crystal growth, and recrystallization) interacted with inferred microbial processes (including localized growth of biofilms, trapping and binding of grains in mats, nucleation of gypsum on cells) to produce distinct morphological-textural assemblages. Evidence for biological origins is clear in some stromatolite morphotypes and can come from the presence of microfossils, the spatial distribution of organic matter, and stromatolite morphology. In one stromatolite morphotype, the presence of the stromatolite, or the biota associated with it, may have determined the morphology of gypsum crystals. In some stromatolite morphotypes, definitive evidence of a microbial influence is not as clear.

There are broad similarities between the Messinian gypsum stromatolites and carbonate stromatolites elsewhere in the geologic record, such as the formation of precipitated and granular layers; the development of domed, columnar, and conical morphotypes; the potential for microbes to influence mineral precipitation; and the recrystallization of deposits during burial. However, in detail the array of microbial-sedimentary-diagenetic process interactions is quite distinct in gypsic systems due to differences in the way gypsum typically forms and evolves in the paleoenvironment compared to carbonate. Unique aspects of the taphonomy of gypsum compared to carbonate sediments, generally speaking, include the following: the potential for growth of individual crystals to determine the shape of a stromatolite (and possibly vice versa), a more diverse set of outcomes relating to preservation versus destruction of textures through crystal growth and recrystallization, and a greater likelihood of preserving microfossils through encapsulation in large crystals. These insights gained from the study of terrestrial gypsum sedimentary rocks provide valuable guidance for the search for clues to past life in sulfate chemical sediments on Mars. Key Words: Stromatolites—Gypsum—Evaporites—Mars—Biosignature.

1. Introduction

Interactions between microbial communities and chemical sediments have played an important role in preserving evidence of the history of microbial life on Earth. Similarly, chemical sediments may have been important for preserving evidence of microbial life on Mars, if life ever existed there. The synsedimentary mineralization that occurs in chemical sedimentary environments such as evaporites can rapidly entomb and preserve cellular fossils and organic material (e.g., Oehler and Schopf, 1971; Westall et al., 1995; Schopf et al., 2012), record chemical signatures of biological processing such as isotopic and trace element patterns, and promote the formation of biosedimentary structures and textures. One of the most notable outcomes of such microbe-chemical sediment interactions is the production of macroscopic morphological features called stromatolites (internally laminated sedimentary structures of probable biological
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The importance of this taphonomic pathway is highlighted by the association between carbonate mineral precipitation from the Precambrian ocean and the widespread occurrence of stromatolitic carbonate buildups in the first ∼2.5 to 3.0 billion years of the record of life on Earth (e.g., Grotzinger and Rothmann, 1996; Grotzinger and Knoll, 1999). The distinction of biogenic from nonbiological mineral precipitation and crystal growth processes in evaporitic depositional systems in order to highlight the types of processes that must be considered in the analysis and interpretation of potentially biogenic features in gypsum deposits. More detailed reviews of sedimentary processes in evaporitic systems can be found in the work of Warren (1999, 2006) and Babel (2004). For reviews of gypsum microbial sediments, see the work of Rouchy and Monty (2000) and Babel (2004). For a review of modern evaporite microbial sediments, see the work of Gerdes et al. (2000).

Mineral precipitation in the water column: Fine-grained gypsum may precipitate at the air-water interface or in the brine column and settle to the bottom, where it may be transported by currents and re-deposited; this type of sediment can be thought of as both chemical and detrital. Precipitation may be nucleated on microbial cells in the water column (Thompson and Ferris, 1990). Precipitation of fine-grained gypsum is common in shallow to semi-emerged areas such as ephemeral saline pans and shoals intertently crossed by migrating brine sheets (Logan, 1987; Babel, 2004). However, fine-grained gypsum deposits are also common in the deeper parts of basins (Warren, 1999).

Bottom-nucleated mineral precipitation: Fine- or coarse-grained gypsum may precipitate at the sediment-water interface and form layers or crusts of varying thickness and character. The fabric typically consists of vertically oriented crystals (palisades fabric), although many other fabric types are known, such as radial, stellate, and domal. Layers can be a few millimeters to several meters thick. Isolated single or clustered crystals are also known (Schreiber, 1978; Dronkert, 1985; Babel, 2004).

Mineral crystal growth in the subsurface: Gypsum crystals can grow in the subsurface and modify or destroy the original sedimentary fabric, or in some cases preserve components of the original sediment. The gypsum can take on different habits, including swallowtail twins, massive meter-scale intergrowths, and large, foliated crystals of selenite (Babel, 2004, 2005 and references therein).

Clastic sedimentation: Clastic sedimentation may consist of detrital sediment transported from outside the basin or...
intrabasinal sediments such as intraclast conglomerates formed during storms and other high-energy events. Thick clastic deposits laid down in high-energy events may terminate the growth of microbial mats and bottom-nucleated crystals. Mechanically deposited sediments have been described in a number of evaporitic basins even if chemical sedimentary processes and early interlocking and cementation of crystals are usually prevailing in these settings (Warren, 1999).

Precipitation of gypsum on microbial cells: Experiments have shown that microbes can influence gypsum precipitation when calcium binds to the cell wall or extracellular glyco-calx (Morita, 1980; Costerton et al., 1981; Beveridge and Fyfe, 1985). The bound calcium acts as a nucleation site such that, if the surrounding fluids have high sulfate concentration, gypsum can precipitate (Thompson and Ferris, 1990).

