



Benthic cyanobacteria and their influence on the sedimentary dynamics of peritidal depositional systems (siliciclastic, evaporitic salty, and evaporitic carbonatic)

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Abstract

Peritidal sedimentary systems are widely colonized by benthic cyanobacteria that form biofilms and microbial mats. The bacterial communities interfere with physical and chemical sedimentary dynamics, which is documented by the formation of Microbially Induced Sedimentary Structures (MISS). The structures form a new fifth category in the existing Classification of Primary Sedimentary Structures.

Siliciclastic depositional systems are dominated by physical dynamics. By biostabilization, cyanobacteria shelter their substrata against erosion during periods of intensive hydraulic reworking, or they permit flexible deformation of sandy sediments. During low hydrodynamic disturbance, the bacteria enhance deposition of sediments by baffling, trapping, and binding. Such biotic-physical interference is recorded by MISS such as erosional remnants and pockets or planar stromatolites.

Chemical depositional systems include (i) evaporitic salty environments characterized by evaporation and dissolution and (ii) evaporitic carbonatic environments that include evaporation, dissolution, and in situ lithification of organic matter. Here, cyanobacterial mats experience periodical desiccation or evaporation of crystals and mat-related structures such as petees, and polygonal patterns of cracks are formed. Cyanobacteria and heterotrophic bacteria provide a chemical microenvironment that supports in situ lithification of organic matter. In thin-sections, carbonate precipitates as ooids or lines of decaying filaments are visible.

MISS occur in modern and ancient depositional systems. They record (i) biological abilities of benthic cyanobacteria to cope with sedimentary dynamics and (ii) paleoclimate and paleoenvironmental conditions during Earth history. Similar structures are also expected in extraterrestrial (paleo)environments.

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1. Introduction

The significance of biota for the interpretation of geological processes is increasingly becoming the

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focus of study for geologists, paleontologists, and microbiologists. The interdisciplinary approach to deciphering complex biological interaction with geological parameters is reflected by the modern and strongly evolving research field of ‘geobiology’ (symposium of Noffke and Knoll, 2001). This paper presents geobiological studies on the influence of benthic cyanobacteria on dynamic sedimentary processes in different depositional systems of peritidal areas.

In general, three main types of sedimentary systems are distinguished: siliciclastic, evaporitic salty, and evaporitic carbonatic (Warren, 1999; Prothero and Schwab, 1996). Sedimentary systems are governed by various physical and chemical parameters, which are functions of environmental conditions like hydrodynamics, ocean water chemistry, atmosphere composition, and climate (Friedman et al., 1992). In sediments and sedimentary rocks, physical and chemical processes are evidenced by characteristic sedimentary structures or by minerals formed in situ. Peritidal settings are unique insofar as they undergo a regular rhythm of inundation by seawater and subaerial exposure (including episodic desiccation or episodic strong influence by freshwater during heavy rains). Sediments are not only influenced by physical and chemical but also by biological factors. Mechanical disturbance of sediments by burrowing, grazing, or resting of macroorganisms causes a variety of traces in the deposits, later preserved as trace fossils (Bromley, 1990). Intensive chemical precipitation of carbonate minerals is a consequence of skeleton formation of macroorganisms. But even if trace fossils or thick beds of shells are striking phenomena in sediments and sedimentary rocks, it is not macroorganisms alone that play a role in sedimentary processes. Microbes, like bacteria, including cyanobacteria, fungi, microalgae, and others, have a significant influence on rock and structure formation (Krumbein, 1986; Krumbein et al., 1994; Ehrlich, 1996; Neelson, 1997; Riding, 2000; Riding and Awramik, 2000; Nisbet and Sleep, 2001). This is especially the case in peritidal coastal environments. In the past, geoscientific studies especially focused on domal stromatolites that are induced by metabolic activity of cyanobacteria and heterotrophic bacteria and occur mainly, but not exclusively, in evaporitic carbonatic environments (classical volume Walter, 1976; see also Awramik, 1984; Knoll and

Golubic, 1992; Grotzinger and Knoll, 1999; Reid et al., 2000; Vischer et al., 2000). However, recent work revealed a great variety of other structures besides common stromatolites (Gerdes et al., 1994b, 2000b; Noffke et al., 2001b; Noffke, in press (a)). These structures rise from microbial responsive behaviour to sediment dynamics in different peritidal areas. They were summarized and defined as a unique category, Microbially Induced Sedimentary Structures (MISS) (Noffke et al., 2001b). The category was placed as the 5th group into the existing Classification of Primary Sedimentary Structures (sensu Pettijohn and Potter, 1964).

This paper gives an overview on cyanobacteria forming biofilms and microbial mats; it demonstrates how the microepibenthos influences sedimentary processes in siliciclastic, evaporitic salty, and evaporitic carbonatic peritidal systems, how MISS originate, and how the structures serve as indicators for paleoenvironmental conditions; finally, a definition for MISS is proposed.

