

MICROBIALITES, MODERN

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Synonyms

“Cryptalgal sedimentary rock” (Aitken, 1967);
Microbolite (Riding, 1991)

Definition

Microbialite: “Organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding sediment and/or forming the locus of mineral precipitation” (Burne and Moore, 1987), or “Benthic microbial deposits” (Riding, 1991).

Introduction

In this encyclopedia, microbialite is discussed under two chapters: (1) modern and (2) fossil. This part discusses modern microbialites, with emphasis on processes of formation. The fossil extension and classification of microbial deposits (fossil forms being more diverse) are treated in the “fossil microbialite” section of the encyclopedia (see Chapter *Microbialites, Stromatolites, and Thrombolites*). Microbialites are composed of trapped, bound, and/or precipitated sediment, and exhibit a range of mineralogies (Figure 1). This chapter focuses on carbonate microbialites, which are the most widespread and the most studied.

Microbialites are “rocks” that are produced, induced, or influenced by benthic microbial communities, primarily bacteria and sometimes also microeukaryotes, such as diatoms. These microbial communities are organized in mats or biofilms (e.g., Stolz, 2000), consisting of microscopic organisms enveloped in an organic matrix of extracellular polymeric substances (EPS; Decho, 1990; Bhaskar and Bhosle, 2005; see Chapter *Extracellular Polymeric Substances (EPS)*). Because the microbial mat is dominantly organic, it is rarely preserved in the fossil record. In some unusual cases, exceptional taphonomic conditions can preserve intact cells and even the EPS structure (e.g., silicification or preserved remnants of EPS matrices, Golubic and Hofmann, 1976; Barbieri et al., 2004; Barbieri and Cavalazzi, 2005; Altermann et al., 2006; Benzerara et al., 2006; Kumar and Pandey, 2008; Lepot et al., 2008). More commonly, the organic matter decomposes to carbon dioxide (CO₂) or methane (CH₄), although in some cases incomplete degradation can lead to organic matter enrichment of the sediment. Evidence of the original microbial mat or biofilm is generally indirect (e.g., specific sedimentary (bio)structure, micromorphology, organic biomarkers, and stable isotopic fractionation). Microbial mats can help preserve sedimentary structures in the fossil record (“microbially-induced sedimentary structures” – MISS; Noffke et al., 2003). The most

spectacular examples are carbonate microbialites. Examples of modern microbialites in the following section are followed by a discussion of processes of formation.

Types of modern microbialite

Microbialite descriptions incorporate a range of scales, from macrometers to micro/nanometers (e.g., Shapiro, 2000). Megastructure relates to the geographical extension of a microbial deposit and overall deposit morphology (e.g., ridges, biostrome, and bioherm). Macrostructure characterizes the morphology of an individual buildup (e.g., domal, branching, knobby). Mesostructure refers to structures visible with the naked eye, such as lamination. Microstructure is observed with a microscope, such as light, confocal, scanning electron (SEM), or transmission electron microscope (TEM).

Microbialite classification is based on mesostructure with four common types (Figure 2): laminated microbialites classified as stromatolites, thrombolites are clotted, leiolites are structureless, and dendrolites are dendritic (Burne and Moore, 1987; Riding, 1991, 2000; Dupraz and Strasser, 1999, 2002). All of these structures exhibit a wide range of microstructures including micropeloidal, densely micritic, or agglutinated microfabrics (Riding, 1991; Dupraz and Strasser, 1999). Three types of modern microbialites are described in the following section; dendrolites have not yet been found in modern environments. For further description of microbialite classification and microstructure see Chapter *Microbialites, Stromatolites, and Thrombolites*.

Stromatolite

The term stromatolite is derived from the Greek “stroma,” meaning mattress or stratum and “lithos,” meaning rock. The term was first introduced by Kalkowsky in 1908 to refer to “laminated benthic microbial deposits” (see also Riding, 1999; Chapter *Microbialites, Stromatolites, and Thrombolites*). The first modern stromatolites were found in the Shark Bay, Western Australia in 1954 in the hypersaline water of Hamelin Pool. Until this date, scientists believed that stromatolites were extinct, found only in the fossil record. Although the biogenicity of 3.5 Ga stromatolites has been questioned (Buick et al., 1981; Lowe, 1994; Grotzinger and Knoll, 1999; Lindsay et al., 2003), all modern microbialites called stromatolites are associated with microbial communities that induce, or serve as organic substrate for, precipitation (Riding, 2000). Modern stromatolites are found in many different locations including marine, hypersaline, freshwater, and even continental environments.

Open marine stromatolites

The Bahamas hosts the only known examples of open marine stromatolites. These structures are found at a variety of locations on the margins of Exuma Sound including Schooner Cays, Lee Stocking Island, Stocking Island Highborne Cay, and Darby Island (Dravis, 1983;

Carbonates

Calcite - CaCO_3
 Mg-Calcite - $(\text{Mg}_x\text{Ca}_{1-x})\text{CO}_3$
 Aragonite - CaCO_3
 Vaterite - CaCO_3
 Monohydrocalcite - $\text{CaCO}_3 \cdot \text{H}_2\text{O}$
 Protodolomite - $\text{MgCa}(\text{CO}_3)$
 Hydrocerussite - $\text{Pb}_3(\text{CO}_3)_2(\text{OH})_2$
 Amorphous forms - $\text{CaCO}_3 \cdot \text{H}_2\text{O}$ or CaCO_3

Phosphates

Octacalcium phosphate - $\text{Ca}_8\text{H}_2(\text{PO}_4)_6$
 Brushite - $\text{CaHPO}_4 \cdot 2\text{H}_2\text{O}$
 Francolite - $\text{Ca}_{10}(\text{PO}_4)_6\text{F}_2$
 Carbonated-hydroxylapatite (dahllite) - $\text{Ca}_5(\text{PO}_4)_3(\text{CO}_3)(\text{OH})$
 Whitlockite - $\text{Ca}_8\text{H}_2(\text{Mg},\text{Fe})_2+2(\text{PO}_4)_4$
 Struvite - $\text{Mg}(\text{NH}_4)(\text{PO}_4) \cdot 6\text{H}_2\text{O}$
 Vivianite - $\text{Fe}_3+2(\text{PO}_4)_2 \cdot 8\text{H}_2\text{O}$
 Amorphous Calcium Phosphate (at least 6 forms) variable
 Amorphous Calcium Pyrophosphate - $\text{Ca}_2\text{P}_2\text{O}_7 \cdot 2\text{H}_2\text{O}$

Sulfates

Gypsum - $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$
 Barite - BaSO_4
 Celestite - SrSO_4
 Jarosite - $\text{KFe}_3^{+3}(\text{SO}_4)_2(\text{OH})_6$

Sulfides

Pyrite - FeS_2
 Hydrotroilite - $\text{FeS} \cdot n\text{H}_2\text{O}$
 Sphalerite - ZnS
 Galena - PbS
 Hydrotroilite $\text{FeS} \cdot n\text{H}_2\text{O}$
 Sphalerite ZnS
 Wurtzite ZnS
 Greigite Fe_3S_4
 Mackinawite $(\text{Fe},\text{Ni})_9\text{S}_8$
 Amorphous Pyrrhotite Fe_{1-x}S ($x = 0-0.17$)
 Acanthite Ag_2S

Arsenates

Orpiment - As_2S_3

Hydrated Silica

Amorphous Silica - $\text{SiO}_2 \cdot n\text{H}_2\text{O}$

Chlorides

Atacamite - $\text{Cu}_2\text{Cl}(\text{OH})_3$

Fluorides

Fluorite - CaF_2
 Hieratite - K_2SiF_6

Oxides

Magnetite - Fe_3O_4
 Amorphous Iron Oxide - Fe_2O_3
 Amorphous Mn Oxide - Mn_3O_4
 Amorphous Ilmenite $\text{Fe}^{+2}\text{TiO}_3$