Microbial baffling, trapping, and binding: Microbes may form benthic communities that can baffle, trap, and bind sediment grains. Although most commonly associated with clastic and carbonate-precipitating environments, microbial trapping and binding (Black, 1933; Noffke et al., 2001) may involve detrital or precipitated particles of different compositions including gypsum. Grains may become trapped among intertwined filamentous microbes or in sticky extracellular polysaccharides (Burne and Moore, 1987). Trapping and binding in ancient stromatolites may be associated with such textural hallmarks as grainy textures that result from particle deposition and wrinkly laminations that arise from the formation of thick, irregular microbial mats.

Adhesion of particles to thin biofilms: The adhesion of fine particles to thin biofilms is a process inferred as a mechanism for the formation of thin laminae in Early Archean carbonate stromatolites (Allwood et al., 2009). Adhesion may require only a thin biofilm and may not necessarily result in the wrinkly or irregular textural features normally associated with development of a thick mat. Particle adhesion to biofilms has been observed in streams (Battin et al., 2003) and demonstrated experimentally (Salant and Hassan, 2007).

Microbial mat nucleation of crystal growth: Microbial mats may provide a template for precipitation of crystals at the sediment-water interface. This process was interpreted as contributing to the formation of carbonate Mesoproterozoic O. omachtensis stromatolites (Knoll and Semikhatov, 1998) and Early Archean coniform and domical stromatolites (Allwood et al., 2009). Nucleation of crystals on the surface—or in the interior—of microbial mats also occurs in gypsum microbial sediments (Babel, 2004).

Microbial mat termination of crystal growth: Where dense microbial mats form, brine may be prevented from reaching the crystals in the subsurface, which can cause a new layer of crystals to nucleate instead and keep crystal sizes small. Conversely, where only a flocculous biofilm forms (as is typical of microbes that dominate evaporite basin ecosystems at higher salinities), brines are able to penetrate, and syntaxial crystal growth will continue, allowing larger crystals to form. On Earth, large selenite crystal beds predominate in high-salinity areas that exclude formation of dense mats (Babel, 2004).

Organic matter influence on crystal growth: The presence of organic compounds during the growth of gypsum crystals has been hypothesized as a likely cause of the curved shape of some gypsum crystals, such as “sabre gypsum.” This is thought to be because organic molecules of different chirality interfere with growth along different faces of the crystal (Babel, 1990).

Intimate combination of chemical and physical sedimentary processes: A major distinguishing characteristic of evaporite sediments is the prevalence of chemical sedimentary processes over physical sedimentary processes. Even though particulate sediment can form in the brine column or at the sediment-water interface, those particles, once deposited, tend to rapidly become cemented in place (Warren, 1999). Because chemical sedimentation is so prevalent, stromatolites and other potentially microbial sedimentary features are more likely to form due to the rapid cementation of microbial layers. However, abiotic accretionary structures are also more likely to form, and the role of microbes in the accretion of any given set of structures can be hard to distinguish.

2.1. Stromatolites in gypsum evaporites

Stromatolitic structures composed of gypsum are preserved in upper Miocene evaporitic gypsum deposits in Cyprus (Orszag-Sperber et al., 1980; Rouchy and Monty, 1981, 2000; Rouchy, 1982) and Crete, and in Sicily (Hardie and Eugster, 1971; Schreiber, 1988; Rouchy and Monty, 2000), where extensive evaporite deposition took place during the Messinian. The Cyprus and Crete structures are among the best developed gypsumiferous stromatolites and exemplify the range of types known in the Miocene gypsum successions. Other examples of gypsum stromatolites occur in upper Miocene gypsum deposits of the Apennines, Italy (Vai and Ricci-Lucchi, 1977), Bulgaria (Trashlhev, 1969); Middle Miocene deposits of Poland and Ukraine (Kasprzyk, 1993; Peryt et al., 1994); Middle Miocene deposits of Egypt (Monty et al., 1987; Youssef, 1988); and Paleogene deposits of Bresse, France (Guillevin, 1980).

The Messinian gypsum deposits of Cyprus and Crete contain several different types of stromatolites that illustrate the diverse interaction of microbial communities with gypsum sedimentation regimes and the variety of preservation pathways during subsequent diagenesis.

3. Messinian Gypsum Stromatolites of Cyprus and Crete: Description and Analysis

The gypsum stromatolites of Cyprus and Crete are part of an extensive evaporitic succession deposited during the Messinian salinity crisis in the Mediterranean region. In Cyprus, these deposits occur in the southern part of the island, where a Tertiary sedimentary cover fringes the central Troodos Massif. Neogene sediments are distributed in sub-basins, including the Poleni and Psematismenos basins (Fig. 1) (Orszag-Sperber et al., 1980; Rouchy, 1982). In Crete, gypsum stromatolites occur in the Messinian succession of the Heraklion basin (Fig. 2) (Rouchy, 1982), which is a Neogene-Quaternary graben structure located in central Crete between the Psiloritis and Dicti Mountains (Fassoulas, 2000). Stromatolites and other microbial features in the Messinian gypsum deposits of Cyprus and Crete were described by Rouchy and Monty (1981, 2000).