2. Benthic cyanobacteria, biofilms, and microbial mats

Cyanobacteria are photoautotrophic microorganisms that are known from earliest Earth history (overview in Knoll, 1996, 1999). Two morphological types are distinguished (Fig. 1): filamentous species that form elongated cell chains (trichomes) often bundled together (multitrichomous species; Fig. 1A) and coccoid species that form spheroidal cells often arranged into cell clusters (Fig. 1B; systematic biology: Staley et al., 1989; ecology: Whitton and Potts, 2000). From the geological point of view, benthic microbiota are important because they colonize the interface between sediments and water and affect fluid flow dynamics and structure formation.

Cyanobacteria envelope the mineral grains of depositional surfaces forming ‘biofilms’ (Charaklis and Wilderer, 1989; Charaklis and Marshall, 1990) that are organic coatings composed of the cells themselves plus their extracellular polymeric secretions (EPS; for an overview on structure and ecological function, see Decho, 1990, 2000). Such secretions are adhesive mucilages that are produced by many groups of microorganisms. They provide a protective microen-

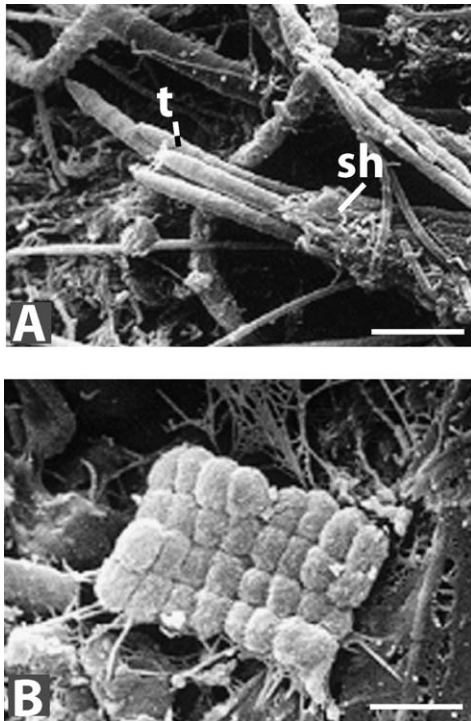


Fig. 1. Filamentous and coccoid cyanobacteria in SEM. (A) Filamentous species form elongated trichomes (t) often bundled together by a sheath (sh). Scale=20 μm . (B) Coccoid taxa form spheroidal cells that may be arranged to cell clusters. Scale=6 μm .

environment for the small cells against external chemical or physical stress factors affecting the microbes. Additionally, the adhesive mucilages aid benthic species to attach firmly to their mineral substratum (Fig. 2A) or serve as medium to transport nutrients (Dade et al., 1990; Decho, 1990).

At sites of favorable environmental conditions, initial biofilms of cyanobacteria grow to form thick organic layers that can cover large areas of sedimentary surfaces of up to several square kilometers. Because such organic layers resemble carpets or tissues (Fig. 2B), they were termed ‘microbial mats’ (Krumbein, 1983 for discussion of term; Cohen and Rosenberg, 1989; Stal and Caumette, 1994; Stolz, 2000).

The mucous-rich layers are composed not only of cyanobacteria but also include heterotrophic bacteria and other groups of microorganisms such as fungi or diatoms. The bacteria form a very complex stratified ecosystem of interfering metabolic cycles, which is

not yet fully understood (Krumbein, 1986; Stolz, 2000; Stal, 2000; Noffke, in press (b)).

Cyanobacteria are well adapted to extreme environments of various types. For example, at sites of high hydrodynamic energy, where the substrata are constantly reworked, many cyanobacterial species are able to move to escape burial by freshly deposited sediment or to reach an optimal position in terms of light climate (Gerdes et al., 1991; Golubic and Knoll, 1993; Kruschel and Castenholz, 1998). Another example of biofilm formation are sabkha-like environments, where the microbes must withstand high salinities or long lasting periods of desiccation (classical papers are Cohen et al., 1977; Friedman and Krumbein, 1985; Gerdes and Krumbein, 1987; see also Friedman et al., 1992; Gerdes et al., 2000a).

Due to their ability to respond successfully to environmental conditions, cyanobacteria grow in

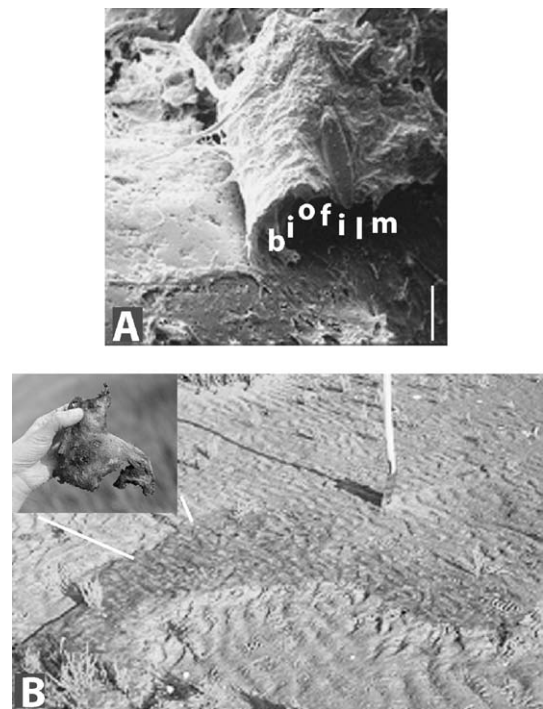


Fig. 2. Epibenthic cyanobacteria form biofilms and microbial mats. (A) Biofilms are organic coatings that consist of the cells and their slimy, adhesive ‘extracellular polymeric substances’. This biofilm envelopes a quartz grain. Photo taken by SEM. Scale=20 μm . (B) A microbial mat patch overgrows ripple marks of a sandy tidal flat. Scale=blade of spade (20-cm wide). The small picture shows a piece of the coherent, carpet-like microbial mat.