Metals

Sulfur - S

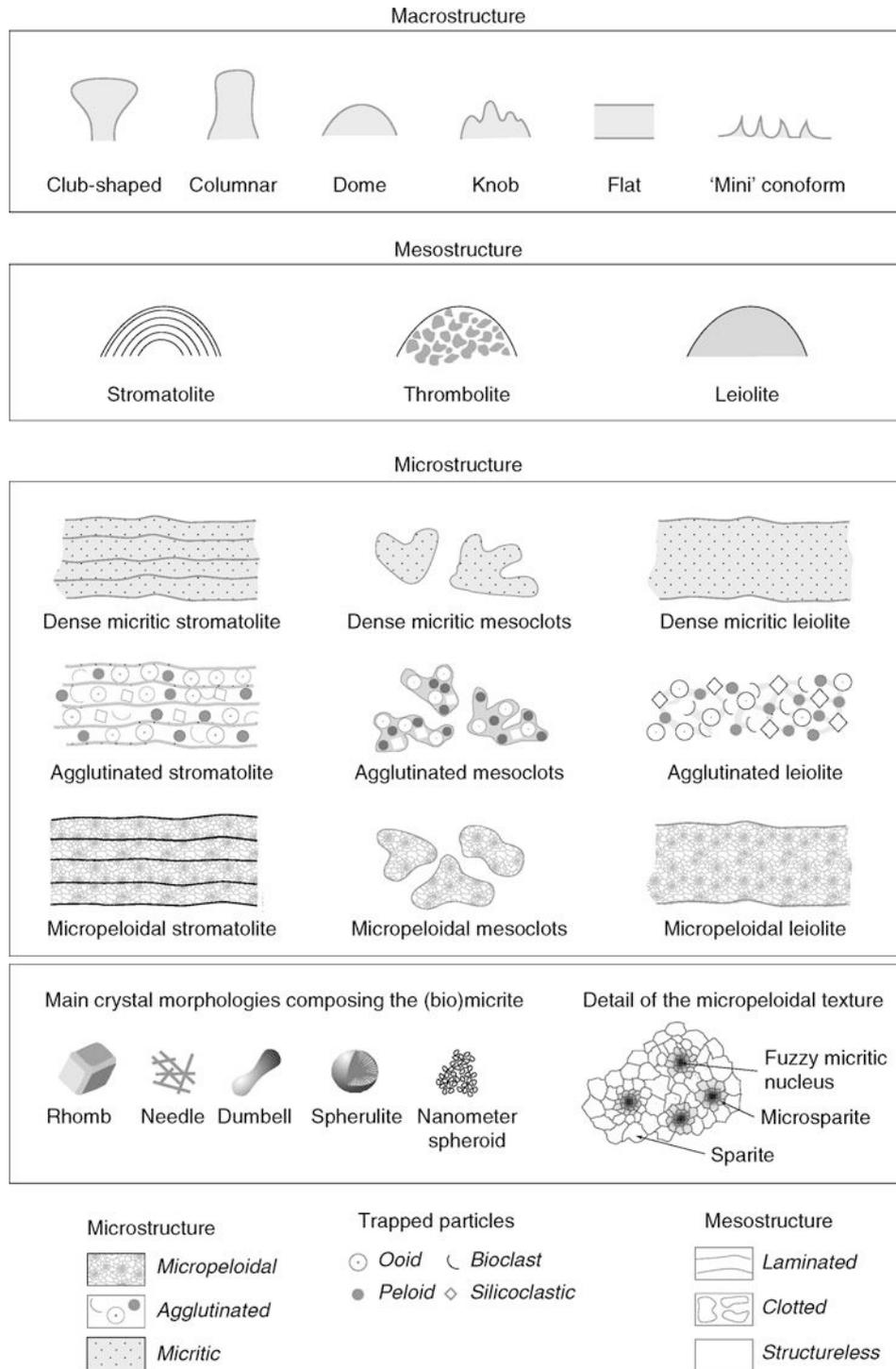
Hydroxides and Hydrus Oxides

Goethite - $\alpha\text{-FeOOH}$
 Ferrihydrite - $5\text{Fe}_2\text{O}_3 \cdot 9\text{H}_2\text{O}$
 Lepidocrocite - $\gamma\text{-FeOOH}$
 Ferrihydrite - $5\text{Fe}_2\text{O}_3 \cdot 9\text{H}_2\text{O}$
 Todorokite - $(\text{Mn}^{+2}\text{CaMg})\text{Mn}_3^{+4}\text{O}_7 \cdot \text{H}_2\text{O}$
 Birnessite - $\text{Na}_4\text{Mn}_{14}\text{O}_{27} \cdot 9\text{H}_2\text{O}$

Organic Crystals following Lowenstam & Weiner (1989)

Whewellite - $\text{CaC}_2\text{O}_4 \cdot \text{H}_2\text{O}$
 Weddellite - $\text{CaC}_2\text{O}_4 \cdot (2+x)\text{H}_2\text{O}$
 Mn Oxalate - $\text{Mn}_2\text{C}_2\text{O}_4 \cdot 2\text{H}_2\text{O}$
 Earlandite - $\text{Ca}_3(\text{C}_6\text{H}_5\text{O}_2)_2 \cdot 4\text{H}_2\text{O}$
 Glushinskite - $\text{MgC}_2\text{O}_4 \cdot 4\text{H}_2\text{O}$
 Manganese Oxalate - $\text{Mn}_2\text{C}_2\text{O}_4 \cdot 2\text{H}_2\text{O}$
 Sodium urate - $\text{C}_5\text{H}_3\text{N}_4\text{NaO}_3$
 Uric Acid - $\text{C}_5\text{H}_4\text{N}_4\text{O}_3$
 Ca tartrate - $\text{C}_4\text{H}_4\text{CaO}_6$
 Ca malate - $\text{C}_4\text{H}_4\text{CaO}_5$
 Paraffin Hydrocarbon
 Guanine - $\text{C}_5\text{H}_3(\text{NH}_2)\text{N}_4\text{O}$

Microbialites, Modern, Figure 1 Nomenclature and chemical compositions of minerals produced by biologically-related mineralization processes. (Modified from Weiner and Dove, 2003; data from Lowenstam and Weiner, 1989; Simkiss and Wilbur, 1989; Mann, 2001; Weiner and Addadi, 2002.)



Microbialites, Modern, Figure 2 Descriptive terminology for microbialite macro-, meso-, and microfabrics. (From Kennard and James, 1986; Riding, 1991; Schmid, 1996; Dupraz and Strasser, 1999; Shapiro, 2000.)



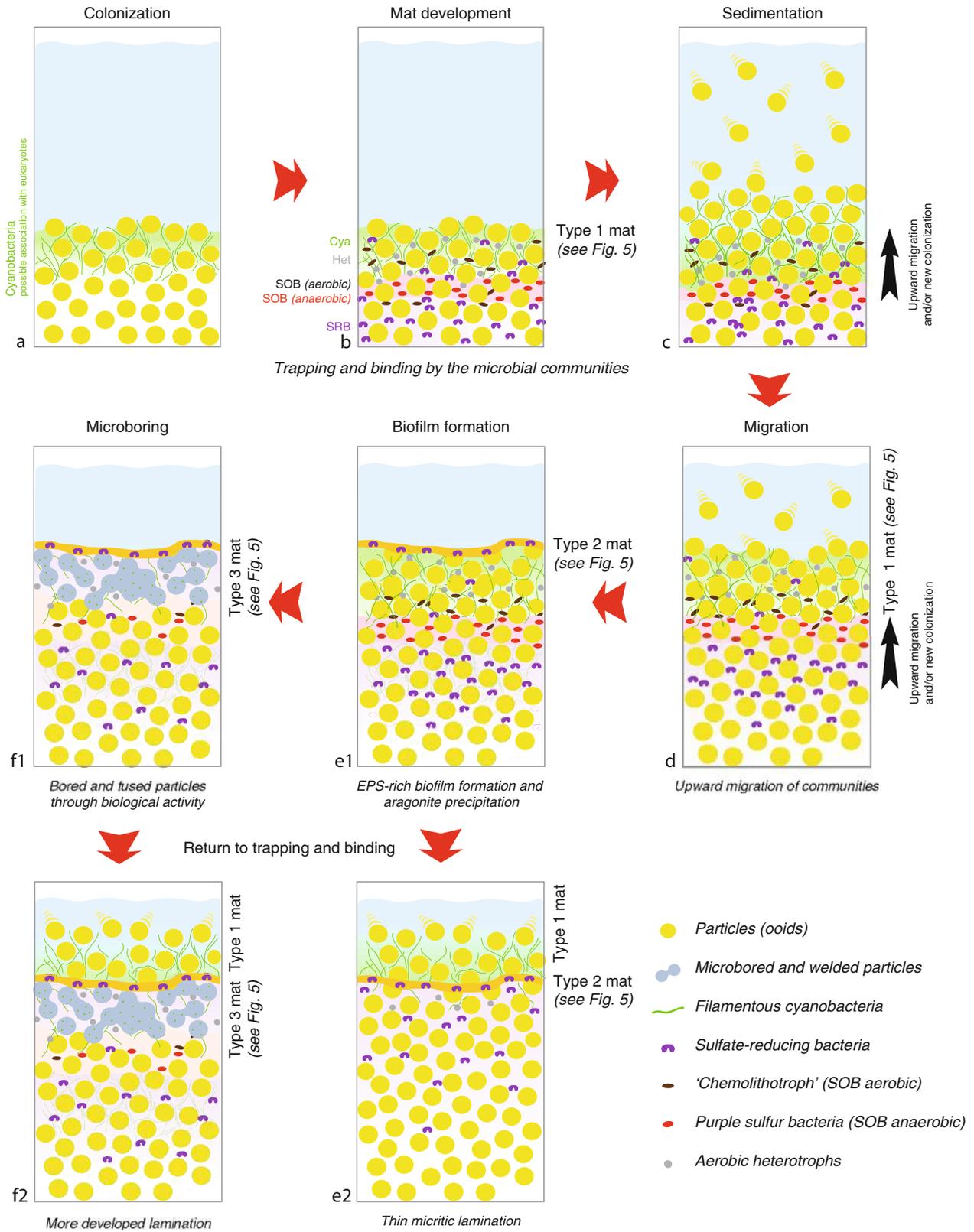
Microbialites, Modern, Figure 3 Underwater photograph showing shallow subtidal stromatolites (Darby Island, Bahamas) with a vertical section (upper left hand insert) showing well-developed lamination.

Dill et al., 1986; Reid et al., 1995). These stromatolites are coarse grained structures, composed of ooid sand; they form in intertidal and subtidal environments, exposed to high wave energy and strong tidal currents (e.g., Gebelein, 1976; Reid et al., 2000). Many of the stromatolites exhibit well-developed laminae (Figure 3; e.g., Reid et al., 2000). The lamination results from iterative growth of different types of microbial mats on the top of the build-ups (Figure 4). Each microbial mat forms a distinct mineral product, which can be recognized in thin section and SEM (Figure 5; Reid et al., 2000). The first mat type (1) is dominated by the filamentous cyanobacterium *Schizothrix*, which traps and binds ooids. The stickiness of the mat EPS results in the trapping of particles, which are subsequently bound by the upward growth of the cyanobacterial filaments. Other microorganisms (e.g., diatoms that produce copious amounts of EPS) can also participate in trapping grains. The second mat community (2) consists of a thin biofilm with abundant heterotrophic bacteria. Precipitation of aragonite within this biofilm forms a micritic lamina, which caps the underlying ooids. The third mat type (3) is characterized by an abundance of the endolithic coccoid cyanobacterium *Solentia* spp. *Solentia* tunnels through grains, leaving bore holes filled with EPS. Aragonite precipitation within the EPS results in micritization of the grains and, when tunnels cross between grains, welds the grains together. This process forms a well-cemented layer (Macintyre et al., 2000; Reid and Macintyre, 2000; Reid et al., 2000). The in situ precipitation of carbonate, which leads to early lithification of

the stromatolite-forming mats, is a result of prokaryotic activity (Visscher et al., 2000; Reid et al., 2003a).