Rouchy and Monty (2000) described two types of gypsum microbial sediments in evaporitic gypsum deposits, which were distinguished on the basis of crystal morphology. The first type—microcrystalline gypsum microbial sediments—consists of laminated gypsum with planar, undulating,
domical, and conical morphologies. In examples from Crete, selenite crystals deform laminae or are enveloped by microbial mats (selenite = crystalline gypsum variety). The laminae are defined by variations in calcite content, organic content, and gypsum crystal size and are thought to represent a primary calcitic lamination coupled with secondary gypsum precipitation within microbial mats. The second type—microbial laminites in large selenite crystals—consists of vertical selenite crystals with laminae composed of interwoven microbial filaments “floating” in the translucent selenite matrix. Two different subtypes were recognized: centimeter-scale crystals with flattened laminae composed of calcified filaments, or centimeter- to meter-scale crystals that form laterally continuous beds and contain laterally continuous flat to undulose or rare domal laminae composed of filaments (Rouchy and Monty, 2000).

Based on new observations of stromatolites in the Polemi, Psematismenos, and Heraklion basins, we recognize four different types of stromatolite that are characterized either by selenitic or fine-grained gypsum composition and reflect differences in interactions between microbes, sedimentation, and diagenesis. Two morphotypes composed of fine-grained gypsum are (1) columnar stromatolites and (2) laterally linked domical stromatolites. Two morphotypes composed of large selenite crystals are (1) flat/undulose, laterally continuous microbial laminites and (2) selenitic columnar stromatolites. Each of these subtypes was analyzed to evaluate its processes of formation.

3.1. Type 1: Columnar stromatolites in fine-grained gypsum

The columnar stromatolites occur in the ~3 m thick, uppermost gypsum bed of the Upper Evaporite Unit in the Polemi basin, Cyprus (Rouchy and Monty, 1981, 2000). The gypsum in the Upper Evaporite Unit precipitated from
brines formed through evaporative concentration of brackish waters (e.g., Orszag-Sperber et al., 1980; Rouchy, 1982). The stromatolites formed in extremely shallow water environments near the margins of the evaporite basin (Rouchy, 1982).

The columnar stromatolites sampled here occur in outcrops approximately 1.3 km east of the abandoned village of Theletra in western Cyprus. Outcrops of similar stromatolites previously existed approximately 1 km to the northeast, near Yiolou (Rouchy and Monty, 1981, 2000), but those outcrops have been covered by urban development. The stromatolitic outcrops are part of an east-dipping succession of bedded gypsum exposed along several roadside outcrops on the eastern side of a valley. From base to top, the succession consists of (1) cream-colored carbonate (locally conglomeratic); (2) massive fine-grained, laminated, and stromatolitic gypsum, and stromatolitic gypsum breccia; and (3) massive coarse-grained gypsum (including randomly oriented selenite crystals and massive “sabre” gypsum intergrowths). The fine-grained/conglomeratic/stromatolitic gypsum is absent in the more northerly outcrops (~300 m north), where carbonate is unconformably overlain by meter-scale selenite intergrowths.

The stromatolites occur in 20–30 cm thick beds that are intercalated with beds of massive gypsum breccia made up of stromatolitic intraclasts (Rouchy and Monty, 2000). The stromatolites consist of subhorizontal, 2–5 mm thick, irregular laminae with rounded, overhanging margins and are stacked into short columns typically 1–4 cm high and 3–10 cm wide (Fig. 3a). Stromatolite columns tend to be shorter (i.e., in terms of “stratigraphic height”) and more poorly formed in the lower parts of the beds, gradually increasing in stratigraphic height toward the top of the bed. The thick laminae that make up the stromatolites have a distinct gradation from their base to their top. The lower parts of the laminae consist of light-colored, fine-grained gypsum with abundant poorly sorted, sand-sized gypsum crystals and rare quartz grains; the upper parts of the laminae are darker deposits composed of fine-grained gypsum with abundant carbonate micrite and organic matter. The organic matter and calcite are spatially associated, and both terminate at the edges of the stromatolites. Areas between the stromatolites contain the same material as the lower parts of the stromatolite laminae, namely, light-colored fine-grained gypsum with rounded gypsum clasts and rare quartz grains, but with no organic deposits.

FIG. 3. Columnar stromatolites in fine-grained gypsum. (a) Polished slab. Light layers consist mainly of very fine-grained gypsum, with some sand-sized gypsum clasts and minor detrital quartz. Darker layers contain carbonate micrite and fine, anastomosing organic laminae. (b) Composite thin section stromatolite photomicrograph (plane polarized light) showing detail of a dark lamina: thin, irregular dark layer contains organic matter.
In thin section (Fig. 3b), the stromatolite laminae are seen to primarily consist of a roughly equigranular, interlocking mosaic of gypsum crystals. The grain size varies between upper and lower parts of the laminae. Fine, anastomosing layers of carbonate micrite and organic matter occur at the top of each lamina.

3.1.1. Formation processes and preserved evidence of microbial activity. The internal textures of the stromatolites suggest both physical and chemical sedimentation processes occurred during stromatolite formation, while the presence and distribution of organic material, combined with the morphology of the stromatolites, suggest that microbes were present during deposition and influenced the formation of the stromatolites. The interlocking gypsum crystal mosaic fabric in stromatolite laminae is consistent with in situ gypsum crystal growth (Rouchy and Monty, 2000) or with recrystallization of particulate gypsum (i.e., water-column-nucleated gypsum particles that settled out and recrystallized). On the other hand, the abundance of rounded detrital grains in and between the columnar stromatolites indicates a significant component of detrital sediment. To explain all the observed sedimentary textures, the most plausible hypothesis is a combination of the latter three processes: in situ precipitation, clast and particle deposition, and particle recrystallization.