almost every habitat (overview in Knoll and Bauld, 1989). The only essential ecological factors are solar radiation and water. The climate seems to play a minor role as a controlling parameter of mat distribution, but influences mat fabrics and species compositions. Cyanobacteria-dominated mats were detected underneath the ice cover of Antarctic lakes (Wharton, 1994), in coastal areas of moderate climates like the northeastern coast of USA (Cameron et al., 1985), or the tidal flats of the North Sea (Gerdes and Krumbein, 1987; Noffke and Krumbein, 1999; Gerdes et al., 2000b; Noffke et al., 2001b). In the Mediterranean area, thick microbial mats fringe the coast of southern Tunisia (Gerdes et al., 2000b; Noffke et al., 2001a). Well known are the microbial mats from the Red Sea area (for example, Solar Lake and Gavish Sabkha) representing an arid-tropical climate zone (Cohen et al., 1984; Friedman and Krumbein, 1985). Significant microbial mats are harbored in the Guerrero Negro Lagoon, Baja California (classical study by Horodyski et al., 1977; see also DesMarais et al., 1992). Most coastal sites, where mats occur, are located behind a morphological barrier, like in a lagoon or embayment, that shelter the microbial carpets against major reworking by strong water agitation.

3. Types of peritidal sedimentary systems

Siliciclastic, evaporitic salty, and evaporitic carbonatic sedimentary systems are each characterized by specific dynamic parameters that control the prevail-

ing conditions (Fig. 3). Dynamic processes in siliciclastic sedimentary systems are mainly physical, such as wave action or bottom currents, and cause erosion, deposition, and deformation of sediment. In evaporitic salty and carbonatic systems, water motion also plays a significant role, but additional effective factors are chemical processes. Evaporitic salty sedimentary systems are characterized by abiotic precipitation of salt minerals such as sulfates (for example, anhydrite and gypsum) as consequence of evaporation. Evaporitic carbonatic sedimentary systems show in situ biogenic carbonate formation (Friedman et al., 1992; Warren, 1999).

The division of sedimentary systems into the three groups is not strict, and many intermediate systems exist. These can be related in part to climatic factors. For example, investigations showed that in the tidal flats of the North Sea, which clearly represent a siliciclastic sedimentary system, carbonate formation as consequence of bacterial decay may take place. Requirements for this process are extreme high temperatures and high humidity during the summer months. Of course, carbonate formation is exceptional and temporary, and only very small particles of microscopic sizes are formed (Kropp et al., 1997; Von Knorre and Krumbein, 2000). Evaporitic salty sedimentary systems characterize climate zones that are hot and arid, such as sabkha-like settings along the coast of the Red Sea or the Persian Gulf (Friedman and Krumbein, 1985; Purser, 1973; Gerdes and Krumbein, 1987; Gerdes et al., 2000a,b). In contrast, evaporitic carbonatic depositional areas indicate a

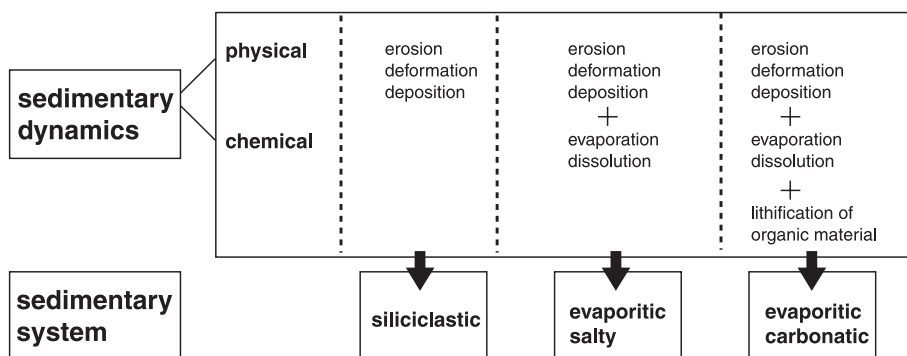


Fig. 3. Sedimentary systems are defined by physical and chemical sedimentary dynamics. Physical dynamics comprises erosion, deposition, and deformation. Chemical dynamics includes evaporation, dissolution, and lithification of organic material. In accordance with prevailing dynamics, three types of sedimentary systems are distinguished: siliciclastic, evaporitic salty, and evaporitic carbonatic.

hot-humid climate. A famous example of such an environment are the shallow-marine areas of the Bahamas, where numerous sedimentological and paleontological studies have been and are conducted.