Dominance of prokaryotic communities on the surfaces of modern marine stromatolites, is favored by the selective environmental pressure of periodic burial by sand (Andres and Reid, 2006; Kromkamp et al., 2007). In contrast to eukaryotes, which are typically killed when buried for periods of weeks to months, prokaryotes such as cyanobacteria are able to survive and recover from long burial events (Kromkamp et al., 2007). This attribute may contribute to the success of stromatolites in modern and past environments. Eukaryotic colonization (macroalgae: e.g., *Batophora*), during week- to month-long periods of exposure disrupts the lamination resulting from the cycling of prokaryotic mats, producing intervals of crude to no lamination within the stromatolite head.

It should be noted that trapping and binding alone does not form a stromatolite. The key factor in allowing development of a lithified laminated buildup is a hiatus in sediment accretion and corresponding development and lithification of a microbial biofilm. During long hiatal periods (i.e., several weeks), surfaces infested with the coccoid bacterium *Solentia* forms thicker, well-cemented lamina of fused ooid grains. Precipitation of aragonitic needles associated with the activity of sulfate-reducing bacteria is a key feature in carbonate precipitation within Bahamian stromatolites (Visscher et al., 2000). Precipitation resulting from anaerobic heterotrophic activity is supported by isotopic data (Andres et al., 2005).



Microbialites, Modern, Figure 4 (Continued)

Factors leading to the cycling of surface communities responsible for lamination in Bahamian stromatolites are currently under investigation (Andres and Reid, 2006). Both biological and environmental factors may be important (Figure 6; Seong-Joo et al., 2000; Reid et al., 2003a). Biological factors include microbial ecological interactions, and production and consumption of organic and inorganic compounds. Extrinsic factors include temperature, light, nutrients, and hydrodynamics, which could affect the stickiness of EPS and/or sediment supply (Figure 6).

Hypersaline and saline stromatolites

In contrast to open marine environments, where modern stromatolites are rare, living stromatolites are more common in hypersaline environments. This is because microbial communities are able to cope with high salinity, whereas most eukaryotes, such as macroalgae and burrowing/grazing invertebrates, which compete with or ingest cyanobacteria and disrupt lamination, are largely excluded (Fischer, 1965; Awramik, 1971, 1982, 1992; Walter and Heys, 1985; Riding, 2006).

Stromatolites in Shark Bay, Western Australia are the most famous stromatolites thriving in hypersaline water. They are found in the Hamelin Pool Marine Nature Reserve of the Shark Bay UNESCO World Heritage Site. Ranging from 55–70 ppt throughout the year (Playford, 1990), Hamelin Pool has approximately double normal marine salinity and hosts abundant and diverse stromatolites. Shark Bay stromatolites were discovered in 1954 by Johnstone, Playford, and Chase of the West Australian Petroleum Pty. Ltd (Playford and Cockbain, 1976). They were the first modern stromatolites discovered with sizes and shapes comparable to fossil counterparts (Logan, 1961; Logan et al., 1974; Playford and Cockbain, 1976; Playford, 1979; Bauld et al., 1979; Bauld, 1981; Burns et al., 2004). Like Bahamian stromatolites, Shark Bay structures are formed by both (1) microbial trapping and binding and (2) microbial precipitation. Both processes are important in the intertidal zone, forming coarse grained sandy stromatolites. Microbial precipitation is the primary accretionary mechanism in the subtidal zone of Shark Bay, forming muddy, micritic stromatolites (Reid et al., 2003b).

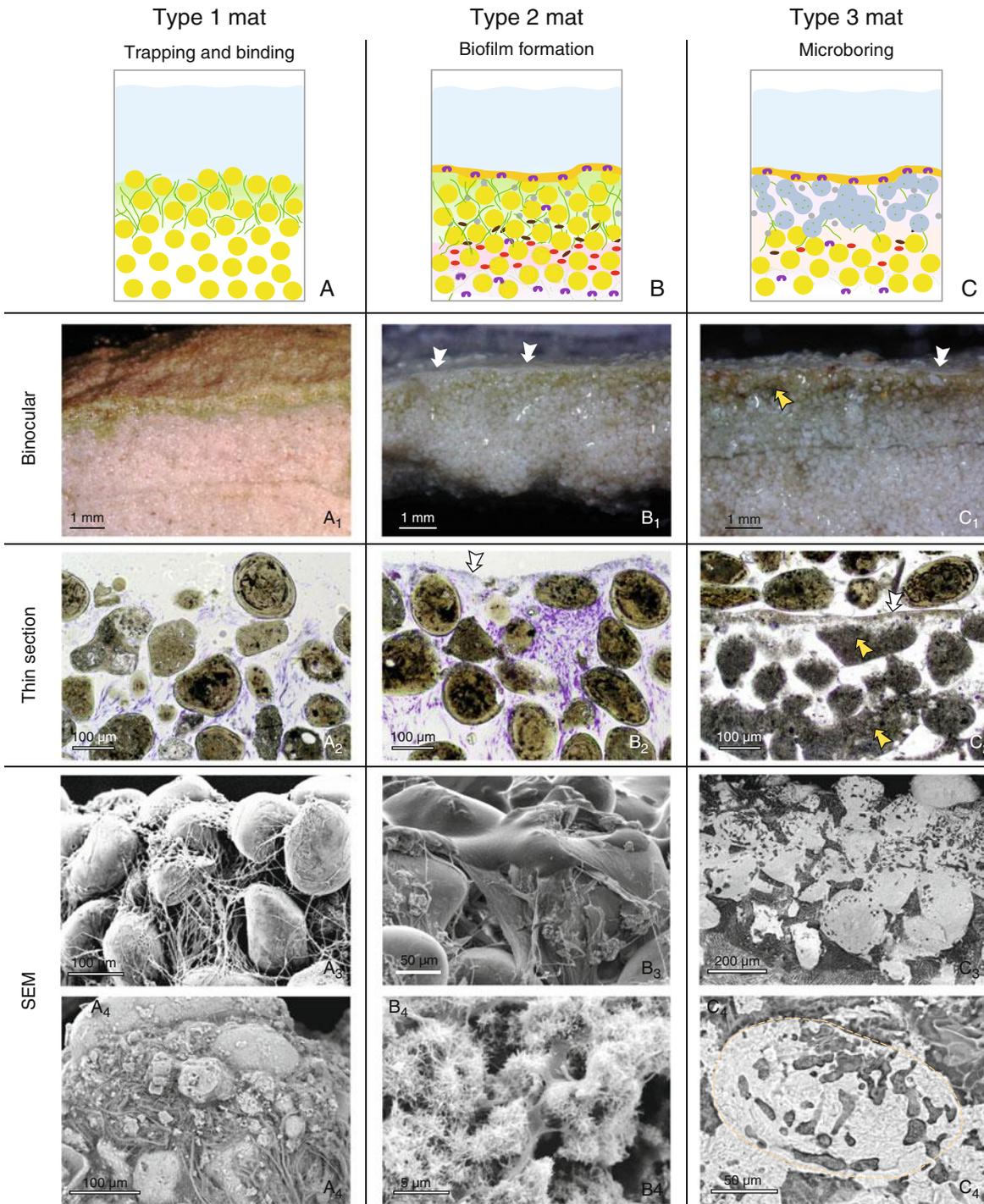
As a result of the dominant sandy textures of Shark Bay stromatolites and open marine stromatolites in the Bahamas, some authors have proposed that these stromatolites are not appropriate analogs for fossil stromatolites, which are generally display fine-grained, micritic microstructures (Awramik and Riding, 1988). Despite their overall coarse-grained texture, these modern stromatolites have micritic laminae formed as a result of microbially-induced precipitation (Reid et al., 2000; Visscher et al., 2000). Moreover, the ecological model developed for Bahamian stromatolites, in which lamination results from the cycling of prokaryotic communities on the stromatolite surface, is likely applicable to the growth of Shark Bay stromatolites. Indeed, a model of iterative accretion of laminae, which record both microbial and environmental fingerprints and progressively shape the emergent morphology, may serve as a conceptual model for the growth of fossil stromatolites.

In addition to Shark Bay, living stromatolites are also present in many other saline and hypersaline environments. Several saline lakes in Australia harbor stromatolites, including Lake Thetis, near Cervantes, lakes on Rottneest Island (Reitner et al., 1996), and Lake Clifton near Mandurah (e.g., Grey et al., 1990). Cyanobacterial stromatolitic domes have been described in the intertidal zone of Bermuda (e.g., Sharp, 1969; Golubic and Focke, 1978) and small crudely laminated knobs have been found in a hypersaline lake on Bonaire Island in the Netherlands Antilles (Golubic and Focke, 1978). Various islands in the Bahamas also have hypersaline lakes with well-developed microbial mats and stromatolites, including Storr's Lake on San Salvador. Storr's lake harbors alternating stromatolitic and thrombolitic buildups (Mann and Hoffman, 1984; McNeese, 1988; Neumann et al., 1988; Mann and Nelson, 1989; Pentecost, 1989; Zabielski, 1991).