Despite the lack of microfossils in these structures, it is possible to infer the former presence of microbial mats and their role in stromatolite formation from the shape of the organic laminations, which span the stromatolites from edge to edge, adhere to the steep margins, and do not exist in the stromatolite interspaces. A major morphological clue to a microbial influence lies in the observation that the sediment consisted of a significant portion of loose particles yet formed high-standing, steep-sided, lithified structures. However, direct evidence of microbes (i.e., microfossils) is absent. Organic matter is preserved, but if cellular structures were formerly present, they were deformed or destroyed during interstitial crystal growth.

The laminae shape, vertical variations in laminae fabric, and the nature of deposits surrounding the stromatolites suggest that stromatolite formation involved episodic detrital sedimentation, followed by quiescent periods when benthic microbial communities established themselves on bathymetric highs (Fig. 4). The presence of microbial communities may have caused or enhanced the precipitation of minerals (calcite and gypsum) on the stromatolite surfaces. While no direct evidence is preserved for microbial influence on gypsum precipitation, experiments have shown that microbes can influence gypsum precipitation through modification of the local microenvironment and provision of nucleation sites on cell walls (e.g., Thompson and Ferris, 1990). Gypsum precipitation may have also been enhanced at the tops of stromatolites due to capillary evaporation during periods of exposure (Rouchy and Monty, 2000). The presence of microbial mats—and the in situ mineralization (which they may have caused)—would have stabilized the sediment and enabled formation of the high-standing, lithified stromatolitic structures. The increasing paleo-height of stromatolites through time may reflect a positive feedback between a benthic community’s preference for high areas and the building up of those highs as the presence of benthic communities promoted chemical sedimentation in their local environment.

3.2. Type 2: Laterally linked domical stromatolites in fine-grained gypsum

The domical stromatolites occur in outcrops of the Upper Evaporite Unit in the Heraklion basin, Crete. Deposition of the evaporites occurred at very shallow depths in residual lagoonal water bodies of limited extent, which were concentrated at the lowest parts of the paleogeography (Rouchy, 1982). These domical stromatolites occur in deposits near the basin margin and are currently exposed in a section approximately 1 km northeast of Profitas Ilias.

The outcrop is near the site of domical stromatolites near Tsangaraki (Rouchy and Monty, 1981). The stromatolitic outcrops examined here are part of a ~10 m thick, north-dipping succession of bedded gypsum exposed along roadsides outcrops on a southeast-facing slope. The succession consists of laminated, stromatolitic gypsum with several layers that contain selenite crystals, which are overlain by massive, coarse-grained (selenitic) gypsum.

The domical stromatolites, which occur in the lower 2–3 m of the succession, consist of short vertical stacks of domeshaped, generally isopachous laminae (Fig. 5a). In thin section, laminae are composed of an interlocking mosaic of fine-grained gypsum crystals, with thin, diffuse laminae of micritic calcite and brown organic matter (Fig. 5d). The organic matter consists of amorphous particles accumulated along crystal boundaries. The laminae are continuous across the dome and interdome areas. A selenite crystal occurs at

![FIG. 4. Schematic diagram showing interpretation of the development of columnar stromatolites through time.](image-url)
FIG. 5. Domical stromatolites. (a) Outcrop showing a series of small, abutting domes overlain by flat-lying laminated gypsum. Box shows location of (b). (b) Polished slab showing early diagenetic selenite crystals that formed a topographic template for dome accretion. (c) Polished slab showing details of lamination. (d) Thin section photomicrograph showing gypsum laminae separated by thin laminae of calcite and organic matter (o.m.). (e) Polished slab showing detail of a selenite crystal and its textural and geometric relationship to laminae. (f) Line drawing highlighting the key features of (e). (g) Thin section photomicrograph showing selenite crystal containing inclusions of finer-grained gypsum and calcite on the left, and groundmass of fine-grained gypsum and calcite on the right.
the base of each dome, though the crystals are commonly not visible in outcrop and are only exposed when the stromatolite is cut in half (Fig. 5b, 5c). Laminae generally terminate at the edge of the crystal, although feint relics of the laminae can be seen locally inside the crystals in reflected light (polished slab view: Fig. 5e, 5f). Additionally, in thin section (cross-polarized light), optical discontinuities in the selenite reveal relics of a fine-grained fabric, similar to the fabric of sediment surrounding the crystal (Figs. 5g, 6), that was replaced by (or perhaps recrystallized into) the selenite crystal.

While laminae adjacent to the crystal were replaced or recrystallized, the laminae that immediately overlie the crystal are convex upward over the crystal, which indicates that their geometry was influenced by the presence of the pre-existing crystal. The first few laminae at the top of the crystals appear to have been pushed upward by the growing crystal, whereas successive overlying laminae appear to have encrusted the initial template provided by the crystal and deformed laminae. The domed layers increase in radius up section, each encrusting (not draping) the one below, creating larger and larger accretionary dome structures that gradually coalesce up section and flatten out to horizontal gypsum laminites (Fig 5a).

3.2.1. Formation processes and preserved evidence of microbial activity. The lack of clastic sedimentary textures observed around these stromatolitic structures argues against detrital deposition as a dominant mode of sedimentation. Rather, the laterally continuous, near-isopachous laminae and the radially expanding dome morphology of the stromatolites indicate in situ precipitation of crusts (e.g., Batchelor et al., 2005; Allwood et al., 2009). The fine-grained texture indicates that in situ precipitated crusts were composed of small particles. Precipitation may have nucleated on, or within, microbial mats, and the presence of organic deposits associated with each gypsum layer is consistent with this hypothesis. Nonetheless, the nearly isopachous geometry of the laminae suggests that in situ crystal growth processes were the most influential factor in the formation of the structures.