4. Interaction of cyanobacteria with sediment-dynamic parameters and the formation of Microbially Induced Sedimentary Structures

Cyanobacteria occur in all groups of sedimentary systems, and they construct mats of varying species compositions and fabrics (Noffke and Krumbein, 1999; Noffke et al., 2001a; Noffke, in press (c)). It is easy to imagine that thick and coherent microbial mats of great metabolic complexity must have decisive influence on the physical and chemical micro-environment within sediments. In sum, influences by mats can overprint the dynamic pattern of whole sedimentary systems, as it will be shown below. Mechanisms and processes of biotic-physical and biochemical sedimentary interaction can be studied easily in the present, but we also can trace structural evidence of the processes back to the cyanobacterial life in the early history of the Earth (Noffke et al., 1996, 2002; Gerdes et al., 2000b).

4.1. Siliciclastic environments

In siliciclastic environments, mat colonization is favored by clean, translucent, and fine-grained quartz sands deposited at sites where hydrodynamic flow is sufficient to sweep clay minerals from mat surfaces but insufficient to erode biostabilized laminae (Noffke et al., 2002). A high percentage of ‘clear’ (translucent) quartz particles enables cyanobacteria to form thicker mats because the grains serve as light channeling systems if they are incorporated into the mat fabrics. By this mechanism, solar radiation is conducted deeper into the organic layer, and the photic thickness of the microbial mat is increased (Gerdes et al., 1985; Noffke, 2000; Noffke et al., 2002). Ancient cyanobacterial mats occur in lithologies that record the same sedimentary facies as are found in modern environments. For example, fossil mats have been detected from late Archean to Meso- and Neoproterozoic ages (e.g., Horodyski, 1993; Hagadorn and Bottjer, 1997, 1999; Gehling, 1999; Hagadorn et al., 1999; Noffke et

al., 2002), as well as from a great variety of Phanerozoic rocks (MacKenzie, 1968; Pflüger, 1999; Noffke, 2000; Noffke et al., 2001a,b).

Cyanobacteria interfere with erosion, deposition, and deformation caused by wave action or currents (Fig. 3). The bacterial activities comprise ‘microbial leveling’, ‘biostabilization’, ‘baffling, trapping, and binding’, ‘microbial grain separation’, and ‘imprinting’ (overview in Noffke et al., 2001b). The microbes induce both surface structures, as well as intrasedimentary structures (compare catalogues of Noffke et al., 1997b, 2001b; Gerdes et al., 1993, 2000b).

‘Biostabilization’ is microbial sediment fixation (introduction of term by Paterson, 1994; volumes by Krumbein et al., 1994; or Paterson, 1997; quantification in Noffke and Krumbein, 1999). How do cyanobacteria stabilize sediments? In close view, microbial mat fabrics are composed of the cyanobacteria themselves and their adhesive mucilages (Fig. 4A, upper photo). Filamentous cyanobacteria construct a network resembling that of a carpet, and by doing so, they interweave depositional grains of the sedimentary surface. Additionally, the adhesive mucous secretions envelope the mineral particles and glue them together. By these effects, the depositional surface is biostabilized.

Three effects on sedimentary dynamics have been distinguished (Gerdes et al., 2000b; Noffke et al., 2001b). First, erosion by bottom currents or wave action is strongly reduced; mineral grains cannot be ripped off from the coherent mat fabrics, and the frictional forces between the smooth mat surface and flowing water are low. The stabilizing effect of cyanobacterial carpets is documented by characteristic depositional surface structures, such as ‘multidirectional ripple marks’ (Noffke, 1998) and ‘erosional remnants and pockets’ (Noffke, 1999; Noffke and Krumbein, 1999), which are most striking in appearance (Fig. 4A, lower photo). In the fossil record, such structures can be found as well (Reineck, 1979; Schieber, 1998; Noffke et al., 2001b). Biostabilization as a protective effect against erosion takes place exclusively at sites of erosive sedimentary dynamics (Noffke et al., 2001b).

Second, biostabilization also includes sealing of the depositional surface by the EPS, which prohibits diffusion of intrasedimentary gases into the water or atmosphere. Fenestrae fabrics such as ‘sponge pore