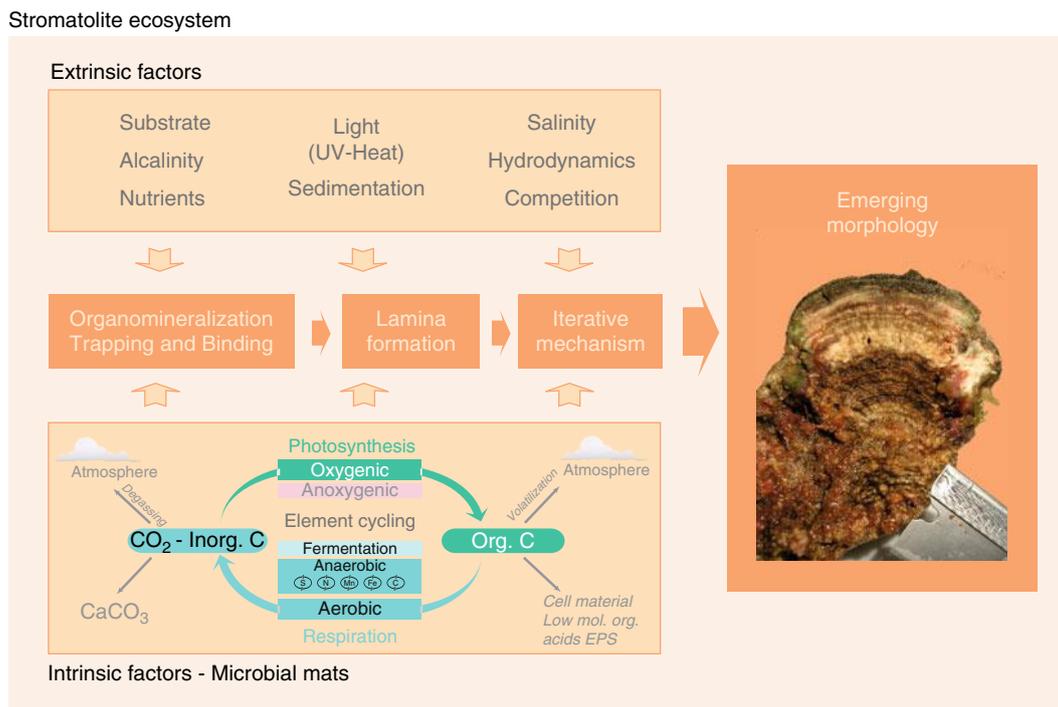
Fresh water and continental stromatolites

Numerous examples of freshwater laminated microbialite have been published. One of the most widespread examples of these microbialites is travertines. Tufa stromatolites (meteoene travertine following Pentecost (2005)) are freshwater fluviatile tufas, which locally exhibit thick laminated crusts formed by calcified cyanobacteria (Pentecost, 1978; Riding, 1991b, 2000). Most of the precipitation of carbonate in these travertines results from physicochemical

Microbialites, Modern, Figure 4 Model of coarse-grained open-marine stromatolite formation. (a) Cyanobacteria colonize and stabilize mobile ooid sand (trapping and binding). (b) A complex microbial mat develops in the upper few millimeters of the sediment (*Cya* cyanobacteria; *SRB* sulfate reducing bacteria; *SOB* sulfide oxidizing bacteria (aerobic and anaerobic); *Het* aerobic heterotrophs; see also Figure 8). (c–d) As a result of sediment accretion, the microbial mat migrates upward, continuing trapping and binding. Cyanobacteria (and heterotrophs) can survive massive burial. No significant in situ precipitation is observed at this stage, which corresponds to the *Type 1 mat* in Figure 5. (e) During a hiatus in sediment accretion, an EPS-rich biofilm develops, draping over the ooids (*Type 2 mat*, Figure 5). This biofilm rapidly lithifies due to the activity of anaerobic heterotrophs (i.e., SRB), forming a thin lamina of micritic aragonite (see Figure 5b4). (f) A prolonged hiatus in trapping and binding results in colonization of ooid grains under the biofilm by the endolithic cocoid cyanobacteria *Solentia* sp. (*Type 3 mat*, Figure 5) Precipitation of aragonite in the bore holes made by these endoliths destroys the internal microstructure of ooids, changing their color from golden brown to gray. Precipitation in bore holes crossing between grains fuses them together (Figure 5c_{2–4}). Resumption of trapping and trapping corresponds to formation of a new *Type 1 mat* (e₂, f₂). The iterative succession of these three different mat types is responsible for the lamination observed in open-marine stromatolite (Figure 3).



Microbialites, Modern, Figure 5 Micrographs illustrating the main features of the surface mats responsible for the formation of modern marine stromatolites. Stromatolite lamination results from the iterative growth at the surface of the build up of three mat types: (1) Type 1 mats are dominated by filamentous cyanobacteria, which trap carbonate sand grains through EPS stickiness (A₁₋₄); (2) Type 2 mats consist of a continuous biofilm, drapping the stromatolite surface (white arrows in B₁₋₃); the biofilm is composed of extracellular polymeric substances (EPS, B₃) containing numerous heterotrophic bacteria. This biofilm rapidly lithifies as a result of precipitation of aragonite needles within the biofilm (B₄); (3) Type 3 mats are characterized by endolith-infested ooid grains (yellow arrows in C₁₋₂), which appear gray and are fused together, below a surface biofilm. (A₁-B₁-C₁) binocular micrographs, (A₂-B₂-C₂) petrographic micrographs, (A₃-B₃-B₄) high vacuum scanning electron microscope images (SEM; chemical drying), and (A₄-C₃-C₄) cryo-SEM (frozen samples) images.



Microbialites, Modern, Figure 6 Interactive processes within the stromatolite ecosystem. Intrinsic (microbial mat-related) and extrinsic (environment-related) factors work together to determine the emergent stromatolite morphology and fabric, which can be described at microscale (biomineralization, trapping, and binding), mesoscale (laminae formation), and macroscale (iterative mechanism leading to morphology) levels.

degassing of CO₂ through resurgence, cascades, or waterfalls. Photosynthetic uptake of CO₂ by cyanobacteria can, however, be responsible for the precipitation of calcium carbonate in slow running and low DIC streams (Verrecchia et al., 1995; Merz-Preiss and Riding, 1999; Arp et al., 2001). Relatively low DIC and high Ca²⁺ concentration is required for photosynthesis to influence carbonate alkalinity and enable precipitation (Arp et al., 2001, 2003).

Fresh water stromatolites are also present in Antarctic lakes, which are permanently ice-covered (Parker et al., 1981). These lakes are seasonally fed by glaciers, which modify salinity from fresh-to-saline while oxygen levels vary from anoxic to supersaturated. The stromatolites are formed through sediment trapping and binding as well as carbonate precipitation in cyanobacterial-dominated (e.g., *Phormidium*, *Oscillatoria*) microbial mats. Other non-marine environments with stromatolites include alkaline lakes, such as the Caldera lakes of Niufo'ou Island (Tonga), with spectacular laminated buildups (Kazmierczak and Kempe, 2006).

Laminated deposits, referred to as terrestrial stromatolites (Verrecchia et al., 1995; Riding, 2000), are observed in "non-water-saturated" environments. These deposits have also been called lichen stromatolites (Klappa, 1979) and subaerial stromatolites (Riding, 1991b). They consist of laminar calcretes formed by microbial activity or in close association with microbial communities.

Determining between biogenic and non-biogenic calcretes is often difficult as carbonate precipitation may be caused by physicochemical evaporation (e.g., Read, 1976), and/or cyanobacterial activity (e.g., Verrecchia et al., 1995).

Thrombolite

The term thrombolite was introduced by Aitken (1967) for microbial "structures related to stromatolites, but lacking lamination and characterized by a macroscopic clotted fabric". Since this initial definition, thrombolites and stromatolites have been recognized as two distinct microbialite structures (Kennard and James, 1986). The key microstructure of thrombolites is mesoclots, which produce the clotted fabric (Shapiro, 2000). The mesoclots consist of polymorphic (simple spheroids to polylobate), millimeter to centimeter-sized, aggregates which display a variety of forms, from simple spheroids to polylobate masses (e.g., Shapiro, 2000). Clotted mesostructures have been described for many fossil thrombolites, which are mostly composed of fine-grained carbonate. Therefore, many authors define mesoclots as mostly composed of micrite or micropeloids (Kennard, and James, 1986; Dupraz and Strasser, 1999; Shapiro, 2000). However, modern thrombolites, as well examples from the Miocene, show agglutinated, clotted fabrics (Riding, 2000). The mesoclots of modern thrombolites thus consist of micrite, micropeloids, or agglutinated particles (Figure 2).

The clotted fabric of thrombolites can have a variety of origins. The fabric can be attributed “to the in situ calcification of coccoid or coccoid-dominated microbial communities” (Kennard and James, 1986). Other mechanisms involve bioturbation and bioerosion, and thrombolitic mesostructures within large Bahamian stromatolites are often due to disruption of the lamination by eukaryotic colonization (e.g., *Batophora* sp. and other algae).

In some cases, environmental conditions may trigger changes between thrombolite and stromatolitic fabrics. In Storr’s Lake (San Salvador, Bahamas), well-developed thrombolites alternate with stromatolitic layers (McNeese, 1988; Mann and Nelson, 1989). This alternation might be triggered by lake-level fluctuations and associated turbidity variability. This mechanism results in a succession of phototrophic-dominated (stromatolites) to heterotrophic-dominated communities (thrombolites) as surface communities, as modeled by Dupraz et al. (2006).

Many other modern lakes host thrombolite deposits: Lake Clifton, Lake Tethys, Lake Richmond and different lakes on Rottneest Island (Australia), Kelly and Pavillon lakes (British Columbia, Canada), lakes on Bonaire Island (Netherlands Antilles, southern Caribbean; Kobluk and Crawford, 1990), Lago Sarmiento (Patagonia, Chile), Poza Azul lake (Cuatro Ciénegas, Mexico), Yellow Stone National Park (USA), Green Lake (Fayetteville, New York, USA). In addition, travertines showing thrombolitic features have been referred to as “Tufa Thrombolite” (Riding, 2000).