A notable aspect of the domical stromatolites is the varying role of growth of large monocrystals in stromatolite morphogenesis and in the preservation, destruction, and modification of fabrics and structures. Crystal growth just beneath the sediment surface resulted in (1) replacement of sedimentary laminae in most places; (2) local preservation of relics of laminae in other places; (3) initial deformation of immediately overlying laminae; and (4) provision of a template for dome accretion (Fig. 7). The domes are not differential compaction features like those associated with anhydrite nodules. The latter show deformation of both underlying and overlying laminae, and laminae are deflected smoothly around the nodule. The domical stromatolites, in contrast, have flat-lying laminae beneath the crystals, and the overlying domical laminae have a distinct cusp at the dome edges.

Notably, no domical stromatolites were found that did not have the crystal template, which suggests that the presence of a growing crystal was the dominant factor causing the domal morphology. This observation, coupled with the fact that the organic laminae continue uniformly beyond the domes into the intervening spaces, suggests that crystal growth and mineral crust formation were the dominant processes of stromatolite morphogenesis. Biological activity played little or no active role in the formation of the dome shape. Rather, the flat-lying and domal laminae were formed by essentially the same processes of mineral crust formation, with the dome shape induced by crystal growth.

Evidence for a biological influence in these structures would be difficult to find if the organic matter was not preserved or could not be detected and mapped along the steep slopes of the domes. The intimate association between micritic calcite and organic laminae suggests that the calcite is a by-product of biological activity and the presence of the calcitic laminae on their own could be taken as suggestive evidence of microbial activity.

FIG. 6. Thin section (cross-polarized light) view of textures in the domical stromatolites. A large selenite crystal at the center of the stromatolite (left part of picture) shows optical discontinuities when rotated toward extinction; these discontinuities resemble the fabric of the surrounding fine-grained gypsum and are interpreted as relics of fine-grained gypsum that was replaced by the selenite.
3.3. Type 3: Microbially laminated selenite

Selenite with microbial lamination occurs in basal parts of Messinian evaporite successions in several locations: the northern Apennines, Sicily, the Ionian Islands, Algeria, Crete, and Cyprus, as well as the Middle Miocene of Sinai (Vai and Ricci-Lucchi, 1977; Rouchy and Monty, 1981, 2000; Rouchy, 1982; Monty et al., 1987). Two types have been identified (Rouchy and Monty, 2000) as follows: (1) monocrystalline selenite that contains flat to undulose microbial laminae, with no crystal discontinuities; (2) centimeter-scale vertical gypsum crystals with millimeter-scale microbial lamination and no lateral discontinuities. Here, we examine examples of the former.

Samples were collected from outcrops adjacent to a quarry near Kalavasos village, in the Psematismenos basin, southern Cyprus. From base to top, the outcrop succession consists of interbedded calcareous mudstone and gravel; 1.1 m of interbedded calcareous mudstone and gypsarenite; 2.5 m of selenite breccia; >8 m of interbedded “balatino” (flat laminated) gypsum, gypsarenite, and selenite breccia. This latter unit passes laterally into a zone of recessive-weathering selenite (Fig. 8a), where the microbial features are observed. However, the contact between the two outcrops is obscured by several meters of scree. When viewed along cleavage planes, the selenite displays subtle, flat to slightly domal lamination defined by calcified filamentous and coccoidal microfossils (Fig. 8b, 8c). The microfossils are composed of micritic calcite and organic matter, within a monocrystalline selenite matrix (Fig. 8d).

3.3.1. Formation processes and preserved evidence of microbial activity. The microbially laminated selenite may have formed when microbial mats on top of crystals growing at the sediment-water interface were encapsulated layer by layer as the crystals grew upward (Rouchy and Monty, 2000; Fig. 9). Another hypothesis that must be considered is that a deposit of gypsiferous sediment and layered microbial mats was recrystallized in the subsurface. This latter hypothesis is potentially supported by the lateral correlation of the structures with laminated, fine-grained gypsum. However, the remarkable morphological preservation of the microbial filaments and the lack of any relict sediment at all are more consistent with rapid permineralization of the organisms. Thus, it is more likely that these structures formed where flocculous mats allowed brines to penetrate through to underlying crystals growing in the subsurface, resulting in continuous syntaxial growth of the crystals around the microbial mat (Babel, 2004). The domical shapes may be related to deformation during crystal growth (Rouchy and Monty, 2000). The alternating filament-rich and filament-poor laminae may reflect seasonal fluctuation in mat development and/or crystal growth rates.

Notably, formation of bottom-nucleated, large selenite crystal beds is thought to represent very high salinity with aggressive precipitation and crystal growth (Ortí Cabo et al., 1984; Babel, 2004). Despite these apparent challenges to biosignature development, the result is excellent textural preservation and, consequently, encapsulation of direct fossil evidence of microorganisms.

3.4. Type 4: Selenitic columnar stromatolites

The selenitic columnar stromatolites occur in outcrops of the Upper Evaporite Unit along the roadside between Profítas Ilias and Tsangaraki, Crete. Rouchy and Monty (2000) described similar selenitic structures but with broad, dome-shaped lamination, from the same unit near Tsangaraki. The selenitic columnar stromatolites immediately overlie the laterally linked domical stromatolites described above.