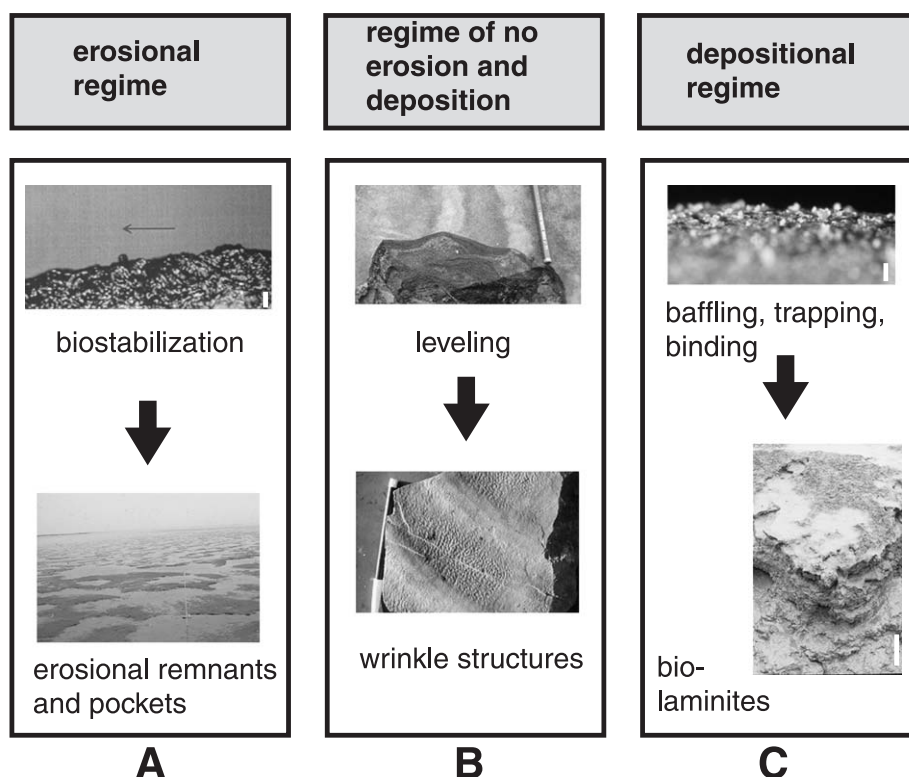


Fig. 4. Interaction of benthic cyanobacteria with physical dynamics of siliciclastic sedimentary systems and structure formation. (A) In erosive hydraulic regimes, cyanobacteria stabilize their substrate by interweaving mineral grains like a network and shelter it against reworking by bottom currents (biostabilization; upper photo; scale=2 mm). Characteristic surface structures like ‘erosional remnants and pockets’ evolve (lower photo; scale=stick 1 m). (B) During periods of no erosion and no deposition, thick microbial mats develop and cover the antecedent depositional surface (leveling; upper photo). In consolidated rocks, ancient microbial mats can be recognized as ‘wrinkle structures’ (lower photo). (C) In depositional regimes, cyanobacteria by their slimy mat surfaces actively accumulate sediment by baffling, trapping, and binding (upper photo; scale=2 mm). This produces biolaminites, that are finely laminated, noncemented build-ups (lower photo; scale=10 cm).

fabrics’ result (Noffke et al., 1997b; Gerdes et al., 2000b). Third, biostabilization also permits flexible deformation of a brittle sediment composed of loose grains, such as sand. Whereas in siliciclastic environments, porous fabrics or structures resulting from deformation of mat-bound sediments are rarely preserved; precipitation or cementation in evaporite and carbonate systems leads to rapid lithification (see sections below).

‘Microbial leveling’ means that a depositional surface is overgrown by a microbial mat, and that any antecedent surface structures like ripple marks are covered by biomass (Fig. 4B, upper photo). The original depositional surface is less or not visible underneath the mat tissue, and mature microbial mats

show typically planar surfaces (quantification in Noffke and Krumbein, 1999). Growth of a microbial mat and leveling takes place during periods of low erosion and lowest rates of deposition (Fig. 4B).

Fossil ‘microbially leveled depositional surfaces’ can easily be detected as ‘wrinkle structures’ (discussion and definition of term by Hagadorn and Bottjer, 1997; compare also Hagadorn and Bottjer, 1999; Pflüger, 1999). These are crinkled bedding planes that rise from loading pressure and dewatering processes during burial of fluid-rich microbial layers (Noffke et al., 2002). Depending on the original thickness of the organic layer that more or less effectively smoothed out the former depositional surface, ‘transparent wrinkle structures’ and ‘nontransparent wrinkle structures’

can be distinguished (Noffke, 2000; Noffke et al., 2002). A thin mat layer produces wrinkles, and underneath, the ripple marks are still visible (transparent; Fig. 4B, lower photo). A thick mat layer hides the surface morphology of its substrate completely (non-transparent), but a vertical section shows that ripple stratification may be preserved.

‘Baffling, trapping, and binding’ is active sediment enrichment by cyanobacteria. The term was introduced in the classical paper of Black (1933). During periods of moderate deposition of sediments and low water motion, filamentous species orient themselves perpendicularly towards the mat surface to reach into the supernatant water column (Noffke et al., 2001b). Thus, mineral particles that are transported by the weak bottom currents across the mat surface become ‘trapped’ by the filaments and settle. The grains are glued to the mat surface by the sticky mucilages of the bacteria (Fig. 4C, upper photo) and over time incorporated into the growing biomass (‘binding’). Also, mineral particles that are aerially transported across the sticky mat surfaces can become trapped by filaments. ‘Baffling, trapping, and binding’ produces laminated patterns within the sediments (Fig. 4C, lower photo). Such laminated patterns are termed ‘biolaminites’ (Gerdes and Krumbein, 1987) or, after lithification, ‘planar stromatolites’ (Krumbein, 1983; Gerdes and Krumbein, 1987).

‘Grain separation’ is the process where particles are pushed aside by their biofilm-envelopes, when a microbial mat grows. In vertical sections through a mature microbial mat (that in a figurative sense consists of a multitude of biofilms surrounding grains, Noffke et al., 2001b), single particles are visible. The grains float independently from each other within the organic matrix, and loading pressure orients them parallel to the depositional surface (Noffke et al., 1997a). In thin-sections through wrinkle structures, this texture is quite common and provides a clear evidence of former mat presence (Noffke, 2000; Noffke et al., 2002).