Leiolite

The term leiolite comes from the Greek word “leios,” meaning uniform or smooth and “lithos,” (meaning rock) and was originally applied to late Miocene (Messinian) deposits in Spain (Figure 2; Braga et al., 1995). Leiolite is characterized by relatively structureless, aphanitic, mesostructure, lacking lamination or clots, and can be a synonym for “cryptomicrobial” as used by Kennard and James (1986). Most authors tend to classify microbialites as either stromatolites or thrombolites, despite the fact that many of these deposits lack the defining mesostructures and would more appropriately be termed leiolite (see Riding, 2000). No examples of modern leiolite have been published. However, examples could include non-laminated, non-thrombolitic portions of Bahamian or Shark Bay stromatolites, carbonate crust formation in hypersaline lakes (Dupraz et al., 2004), and biological stabilization of sand dune by chasmolithic microorganisms (Hillgaertner et al., 2001).

Other types of microbialites

Microbial processes or the presence of microbes are often intimately related to sedimentary processes in modern carbonate systems, although the resulting deposits may not be considered as true microbialite and classified as stromatolite, thrombolite, or leiolite. These microbial carbonate

deposits include meteogene and thermogene travertine (Pentecost, 2005), where microbial influence creates specific microfabrics. Spectacular examples of travertines can be observed in many alkaline lakes, forming carbonate towers (e.g., Pyramid Lake, Nevada (Benson, 1994)), Lake Can, Turkey (Kempe et al., 1991), and Mono Lake, California (e.g., Bischoff et al., 1993; Riding, 2000). Carbonate chimneys are also formed in hydrothermal systems, where microbial activity is important (e.g., “Lost City” Hydrothermal Field; Kelley et al., 2001; Ludwig et al., 2006).

Other deposits that are difficult to classify include microbial calcrite – a terrestrial carbonate the formation of which is strongly influenced by bacteria and fungi (Jones and Wilson, 1986; Wright et al., 1988; Verrecchia and Verrecchia, 1994; Verrecchia et al., 1995). In addition, in continental environments, the formation of needle fiber calcite (NFC) is related to fungi activity (Verrecchia and Verrecchia, 1994; Cailleau et al., 2004, 2005). Mondmilch or Moonmilch – a soft paste-like or powdery cave deposit – includes important microbial populations, which influence precipitation (Thraillkill, 1976; Canaveras et al., 2006). Microbial mats are also involved in the formation of oncoids, which are unattached spherical stromatolites (e.g., Bathurst, 1966), and microbial activity may play a role in the formation of “whitings” (Thompson, and Ferris, 1990; Robbins, and Blackwelder, 1992).

Processes of microbialite formation

Early lithification is a key process in the formation of modern carbonate microbialites and is critical for the preservation of these structures in the fossil record. Lithification processes start at the time of deposition and continue during burial (diagenesis). Lithification consists of in situ precipitation of minerals, which progressively cement trapped grains (if present), and preserve the biosedimentary structures. Two closely coupled components are fundamental in carbonate precipitation within microbial mats: (1) the alkalinity engine and (2) the organic matrix in which this mineral is forming.

The alkalinity engine

The precipitation of carbonate minerals depends on the availability of carbonate ions, specific cations (e.g., Ca^{2+} , Mg^{2+}), and suitable nucleation sites. Carbonate minerals may precipitate when a solution is saturated with respect to that mineral. The degree of saturation is calculated via the saturation index of the specific mineral:

$$\text{SI} = \log(\text{IAP}/K_{\text{ps}}) \quad (1)$$

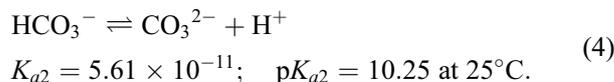
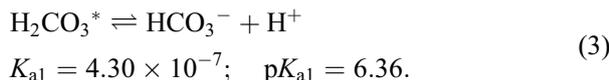
IAP is the “ion activity product” and K_{sp} is the solubility product of the corresponding mineral (solid phase). In the case of CaCO_3 , both the carbonate alkalinity and the activity of the available cations are taken into account

when calculating the saturation index (Stumm and Morgan, 1996):

$$SI_{\text{CaCO}_3} = \text{Log}(\{Ca^{2+}\} * \{CO_3^{2-}\} / K_{sp}). \quad (2)$$

The activity of a given chemical compound corresponds to the concentration of that compound multiplied by the activity coefficient. The solubility products for aragonite and calcite are $10^{-6.19}$ and $10^{-6.37}$, respectively, at 25°C, 1 bar atmospheric pressure and 35 PSU salinity (Zeebe and Wolf-Gladrow, 2001). A solution is supersaturated with respect to a given mineral when SI is greater than 0, meaning that K_{sp} is smaller than IAP. Experimental evidence showed that a supersaturation must be greater than 0.8 in order to have spontaneous precipitation of CaCO_3 (Kempe and Kazmierczak, 1994). Arp et al. (2001) used SI greater than 1 (i.e., a 10-fold supersaturation) as a prerequisite for carbonate precipitation in non-marine environment.

Carbonate ion activity, $\{CO_3^{2-}\}$, depends on the carbonate equilibrium. CO_2 dissolves in water to form carbonic acid (H_2CO_3). The amount of dissolved CO_2 is proportional to the partial pressure of CO_2 ($p\text{CO}_2$) in the gas phase in contact with the liquid (i.e., Henry's Law). This value varies with pressure and temperature. Low temperature and high pressure allow for more CO_2 dissolution in water. Carbonic acid is weak acid that will only partially dissociate in an aqueous solution to produce H^+ ion and the conjugate base. It will deprotonate as follows (with pK_s value for fresh water):

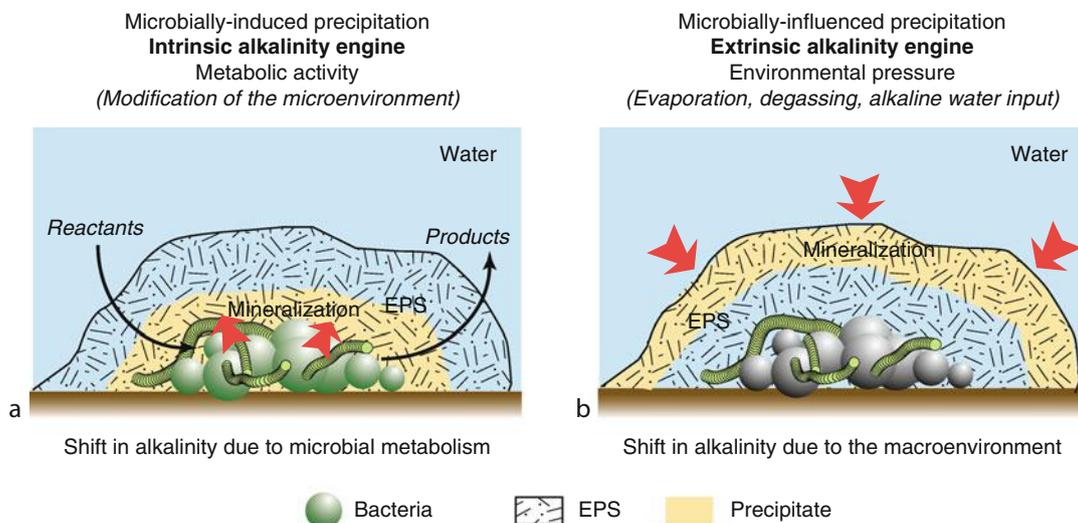


The two pK_s values vary as a function of the salinity. For seawater conditions, pK_{a1} and pK_{a2} are 5.9 and 8.9, respectively (at 25°C, 1 bar atmospheric pressure and 35 PSU salinity; Zeebe and Wolf-Gladrow, 2001).