The stromatolite columns are approximately 5–15 cm wide, with local pseudobranching and a typical paleo-height of 30–80 cm (Fig. 10a, 10b, 10c). The pseudobranching morphology entails subdivision of a lower single column into two upper columns that continued to accrete vertically parallel to one another. In cross-section view, the columns display light and dark, convex upward to conform laminae composed of interwoven calcified microbial filaments, in a matrix of translucent, monocrystalline selenite (Fig. 10c, 10e). The filaments are composed of organic matter with traces of...
micritic calcite; light laminae contain many filaments, whereas dark laminae contain few or no filaments. Within each stromatolite, selenite forms a single, large crystal and exhibits chevron-shaped cleavage patterns. The cleavage planes lie at an angle to the microbial lamination. The crystal edges follow the outline of the stromatolite precisely; where the stromatolite branches, so does the enclosed selenite crystal (Fig. 10c). Notably, swallowtail selenitic gypsum crystals 2 m stratigraphically higher than the coniform structures do not show any microbial lamination (Fig. 10d).

FIG. 8. Selenite-hosted microbial laminites. (a) The outcrop appearance of the selenite laminites—dominated by spalling along crystal cleavage planes. (b) Polished slab cut parallel to crystal cleavage plane. Note convex-upward curvature of laminae. (c) Detail of laminae in polished slab: the stromatolite consists of densely interwoven calcified filamentous microfossils (light-colored) “floating” in a matrix of transparent selenite. Light layers contain many filaments, and dark layers contain very few. White arrow points to a single filament. (d) Thin section photomicrograph oriented parallel to crystal cleavage plane. Light areas = selenite. Dark objects (filaments and parts thereof) consist of micrite (calcite) and organic matter. Plane polarized light.

FIG. 9. Schematic diagram showing interpretation of the development of microbially laminated selenite through time.
FIG. 10. Coniform stromatolites and selenite. (a) Outcrop showing cross section through coniform stromatolite exposed along a selenite cleavage plane. (b) Multiple adjacent coniform stromatolites, mostly viewed obliquely to selenite cleavage planes so that laminations cannot be seen. Note that stromatolites are draped by overlying gypsum sediments that have not been recrystallized to selenite. (c) Branched stromatolite/crystal cut and polished along the vertical axis of the stromatolite column, which is also a cleavage plane of the large selenite crystal contained within the stromatolite. Black dotted line traces a coniform stromatolite lamination; white dotted lines trace crystal growth planes. Sedimentary infill is visible at the top between the two columns of the stromatolite. (d) Selenite crystal showing typical orientation with the twin angle opening upward. (e) Detail of laminae in polished slab: the stromatolite consists of densely interwoven calcified filamentous microfossils (light colored) “floating” in a matrix of transparent selenite. Light layers contain many filaments, and dark layers contain fewer filaments.
The columns are closely spaced (1–3 cm), and the intervening spaces are filled with fine-grained gypsum. Sedimentary fabrics in the intercolumn spaces are poorly preserved but locally exhibit an irregularly layered, detrital fabric. Toward the tops of the columns the intercolumn sediments are seen to onlap and drape the columns, indicating that the columns stood high at the sediment-water interface as discrete stromatolitic structures around which sediment was deposited. The intercolumn sediments grade up into bedded, fine-grained detrital gypsum deposits that buried the stromatolites (Fig. 10b, 10c). The fine-grained gypsum is overlain by massive gypsum breccia and swallowtail gypsum intergrowths.

3.4.1. Formation processes and preserved evidence of microbial activity. The columnar stromatolites are interpreted to have formed by an unusual sequence of sedimentary and crystal growth processes that were microbially influenced. Domical columnar stromatolites from the same unit elsewhere were interpreted to have formed when interstitial growth of selenite crystals caused layered microbial mats to acquire a convex-upward shape (Rouchy and Monty, 2000). In that case, morphogenesis of the structures would have been essentially abiotic, with microbes present but not playing a role in the development of stromatolite morphology. This latter hypothesis is considered for the columnar structures described here.

Certain observations suggest that morphology was not only influenced by interstitial crystal growth processes but also by microbial processes at the sediment-water interface. The onlapping detrital gypsum deposits between the columns indicate that the structures were discrete, stromatolitic features that stood high and separate at the sediment-water interface, which could not happen if the morphology resulted only from interstitial crystal growth within the upper layers of sediment. The further observation of parallel branching is also much more typical of stromatolites than of bottom-nucleated selenite. The fact that in many places the laminae lie at very different angles to the cleavage planes (Fig. 10c) also suggests that laminae acquired their shape by a process other than crystal growth, although crystal growth may have helped reorient the laminae to some extent. Thus, on balance it seems unlikely that stromatolite morphogenesis was controlled purely by crystal growth processes. Instead, the formation of the structures with the observed lamina shape and branching morphology was more likely influenced or determined by microbial processes at the sediment-water interface while syntaxial growth of selenite crystals took place penecontemporaneously within the upper layers of sediment in the stromatolites, preserving the laminae and morphology of the structures (Fig. 11).

If the biomediated hypothesis posed above is correct, the restriction of selenite crystal growth to the interior of the stromatolite is an unusual phenomenon that may be linked to the microbial deposits. That is, the presence of microbial matter within the stromatolite may have influenced or favored the local growth of the selenite crystal. Microbes can cause gypsum precipitation when calcium binds to the cell wall or extracellular glycocalyx (Morita, 1980; Costerton et al., 1981; Beveridge and Fyfe, 1985), which acts as a nucleation site; if the surrounding fluids have high sulfate concentration, gypsum can precipitate (Thompson and Ferris, 1990). It is postulated that this process of microbially influenced precipitation could have promoted interstitial syntaxial crystal growth within the stromatolitic structures (and not between stromatolites), with the crystals growing upward as stromatolite accretion continued. The dense felt of microbial remains inside the stromatolite—and their absence between the stromatolites—is consistent with this hypothesis.