‘Imprinting’ means that we can trace buried depositional surfaces with the aid of their biofilms or microbial mats in vertical sections through sediments. The biofilms ‘line’ (imprint) the antecedent surface. Good examples are ‘sinoidal structures’ that represent buried ripple marks. Such structures are useful tools for the detection of ancient mats in consolidated sediments.

4.2. Evaporitic salty peritidal environments

Evaporitic salty sedimentary systems in subtropical and tropical arid climate zones are influenced not only by physical but also chemical dynamic parameters (compare Fig. 3). Microbial mats experience periodic or episodic desiccation that cause e.g., great ranges of ion concentrations. Additionally, benthic cyanobacteria have to respond to evaporation of minerals. The interference between physical, chemical, and biological factors is documented by very characteristic structures.

‘Bioarvites’ (Gerdes and Krumbein, 1987; Gerdes et al., 1991, 2000b) are patterns of alternating light/dark coloured laminae visible in vertical sections through microbial mats. The laminae are composed by two different cyanobacterial assemblages: the light coloured laminae are composed of coccoid cyanobacteria secreting high amounts of EPS; the dark laminae are composed by filamentous species that construct carpet-like networks. Bioarvites reflect changes in light intensities, temperature, salinities, moisture of substrate, etc., with respect to annual seasons. Coccoid, mucous-enveloped cyanobacteria can well withstand intense solar radiation, and therefore, dominate the summer mat community. Because coccoid species are immobile (unlike many filamentous forms), a layer of coccoid cyanobacteria is formed from cells that are suspended in the seawater, or they are reproduced by cells within the mat itself. In winter, the coccoid layer is overgrown by filamentous species that move through the coccoid population towards the new mat surface (Gerdes et al., 1991, 2000a). Bioarvites may be potentially preserved in carbonate environments by alternating layers of different mineral formations (see below).

During periods of desiccation, characteristic for semi-arid climates, microbial mats shrink and become fractured into a ‘polygonal pattern of cracks’. Fracturing is supported by in situ formation of evaporite crystals and also by pressure of gas that became entrapped underneath the mat, which over time lifts the organic layer separating it from its substrate below. With return of humid climate conditions, the margins of the mats overgrow the fractures forming ‘crack tapestries’. Repetition of breaking and recovering of the mats forms pillow-like ‘bulges’ at the crack margins (Gerdes et al., 2000b; Noffke et al., 2001a).

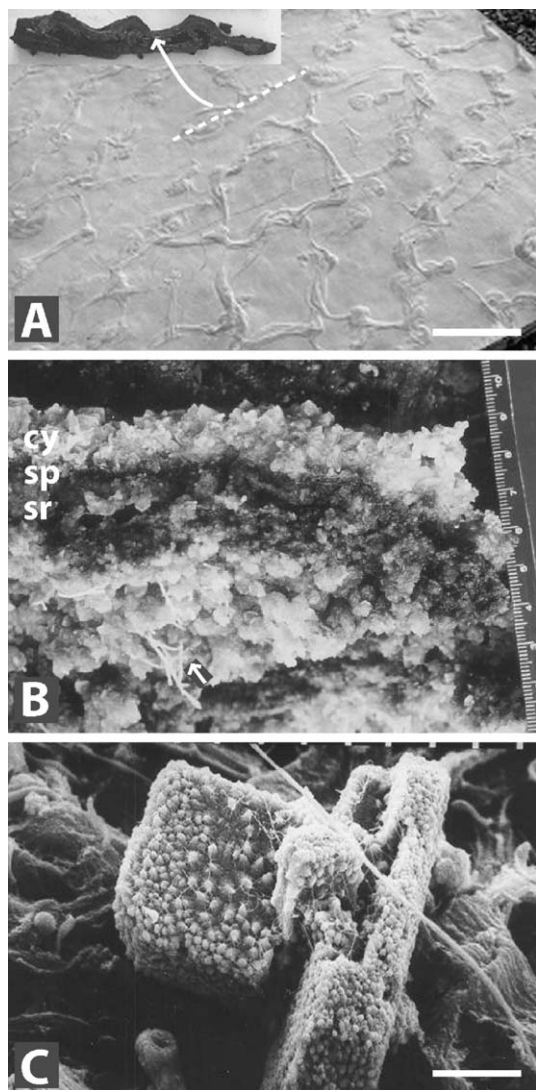


Fig. 5. Interference of microbial mats with chemical dynamics in evaporitic salty sedimentary systems. (A) Petees are polygonal patterns of overfolded mat margins that are visible on mat surfaces. Petees rise from periodical alternation of humid and arid climate conditions. Scale=20 cm. Small picture shows vertical section through petee. Note overfolded laminae. (B) Vertical cut through modern microbial mat. The mat is composed of different bacterial populations: cy=cyanobacteria, sp=sulfur purple bacteria, sr=sulfate reducing bacteria. The mat is filled with gypsum crystals that formed in situ. Arrow indicates cyanobacterial filaments of a former generation. (C) Cubic halite crystal on top of a microbial mat. Note bacteria (probably heterotrophic) that colonize on the halite crystals. Scale=3 μm .