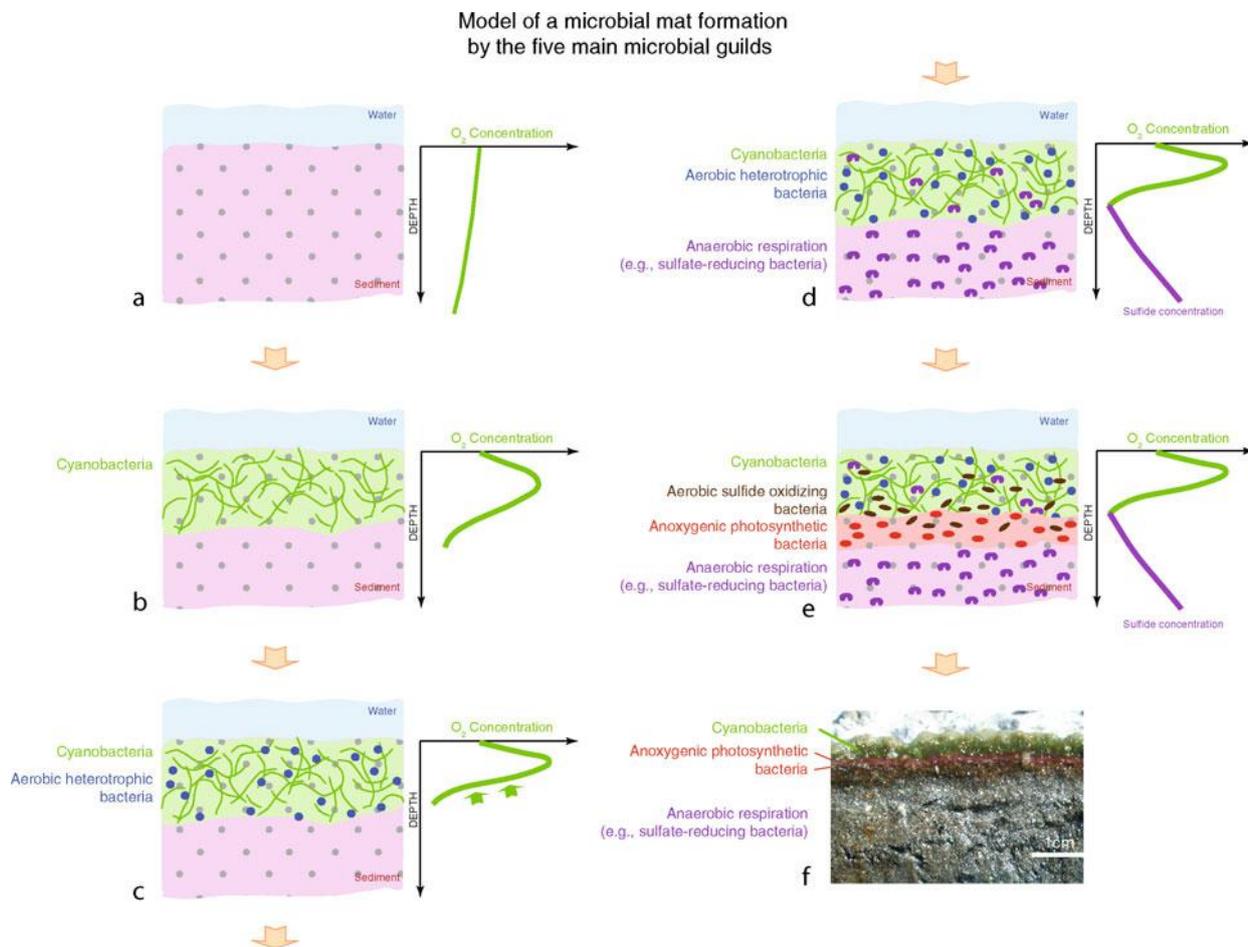
Availability of carbonate ions is a prerequisite for precipitation of carbonate minerals. The amount of bicarbonate and carbonate ions in solution denotes carbonate alkalinity, which is a part of total alkalinity, including borate, hydroxide, phosphate, and silicate. In marine and most of freshwater environments, phosphate and silicate are minor components, and the carbonate equilibrium typically drives global alkalinity. Various processes can have an impact of carbonate alkalinity, indirectly promoting precipitation or dissolution of carbonate mineral. The sum of processes that creates alkalinity represents the "alkalinity engine." This engine is intrinsically driven when alkalinity is affected by microbial communities, or extrinsically driven when physico-chemical processes of the macro-environment cause alkalinity shifts (Figure 7).

Intrinsic alkalinity engine (metabolism)

The way microbial communities acquire their energy and their source of carbon (i.e., through metabolism) can have a strong impact on local carbonate alkalinity. In a simplified view of the microbial carbon cycle, the production of organic matter through photosynthesis (oxygenic or anoxygenic) is coupled with the oxidation of organic carbon by aerobic (oxygen as oxidant) or



Microbialites, Modern, Figure 7 Model of carbonate precipitation within biofilms. Increases in alkalinity leading to precipitation can be (a) intrinsic, resulting from microbial metabolism or (b) extrinsic, resulting from environmental factors (b). In both the cases, the EPS matrix, which embeds the microbial communities, has a pivotal role in determining mineral morphology, composition, and mineralogy.



Microbialites, Modern, Figure 8 Model of microbial mat formation by the five main guilds (van Gernerden, 1993). (a) Typical diffusion of O₂ through the water-sediment interface in the absence of microbial activity. (b) Cyanobacteria colonize the sediment, fixing (reduce) CO₂ to form biomass using solar energy (photosynthesis) and using water as electron donor. O₂ is a byproduct (visible in the upper millimeter of the depth profile). (c) The autotrophically-produced organic carbon is degraded by aerobic heterotrophs (aerobic respiration) using O₂ as final electron acceptor. The consumption of oxygen results in, or is reflected by, a sharper O₂ gradient in the sediment (arrows) and the formation of an anoxic zone below the active cyanobacterial layer. (d) Anaerobic heterotrophs then develop in the anoxic zone (mostly SRB in this example). (e) SRB produces sulfide compounds, which can then feed anoxygenic photosynthesis and aerobic sulfide oxidation. (f) Examples of a hypersaline mat from the Bahamas showing classical zonation of bacterial guilds.

anaerobic (SO₄²⁻, NO₃⁻, Fe³⁺, etc. as oxidant) respiration (Figure 8). Most microbial metabolites (products of metabolism) are efficiently recycled within the mats, completely closing the cycles of major elements. Many microbial mats function as light-driven engines, fueled only by sunlight.

The biogeochemical niche of microorganisms can be described through three overarching metabolic characteristics related to energy generation and biomass acquisition: the energy source, the electron donor used for energy generation, and the carbon source for biomass production. Each of these three properties have two possibilities: potential energy sources are light (photo-) or chemical redox reactions (chemo-), electron donors can be organic (organo-)

or inorganic (litho-), and biomass can be derived from CO₂ fixation (autotrophy) or from carbon that is already fixed (heterotrophy). For example, a cyanobacterium derives energy from light (photo) uses water as electron donor (litho) and fixes CO₂ for biomass (auto-); it is hence designated as a photolithoautotroph (trophos means “to feed”). A typical aerobic bacterium that uses organic carbon is a chemoorganoheterotroph, etc.

Different types of metabolism impact carbonate precipitation and dissolution by taking up (autotrophy) or releasing (respiration) CO₂ and through production or consumption of organic acids. Changes in organic acid concentrations modify alkalinity and pH of the mats (Ehrlich, 1996; Visscher and Stolz, 2005). Mechanisms

that can promote precipitation of carbonate minerals include the following:

1. *Oxygenic photosynthesis* (producing O₂) by cyanobacteria (photolithoautotrophy). Uptake of CO₂ during photosynthetic activity leads to precipitation of carbonate in the sheath or in the direct vicinity of the cyanobacteria (Pentecost and Riding, 1986; Freytag and Verrecchia, 1998, 1999; Merz-Preiss and Riding, 1999; Riding, 2000) (Figure 9). The increase in alkalinity is attributed to an exchange of HCO₃⁻ and OH⁻ through the cell membrane (Figure 9). Photosynthesis is an important mechanism for microbialite formation in freshwater environment (Arp et al., 2001), where it may help overcome the kinetic barrier for CaCO₃ precipitation, even in highly supersaturated freshwater settings (Shiraishi et al., 2008).
2. *Aerobic respiration* (chemoorganoheterotrophy) generally dissolves calcium carbonate through production of CO₂. However, precipitation can occur in a well-buffered alkaline environment when CO₂ produces carbonate ions. Carbonate minerals can also be formed when aerobic respiration consumes strong organic acids and produce CO₂ that will be degassed. This process is proposed for carbonate precipitation in tropical soil associated to the oxalate-carbonate cycle (Braissant et al., 2004). In the absence of O₂, some bacteria can generate energy through fermentation, which process uses the same compound (e.g., organic carbon, inorganic sulfur) both as electron donor and acceptor. Most fermentation of organic carbon will lead to dissolution of carbonate (Visscher and Stolz, 2005).
3. *Anaerobic respiration*: certain bacteria can oxidize organic matter using respiratory chains that do not use O₂ as final electron acceptor (also chemoorganoheterotrophy). These bacteria can use, e.g., sulfate (sulfate-reduction), nitrate (nitrate-reduction), iron (iron-reduction), manganese (manganese reduction), or even HCO₃⁻. These types of metabolism can promote precipitation of carbonate through various processes (e.g., Visscher and Stolz, 2005): consumption of organic acid, production of base (e.g., NH₃), removing precipitation inhibition (removing of SO₄²⁻), etc. Sulfate reduction is the main process in marine environment due to high concentration of SO₄²⁻ in seawater.
4. *Chemolithoautotrophy*: Some bacteria do not oxidize organic matter to generate energy. They will instead use the chemical energy (chemo) produced by the oxidation of inorganic (litho) electron donors such as H₂, CO, Fe²⁺, NH₄⁺ and HS⁻ in order to fix CO₂ (autotrophy). Sulfide (in sediments) and ammonium (in the water column) oxidation are the most abundant chemolithoautotrophic electron donor in marine environment. Aerobic sulfide oxidation and ammonium oxidation is likely to induce dissolution of carbonate minerals, whereas anaerobic sulfide oxidation (e.g., using nitrate as electron acceptor) may induce

precipitation (Visscher and Stolz, 2005). However, most of these types of metabolism are all autotrophic, i.e., fixing CO₂. The uptake of CO₂ can increase carbonate alkalinity and induce precipitation of carbonates in similar way that physicochemical degassing of CO₂ does.

Extrinsic alkalinity engine

The determination of alkalinity-driving forces that form microbialites is generally a complex task. In many cases, a combination of intrinsic and extrinsic factors is responsible for precipitation. There are however, a few examples where the macroenvironment acts as a major player in microbial mat lithification. The two important physicochemical processes that can lead to carbonate precipitation in microbial mats are water evaporation and CO₂ degassing. Even in these cases, however, the microbial communities of the mats can serve as substrates for physicochemical carbonate precipitation and affect mineral mineralogy or morphology.