The selenitic columnar stromatolites may represent an unusual type of microbe-sediment interaction that could serve as a novel biosignature. If microbial communities controlled the development of unique branching columnar crystal morphologies at the sediment-water interface, then the crystal morphology is a potential biosignature—one that is readily identifiable in outcrop.

4. Discussion: Microbial Interactions with Chemical Sedimentation

The Messinian gypsum stromatolites of Cyprus and Crete provide important insights into a diverse array of microbial interactions with mineral precipitation and crystal growth. Some of these insights are unique to gypsum, whereas others are likely also relevant to chemical sediments of carbonate or other compositions.

4.1. Interactions between chemical and microbial processes are diverse and intimately entwined

The Messinian gypsum stromatolites of Cyprus and Crete demonstrate that chemical and microbial processes influencing fabric and morphology are many and varied, and
Nucleation and growth of crystals at the sediment-water interface: small crystals forming thin, isopachous crusts

Nucleation of crystals in brine column, settling to bottom

Long before deposition (transported mineral grains)

Nucleation of small crystals within microbial mats at sediment-water interface

Crystals may be incorporated into microbial mats through trapping, binding, or adhesion, leading to stromatolitic buildups.

Crusts may develop into stromatolitic accretionary structures with or without input from microbes. Morphology, organic deposits, and lamina shape may enable recognition of microbial input.

Microbial mats forming on top of crystals may be fossilized by encapaculation as crystals grow upward.

Microbial mats may form deposits that determine the shape of crystal growth; crystal grows only within bounds of microbial deposit.

Growing crystal may obliterate primary microbial sedimentary fabrics.

Growing crystal may preserve textural relicts locally within neomorphic crystals.

Growing crystals may form protuberances at sediment-water interface that provide a morphological template for accretion.

Crusts may develop into stromatolitic accretionary structures with or without input from microbes. Morphology, organic deposits, and lamina shape may enable recognition of microbial input.

Microbially laminated selenite

Selenitic columnar stromatolites

Crystals may be incorporated into microbial mats through trapping, binding, or adhesion, leading to stromatolitic buildups.

Columnar stromatolites

Columnar stromatolites

Crusts may develop into stromatolitic accretionary structures with or without input from microbes. Morphology, organic deposits, and lamina shape may enable recognition of microbial input.

Laterally linked domical stromatolites

Laterally linked domical stromatolites

Laterally linked domical stromatolites

Laterally linked domical stromatolites

4.2. Crystal habit—and therefore mineralogy—can play important role in development of structures

A major taphonomic influence in the Messinian gypsum deposits is the formation of large single selenite crystals at or near the sediment-water interface. The formation of these crystals has a variety of impacts on morphogenesis and preservation of structures and textures. The same is likely true in any systems where large single mineral crystals form.

For example, a unique taphonomic outcome arising from the growth of selenite crystals occurs in the laterally linked domical stromatolites, where large crystals that grew in shallowly buried sediments created surface protuberances. The protuberances acted as a template for accretion of domical stromatolitic structures by sequential deposition of encrusting, precipitated laminae. The encrusting style of accretion is not unique to gypsum; a similar scenario can arise where a sediment clast provides the topographic template, as observed in some Early Archean carbonate stromatolites (Allwood et al., 2006, 2009). However, the development of a topographic template through diagenetic crystal growth is unusual and resulted from the formation of large crystals or crystal masses in the near subsurface.

These observations imply that the influence of mineral precipitation on morphogenesis will vary between systems of different mineralogy, and that knowledge of mineral crystal habits will allow a better understanding of observed features.

4.3. Crystal growth can destroy or preserve texture, depending on when, where, and how crystal growth proceeds

It is not simply the case that chemical sedimentation and crystal growth processes always obscure morphological and textural evidence of microbial influence; many different taphonomic pathways and outcomes are possible depending on the timing, location, and mode of crystal growth.

Fine-grained gypsum deposits preserve sedimentary fabrics in detail, as observed in the columnar stromatolites, but they tend not to favor preservation of microfossils. While organic deposits are present in all the fine-grained gypsum stromatolites, the small-scale recrystallization has physically deformed any cellular remains (Rouchy and Monty, 2000), leaving only organic accumulations along grain boundaries. Similar outcomes are observed in recrystallized Archean carbonate stromatolites, where relict sedimentary fabrics, but not microfossils, are preserved (e.g., Allwood et al., 2009). The
taphonomic outcomes of fine-scale recrystallization are likely the same irrespective of mineralogy.

The large selenite crystals, however, have different roles in textural development. On the one hand, the selenite crystals can encapsulate and preserve microbial fossils in remarkable detail, as observed in the selenitic columnar stromatolites and microbially laminated selenite. On the other hand, crystal growth can destroy primary sedimentary fabrics, as observed in the laterally linked domical stromatolites. Whether crystals preserve or destroy the primary features appears to depend on the mode of crystal growth. In the two cases where microfossils are preserved, the selenite crystals are interpreted to have nucleated at the sediment-water interface or within the near-surface sediment and grown syntaxially. There are no relicts of primary sediment that was replaced by, or recrystallized into, selenite. Instead, microbial mats residing on top of bottom-nucleated crystals (Babel, 2004) were likely permineralized as the crystals continued their syntaxial upward growth. In the case where primary fabrics were largely destroyed (namely, in the laterally linked domical stromatolites), selenite crystal growth appears to have occurred through replacement of existing fine-grained gypsum. This process is evident where sedimentary and organic laminae terminate at the crystal margins and where relicts of fine-grained gypsum are preserved locally within the crystals (Fig. 5e, 5f).