At sites of high rates of evaporation, gypsum- and halite-encrusted domes, so-termed ‘petees’, form (Reineck et al., 1990; Fig. 5A). Gas pressure also plays a role, similar to the formation of fenestral fabrics (sponge pore fabrics), as described above.

In vertical sections through sabkha-like sediments, gypsum crystals penetrate microbial mats and their laminated bacterial populations (Fig. 5B). It is assumed that the gypsum crystals serve as light channeling system similarly to the clear quartz grains found in mat fabrics in siliciclastic sedimentary systems (Gerdes et al., 1985, 2000a). Because gypsum crystals form diagenetically within the sediments, the crystals often contain embedded laminated mats (Gavish et al., 1985).

Halite crystals (Fig. 5C) are induced by bacterial presence in extremely hypersaline areas and are scattered within mat surfaces (Krumbein, 1986; Lopez-Cortes et al., 1994).

Because of the significant mineral content, polygonal cracks, bulges, crack tapestries, and petees can be well preserved and are known from various fossil successions. Pleistocene sabkha-like sediments show a beautifully preserved succession of these MISS that record the lateral change of hydrologic conditions from the low to the high water lines within an ancient tidal area (Noffke et al., 2001a). Microbial mats of several meter thickness are preserved in Triassic supratidal sediments in SW Germany (Noffke et al., 2001b).

4.3. Evaporitic carbonatic peritidal environments

Evaporitic carbonatic peritidal environments occur in subtropical to tropical humid climate zones. The sedimentary systems are characterized by in situ carbonate formation, often as result of degradation of organic matter, or by biological formation of carbonate skeletons. The most striking phenomena in carbonates are stromatolites. Whereas in early Earth history they have been widely distributed, today only relicts occur, colonizing restricted areas such as small embayments (e.g., Logan, 1961; Logan et al., 1964; Walter, 1976, 1994; Grotzinger and Knoll, 1999; Reid et al., 2000). Of those occurrences, Shark Bay, Australia, is probably the most well known site (e.g., Logan, 1987).

Even if cyanobacteria, by their photoautotrophic metabolism, provide a chemical microenvironment

that supports the formation of carbonate cements in stromatolite development, it is the activity of heterotroph bacteria that actually causes the mineral precipitation (Friedman, 1978; Krumbein, 1979; Cornee et al., 1992; Reid et al., 2000; Von Knorre and Krumbein, 2000). In living mats, decomposition of organic material of primary producers by heterotroph bacteria starts a few millimeters below the surface. Experiments on degradation of organic material and mineral precipitation (Beveridge and Doyle, 1989; Beveridge, 1989; Schulze-Lam et al., 1996), as well as thin-sectioning of modern, not yet lithified microbial mats (Gerdes et al., 1994a, 2000a,b; Noffke et al., 2001a,b), reveal early diagenetic mineral formation along the outer cell walls of deceased bacteria. It is assumed that the electro-negatively charged cell walls attract electro-positive metal ions dissolved in the surrounding seawater, and these first metal ions serve as nuclei for further metal enrichment (Beveridge and Doyle, 1989; reviews by Beveridge, 1989; Schulze-Lam et al., 1996; Douglas and Beveridge, 1998; Ferris, 2000 and references therein). Counter-ions react with the metal ions, and first mineral precipitates settle out. These are amorphous and hydrated because they include molecules of the water film that previously enveloped the bacterial cell. Early steps of aragonite formation on cell walls have been documented by Krumbein (1979), and mechanisms of microbially induced precipitations have been identified by Warthmann et al. (2000). Often, pyrite can be found intimately related to carbonate layers in subrecent, decaying microbial mats (Gerdes et al., 2000a,b).

In thin-sections, fine carbonate and pyrite particles can be dispersed within the mat fabrics, or they can be concentrated to laminae. The distribution pattern of the particles follows obviously the positions of cyanobacterial cells or trichomes within the decaying mat fabrics. Potentially, bioarvites induce alternating layers of different pyrite or carbonate mineral formings.

'Frozen' filaments are filaments that are preserved in an upright position (Gerdes et al., 2000b). Possibly, the cyanobacteria were encrusted by high precipitation rates of carbonate during their lifetime and died from continuing mineralization (Fig. 6A, B). Fossil examples are described by Seong-Joo and Golubic (1998) and Golubic and Seong-Joo (1999).