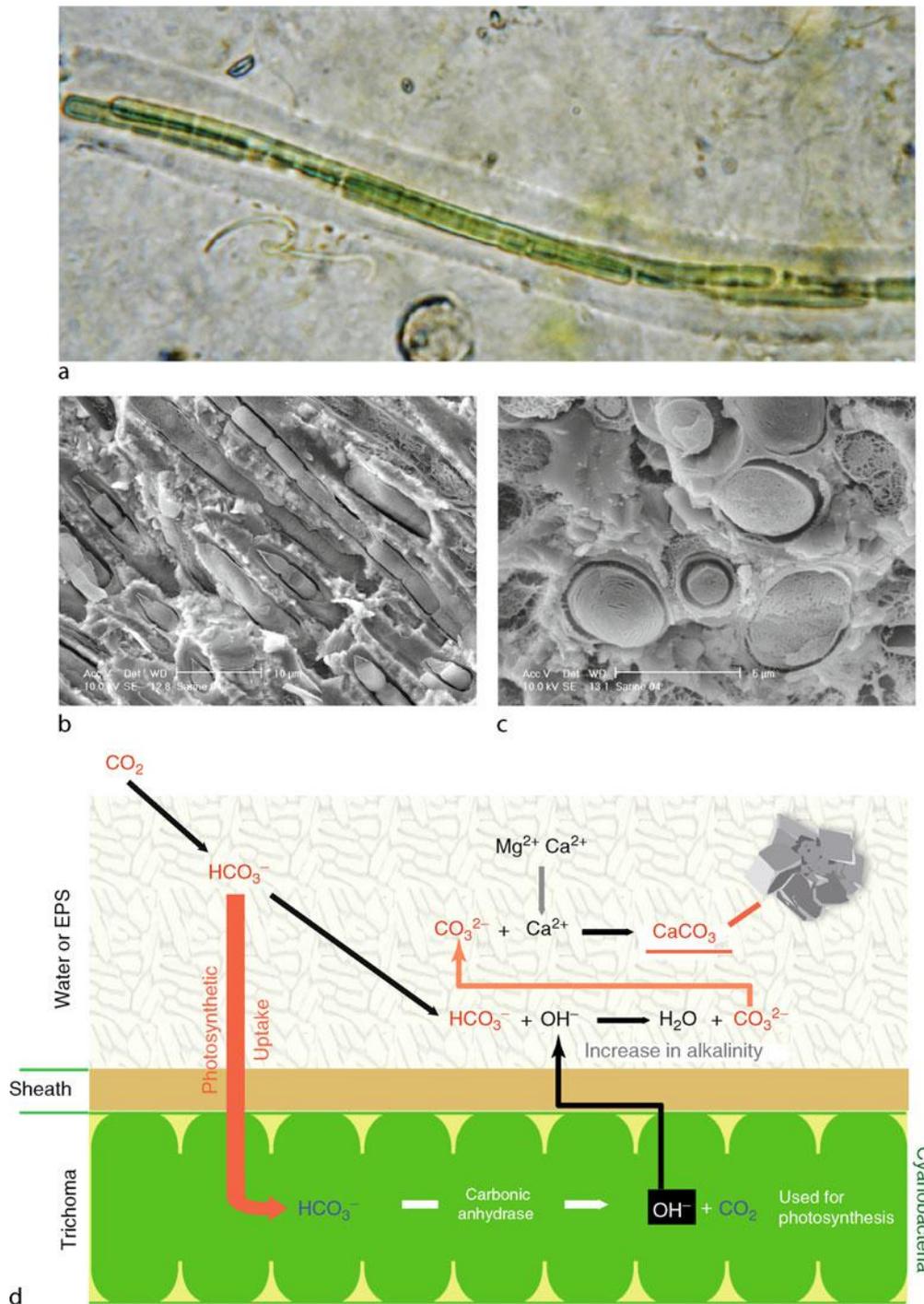
In the marine environment, solar evaporation of water may lead to the formation of evaporitic minerals (e.g., Warren, 2006). Although a variety of carbonate minerals can be produced through this mechanism (e.g., calcite, ikaite, aragonite, Mg-calcite, dolomite, and magnesite), evaporites largely consist of halite and gypsum. Examples of microbial mats associated with gypsum deposits have been described (e.g., Babel, 2004). Moreover, bacteria trapped in gypsum crystals are able to survive for millions of year (Vreeland et al., 2000, 2007). The specific role of microbes in gypsum nucleation is, however, not clear as the evaporation processes generally obscure microbial signatures. For reviews on evaporites, see Yechieli, and Wood (2002) or Warren (2006).

Precipitation of carbonate can also result from degassing of CO₂ and forms travertines. Travertines represent chemically-mediated continental carbonate deposits that form around sinter sources along streams and lakes (Pentecost, 2005). The precipitated minerals, consisting of aragonite or calcite, are mainly related to the release of CO₂ from the system, resulting in supersaturation with respect to calcium carbonate. This can be illustrated by the buffering equation of the carbonate:

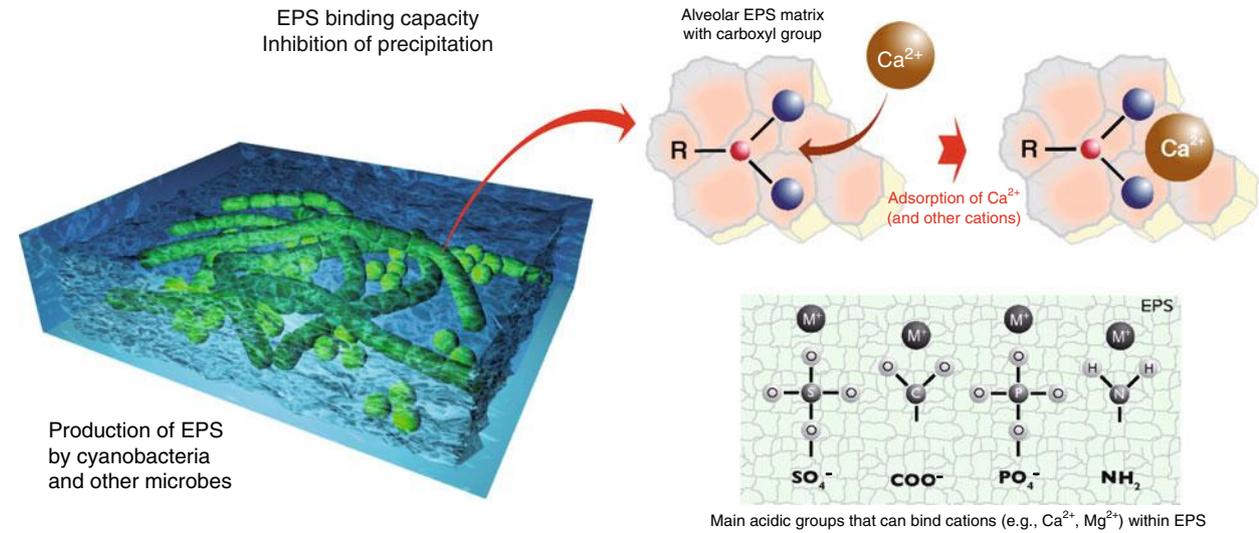


Removal of CO₂ through degassing will drive this equation to the right, promoting precipitation of CaCO₃. Similarly, increasing dissolved CO₂ drive the equation to the left, resulting in dissolution of calcium carbonate.

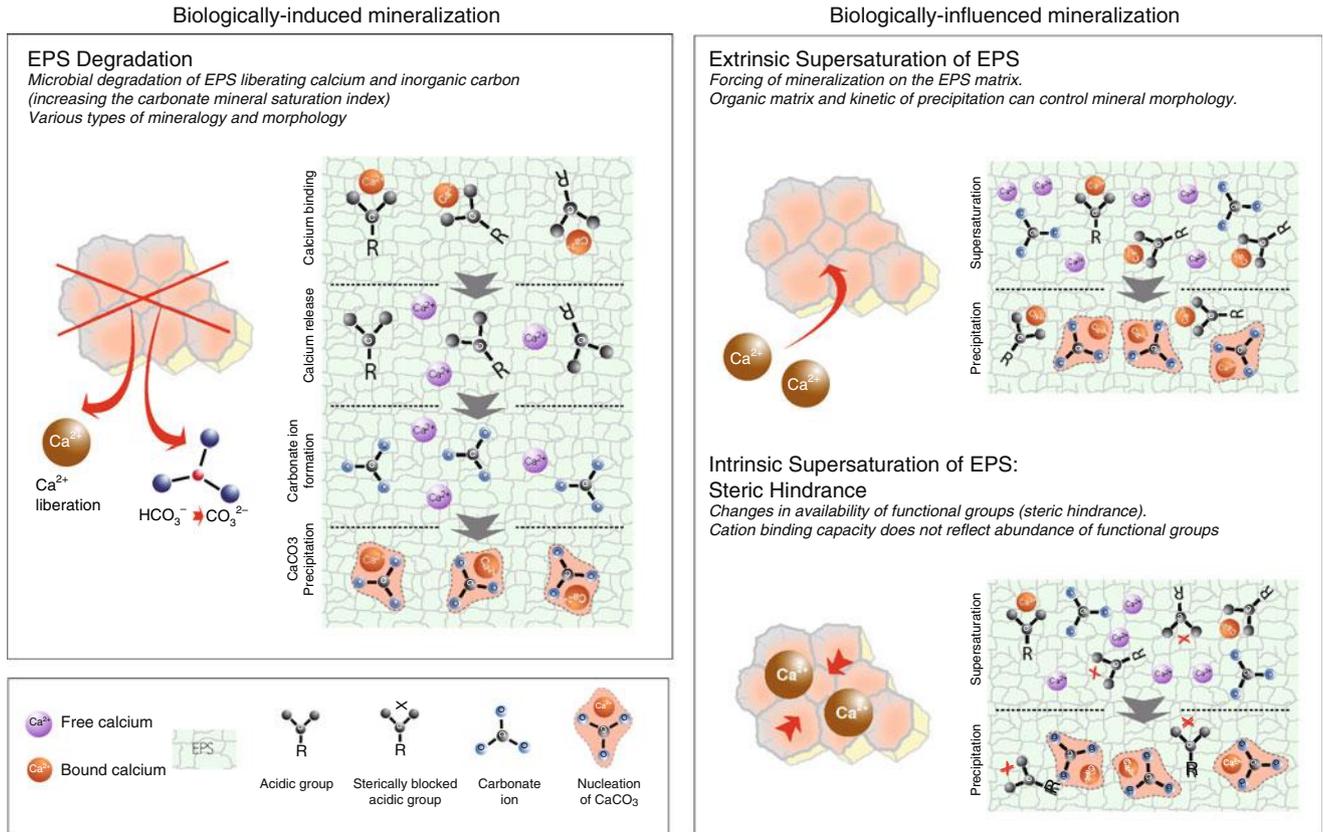
Travertines can be classified based on the source of the CO₂ that is degassed (Pentecost, 2005). "Metogene travertines" are formed by degassing of meteoric carbon dioxide, whereas "thermogene travertines" are formed by the degassing of hydrothermal CO₂. In metogene travertines, the CO₂ can originate from the atmosphere or from the soil-zone. In thermogene travertines, the bulk of the CO₂