The implication of these observations is that clues to sedimentary processes (which in themselves can provide important evidence of microbial activity) can be well preserved in fine-grained deposits but that cellular fossils are best sought in beds of large, bottom-nucleated crystals.

4.4. Crystal growth can influence stromatolite morphology in different ways depending on when, where, and how crystal growth proceeds

The laterally linked domical stromatolites provide a notable example of the multifarious roles of crystal growth in morphogenesis. A crystal growing in the subsurface initially provided a topographic protuberance that acted as a template for accretion at the sediment-water interface. Meanwhile, accretion proceeded due to precipitation of mineral crusts (which may or may not have been influenced by the presence of microbial mats) and led to development of a domical stromatolite at the surface. Then, as the subsurface crystal continued to grow upward, the stromatolite laminae were locally replaced. Thus, two different mineral precipitation processes simultaneously contributed to development of the stromatolite, and a single crystal had a changing role in the development of the stromatolite through time.

In complete contrast, crystal growth played a very minor role in the columnar stromatolites. The abundant grains, laterally tapering laminae, and paucity of precipitated textures indicate that the structures formed largely through microbially mediated accretion of clasts and brine-column-nucleated crystals, although intra-mat nucleation of fine-grained gypsum may also have played a role.

In the case of the microbially laminated selenite, the growing crystals simply acted as a substrate for benthic microbial communities. In cases where the laminae are slightly convex upward, the growing crystals may have deformed originally flat laminae (Rouchy and Monty, 2000). In contrast, the nearby, texturally similar selenitic columnar stromatolites suggest that the microbial laminae determined morphology of the crystals.

4.5. Microbial processes can influence crystal morphogenesis

Previous studies have proposed that the presence of organic compounds can influence the growth of curved crystal faces (e.g., Babel, 1986). However, the selenite columnar stromatolites may provide a novel example where microbial mats appear to have caused a selenite crystal to grow in the shape of a stromatolite. Determining precisely how this occurred requires analysis of additional well-preserved examples. However, a possible explanation is that benthic microbial communities formed layer by layer, and with each layer the microbes could have caused local precipitation of gypsum (Thompson and Ferris, 1990) within the bounds of the microbial community. This process would be similar to the intra-mat precipitation of fine-grained gypsum inferred for the columnar stromatolites, but in this case each microbial layer is inferred to have led to the continued syntaxial growth of a single large crystal, rather than separate small crystals.

An important implication of this observation is that crystal morphology could serve as a clue to microbial activity, even if the microbial remains themselves were not detectable. In the case of the selenitic columnar stromatolites, the crystal morphology retains evidence that the structures were stromatolites that developed parallel branching and stood high at the sediment-water interface. Even without the added evidence of microfossils, these structures would therefore provide clues to microbial activity.

5. Conclusions and Implications for Biosignatures in Gypsiferous Chemical Sediments on Mars

The Messinian gypsum stromatolites of Cyprus and Crete exemplify the considerable variety of interactions between microbes and mineral precipitation in subaqueous chemical sedimentary systems. Among the four stromatolite types in the Messinian gypsum evaporite successions, the major factors controlling development of texture and morphology are mineral crystal habits and the location, timing, and mode of crystal growth processes relative to microbial mat formation. Whereas diagenetic processes can adversely affect biosignature preservation, early diagenetic crystal growth can also play an important role in the development and preservation of morphological biosignatures.

Due to the diverse taphonomic pathways of gypsum chemical sediments, criteria for interpreting potential biosignatures are likely to vary significantly from case to case. As with ancient terrestrial stromatolites of uncertain biogenicity, potential biogenic structures on Mars would be best interpreted by mapping relationships between morphology, lamina architecture, fabric, distribution and composition of any organic materials, and the characteristics of the assemblage of potential biosignatures within the paleoenvironmental context. Insights into microbial metabolisms and environmental conditions can also be gleaned from geochemical studies of the stromatolites and their host rocks, including any preserved organic material (Arp et al., 2008).
To a certain extent, it would be possible to predict where clues to microbial activity might occur in subaqueous gypsum chemical sediments on Mars. The terrestrial gypsum successions that contain stromatolites developed in relatively long-lived, stable, gypsum-precipitating brine basins with low clastic influx. These circumstances would have provided the greatest opportunity for planktonic microbes to successfully establish benthic communities that would have persisted long enough to create macro-structures that were readily preserved and are identifiable in the rock record. Thus, the greatest potential for biosignatures that are readily detectable in situ on Mars would lie in evaporite deposits formed in longer-lived evaporite basins with lower clastic influx.

Within these environments, fine-grained deposits are likely to have undergone small-scale recrystallization and are not likely to have preserved microfossils and microtextures. However, they may nonetheless have preserved organic deposits and stromatolitic structures. Importantly, they are also likely to have preserved relict sedimentary fabrics and structures, which would provide vital contextual information. This contextual information is needed to enable interpretation of potential biosignatures and develop faces models that enable prediction of where biosignatures may occur.

The best place to look for microfossils in gypsum chemical sediments is in beds of large crystals that grew syntaxially at or near the sediment-water interface. This would likely be true of any other chemical sedimentary system where syntectic growth of large translucent crystals enables permineralization and fossilization of cells.

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