'Eye structures' visible in thin-sections through mat layers developed from the growth of round to

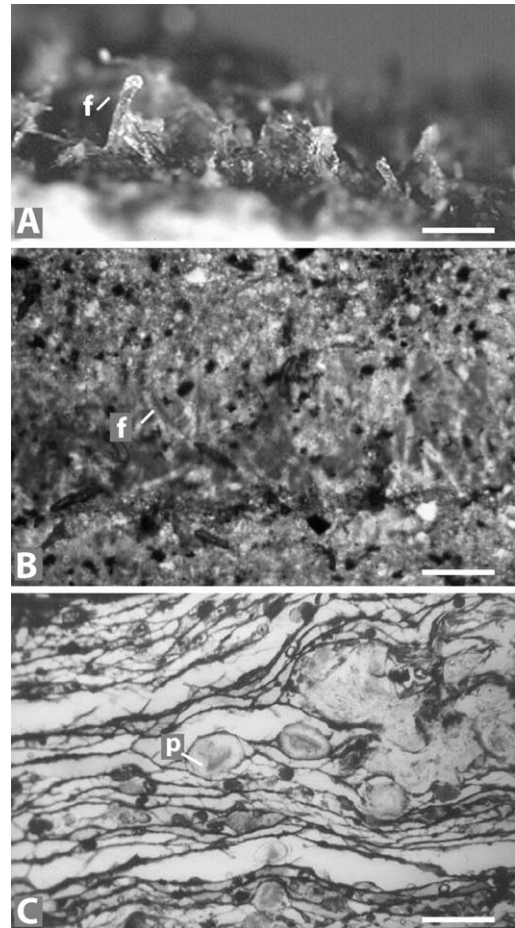


Fig. 6. Cyanobacterially induced mineral formation in evaporitic carbonatic sedimentary systems. (A) Vertically oriented cyanobacterial filaments (f) project from the mat surface. They are encrusted by carbonate envelopes already during life time. Scale=2.5 mm. (B) In thin-sections of both modern and ancient microbial mats, vertically oriented filaments are preserved. Scale=2.5 mm. (C) Within the mat fabrics, round shaped carbonate particles (p) form. They grow in situ and incorporate lithified filaments. Scale=1 mm.

lensoidal shaped carbonate particles within the mats. By growing, the particles push the surrounding, soft mat fabrics aside, and the filamentous cyanobacteria entangle the grain. Several of the in situ forming particles are concentrically laminated due to filamentous organisms incorporated into the carbonate over time (Gerdes et al., 1994b). The name 'eye structure' was given because the final structure resembles 'augengneiss' (Augen=German for 'eyes'; Dahanayake et al., 1985).

Carbonate particles (Fig. 6C) that had been formed in situ represent solid surfaces for biofilms, which subsequently overgrow the grains. Over time, the biofilms again can become encrusted by a subsequent generation of carbonate precipitates. This repetition of mineral precipitation and subsequent attachment of biofilms results in the formation of ooids and oncoids (Gerdes et al., 1994a,b, 2000a,b). Thin-sections through the particles show concentric dark and light laminae. The dark laminae are composed of bacterial cells and EPS, whereas the light laminae represent carbonate (Gerdes et al., 1994a,b).

In addition to these microscale structures, macrostructures can be observed: ‘baffling, trapping, and binding’ produces laminites and stromatolites also in evaporitic carbonatic environments (Gerdes and Krumbein, 1987; Grotzinger and Knoll, 1999, to name a few), biostabilization is recorded by fenestral fabrics and bird’s eye structures (Tebbutt et al., 1965; Dunham, 1962), etc., that can also be observed in siliciclastic environments. Beautifully preserved overfolded microbial mats were found in the Jurassic Alps (Bernier et al., 1991). In contrast to siliciclastic environments, in evaporitic carbonatic depositional regimes, early diagenetic mineral precipitation cements the deposits quickly; the preservation potential of these macrostructures is much higher.

5. Towards a definition of “Microbially Induced Sedimentary Structures”

In this paper, various MISS of different sedimentary systems are shown. The structures develop from interference of sedimentary dynamics, both physical and chemical, by cyanobacterial activities. The structures occur not only in modern deposits, but are known from various fossil sites since the earliest Earth history. Knowledge of modes of formation of MISS that can be observed and measured in the modern environment permits conclusions on the former paleoenvironmental and paleoclimate conditions, if MISS are detected in the consolidated rock. Biostabilization structures such as ‘erosional remnants and pockets’ record erosive hydrodynamic conditions, whereas baffling-, trapping-, and binding-related phenomena reflect low rates of deposition (Fig. 4).

Features like ‘polygonal fractures’ or ‘crack tapestries’ record periodic oscillation of humidity in an arid climate, whereas carbonate formings indicate constant humidity and hot temperatures. The wide distribution in time and space of MISS shows that in peritidal areas (and in the fossil record, also in shelf environments), benthic cyanobacteria are most important parameters controlling the dynamics of sedimentary systems.

In conclusion, we propose a definition for MISS: “Microbially Induced Sedimentary Structures (MISS) are structures of millimeter to meterscale dimensions. They rise from the interference of physical and chemical sedimentary dynamics with biofilms and mats that are mainly, but not exclusively, constructed by cyanobacteria. MISS can be detected in various environments of different climate zones.

In formation, specific dynamic conditions trigger specific responsive behaviour of the cyanobacteria. Their metabolic products or decaying cells allow heterotrophic bacteria to induce mineral precipitation. MISS include ‘planar and domal stromatolites’.

Because MISS occur in modern and ancient depositional systems, they record both biological abilities of benthic cyanobacteria to cope with sedimentary dynamics, and paleoclimate and paleoenvironmental conditions during Earth history. MISS also are expected to be found in extraterrestrial (paleo)environments.”

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