Microbialites, Modern, Figure 9 Role of photosynthesis in the precipitation of carbonate minerals. (a) Photomicrograph of *Microcoleus* spp., a filamentous cyanobacterium showing the trichoma (chains of cells) embedded in a sheath. (b) Longitudinal section through a freshwater travertine (Sarine River, Switzerland) showing precipitation of CaCO_3 in the sheath of the filamentous cyanobacteria *Oscillatoria* sp. and *Phormidium* sp. (c) Perpendicular section through the same travertine. (d) Model of photosynthetically-driven carbonate precipitation. CO_2 dissolve in water, forming bicarbonate ions (the most common form of DIC between pH 5 and 9). The bicarbonate is taken up by cells of the trichoma; the enzyme carbonic anhydrase inside the cells produces CO_2 (used for photosynthesis) and OH^- . The release of hydroxyl ions outside the trichoma increases the alkalinity in the surrounding area of the cyanobacteria and induces precipitation of CaCO_3 (provided Ca^{2+} ions are available).



EPS alteration leading to precipitation of carbonates



Microbialites, Modern, Figure 10 Mechanistic role of the organic EPS matrix in microbial mat lithification. The exopolymeric substances are produced by various groups of bacteria (especially cyanobacteria). EPS can bind large amounts of cations (i.e., Ca²⁺), reducing the calcium carbonate saturation index, inhibiting precipitation. Alteration of the EPS matrix can end this inhibition, allowing carbonate precipitation to commence. EPS alteration is achieved via two main pathways: (1) EPS degradation, (2a) extrinsic, and (2b) intrinsic supersaturation of the EPS binding capacity (modified from Dupraz and Visscher, 2005).

originates from thermal processes. These hydrothermal systems are commonly associated with region of recent volcanic or tectonic activities. It is important to note that the term travertine has variable usage in the literature. Many authors use travertine only for hot water deposits, using “tufa” for cold-water deposits (Pedley, 2000). Other authors use tufa for actively-forming deposits and travertine for non-active, fossil forms (see Chapter *Tufa, Freshwater*).

Although carbonate precipitation in travertines and tufas is driven by abiotic processes, precipitation often initiates on organic substrates, e.g., leaves, woods, algae, or microbial mats. In these cases, mineralogy and morphology are strongly influenced by the organic matrix (e.g., Fouke et al., 2000; Farmer, 2000; Pentecost, 2005; Turner and Jones, 2005). Microbial mats at hot springs, for example, can therefore have a profound impact on thermogene travertine by providing templates for mineralization, even though precipitation is due to vigorous CO₂ degassing (Farmer, 2000; Fouke et al., 2000). Travertine formation is thus an example of biologically-influenced mineralization, since the carbonate precipitation is not due to biological activity, but microorganisms indirectly affect the characteristics of the resulting minerals.

The organic matrix (EPS)

Microbial communities generally produce extracellular polymeric substances (EPS; see Chapter *Extracellular Polymeric Substances (EPS)*). This organic matrix is an important part of the microbial mat, preventing desiccation, retaining essential nutrients, protecting against UV radiation, and providing water channels for transport of metabolites and signaling compounds (Decho, 1990, 2000). Cyanobacteria are often considered to be the major producers of EPS. However, many other bacteria can produce EPS matrix, including aerobic and anaerobic (chemoorgano)heterotrophs, anoxygenic phototrophs, and chemolithoautotrophs (De Philippis et al., 1998, 2001; Stal, 2000, 2003; Richert et al., 2005). Anaerobic bacteria, especially sulfate-reducing bacteria, which play a key role in carbon metabolism in marine microbial mats (Thode-Andersen, and Jorgensen, 1989; Canfield and DesMarais, 1991; Visscher et al., 1991), are known to produce large amounts of EPS (Bosak and Newman, 2005; Braissant et al., 2007).

The EPS matrix is generally the location where the carbonate minerals nucleate and grow (Dupraz et al., 2004). EPS contains negatively-charged acidic groups (e.g., carboxyl, sulfhydryl, amine, hydroxyl groups), which can bind a large amount of mono- and divalent cations, notably Ca²⁺ (Braissant et al., 2007). This binding capacity may inhibit the precipitation of carbonate minerals by depleting calcium from the surrounding microenvironment (Figure 10). The saturation index of calcite depends on the carbonate alkalinity and the availability in calcium. Even if carbonate ions are in solution, the lack of free Ca²⁺ may inhibit precipitation (Dupraz and Visscher, 2005). Therefore, the physicochemical properties of the polymer

matrix, such as the acidity or composition of the functional groups associated with the EPS, are key factors in the formation of modern microbialites.

In order to precipitate calcium carbonate in microbial mats, the Ca²⁺-binding capacity of the EPS has to be reduced. Various mechanisms have been proposed (e.g., Dupraz and Visscher, 2005), which can be grouped into two main processes (Figure 10): (1) degradation of the EPS matrix and (2) intrinsic or extrinsic supersaturation of cation-binding sites (e.g., Dupraz and Visscher, 2005). As EPS is a sugar polymer, it serves as metabolic substrate for (chemoorgano) heterotrophic bacteria. Depolymerization (hydrolysis) of EPS, possibly by fungi and heterotrophs, including spirochetes (Harwood and Canale-Parola, 1984; Weaver and Hicks, 1995), must occur before sugar monomers are available. Microbial degradation of EPS liberates the calcium and produces inorganic carbon (under alkaline conditions, the dominant species is carbonate ion). Alternatively, if the amount of Ca exceeds the number of binding sites in the EPS, free calcium will be present and available for precipitation. These conditions can be achieved through extrinsic factors (the environment) through continuous input of Ca. It can also result from the steric hindrance of acidic groups within the EPS. Although EPS may indeed possess abundant functional groups capable of binding Ca²⁺ or Mg²⁺ ions, these groups may be “sterically-inhibited” (i.e., blocked) via molecular-scale interactions into a structurally complex EPS (Figure 10).

Summary

Microbialites are “organosedimentary deposits that accrete as a result of a benthic microbial community, which traps and binds sediment and/or forms the locus of mineral precipitation” (Kennard and James, 1986). Living examples of these structures can be found in many modern environments including marine, hypersaline, freshwater, and even continental settings. Microbialites are classified based on mesostructure as stromatolites (laminated), thrombolites (clotted), and leiolites (structureless). Among the most spectacular examples are modern stromatolites, which were first discovered in a hypersaline lagoon of Shark Bay in 1954. The only known examples of stromatolites presently forming in open marine environments are in the Bahamas. Lamination in these coarse-grained structures results from the iterative growth of three different types of microbial mats on the surfaces of the build-ups. These microbial communities are responsible for successive “trapping and binding” of sediment (type 1) and in situ precipitation of calcium carbonate (types 2 and 3). Both processes are essential for stromatolites formation. Modern thrombolites and leiolites are less well-studied than modern stromatolites.

Early lithification is a key process in the formation of modern microbialites. Lithification consists of in situ precipitation of minerals, which preserves the biosedimentary structures. Two key and closely coupled components

involved in carbonate precipitation within microbial mats are (1) the alkalinity engine and (2) the organic matrix. The alkalinity engine, which effectively changes the saturation index, is *intrinsically driven* when microbial metabolism is the dominant process causing carbonate precipitation. The alkalinity engine is *extrinsically driven* when the macroenvironment is responsible for microbial mat lithification. In both the cases, the organic matrix of extracellular polymeric substances (EPS), which embed the microbial communities, is the physical location where carbonate minerals nucleate and grow. Fresh EPS contains negatively-charged acidic groups, which bind large amount of cations (e.g., Ca^{2+}), inhibiting CaCO_3 precipitation. In order to precipitate carbonate, this inhibition has to be reduced by degradation of the EPS or by oversaturation of the cation-binding capacity. Microbial activity is ultimately responsible for EPS production and degradation leading mineral precipitation.

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MICROBIALITES, STROMATOLITES, AND THROMBOLITES

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Microbialite Definition

Microbialites are “organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation” (Burne and Moore, 1987, pp. 241–242).

Introduction

Microbial carbonates are produced by the interaction of microbial growth and metabolism, cell surface properties, and extracellular polymeric substances (EPS) with mineral precipitation and grain trapping. The early lithification that is essential for the accretion and preservation of benthic microbial carbonates is both biologically mediated and environmentally dependent. Consequently, microbialite history reflects not only microbial mat evolution, but also long-term changes in seawater and atmospheric chemistry that have influenced microbial metabolism and seawater carbonate saturation state.

Microbialites are in place benthic sediments produced by microbial processes. The term “microbialite” has been most widely used to describe carbonate stromatolites, thrombolites, and similar structures that occur as domes and columns in the shallow waters of lakes and seas, but it can also apply to many additional authigenic accumulations in which microbes are locally conspicuous, such as