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Microbial mats on Earth's
sandy beaches—Today
and 3 billion years ago**

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Nora Noffke

Cover: Multidirectional ripple marks preserved in an ancient siliciclastic tidal flat of the 2.9 Ga Pongola Supergroup, South Africa. Studies in modern settings show that such a chaotic ripple mark pattern is caused by the interaction of sediment-stabilizing microbial mats with episodic storm events. In concert with a multitude of other "microbially induced sedimentary structures" (MISS), these ripple marks potentially record the oldest and most diverse cyanobacterial population in Earth's history. Photo courtesy N. Noffke. See "Turbulent lifestyle: Microbial mats on Earth's sandy beaches—Today and 3 billion years ago" by Nora Noffke, p. 4–9.



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Turbulent lifestyle: Microbial mats on Earth's sandy beaches—Today and 3 billion years ago

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ABSTRACT

Archean Earth history is very difficult to reconstruct. Until recently, only bacterial cells preserved in chert, microborings, and stromatolites provided the few clues to ancient life. Now, siliciclastic “microbially induced sedimentary structures” (MISS) are adding to our knowledge of both past life and paleo-environments. MISS rise from the interaction of photoautotrophic microbial mats with physical sediment dynamics in siliciclastic, shallow-marine settings. Archean MISS can be understood through observations of living microbial mats and modern biotic-physical sedimentary processes. Such geobiological studies are key to the interpretation of the early evolution of prokaryotes. For example, the 2.9 Ga Pongola Supergroup, South Africa, includes MISS that possibly point to the oldest known cyanobacterial community preserved in Earth's history.

INTRODUCTION

The question of where and when the earliest life developed on Earth is a most exciting one but also one that is difficult to answer. Time, tectonism, metamorphism, eons of subsurface microbial activity, and unfamiliar biogeochemical environments make the biota of the Archean notoriously difficult to interpret (Lowe and Tice, 2007). Geobiologists approach this problem by combining studies on living biota in modern settings with historical-geological studies on ancient bacteria and biogenic sedimentary structures preserved in Archean rocks. This paper examines “microbially induced sedimentary structures” (MISS)—traces and trace fossils caused by benthic microbial mats in siliciclastic coastal deposits today and 3 billion years ago.

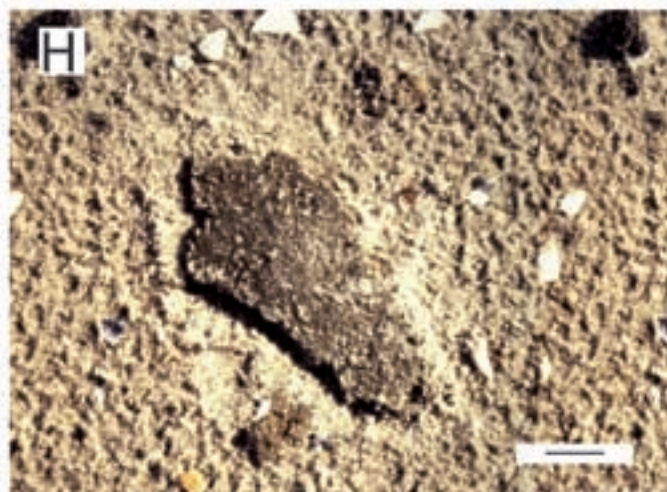
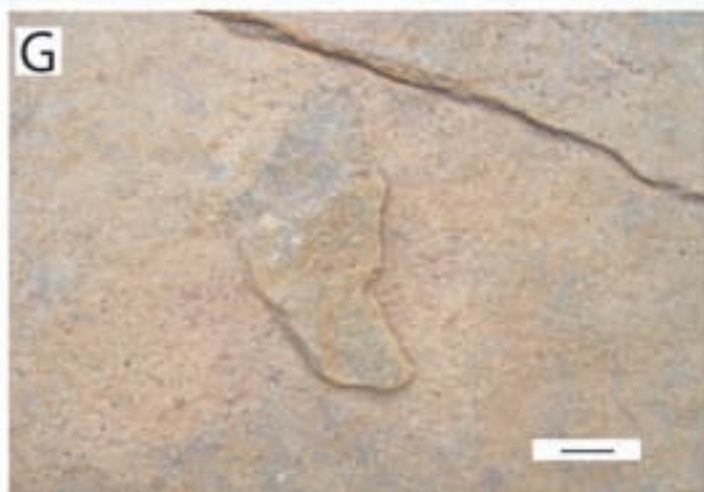
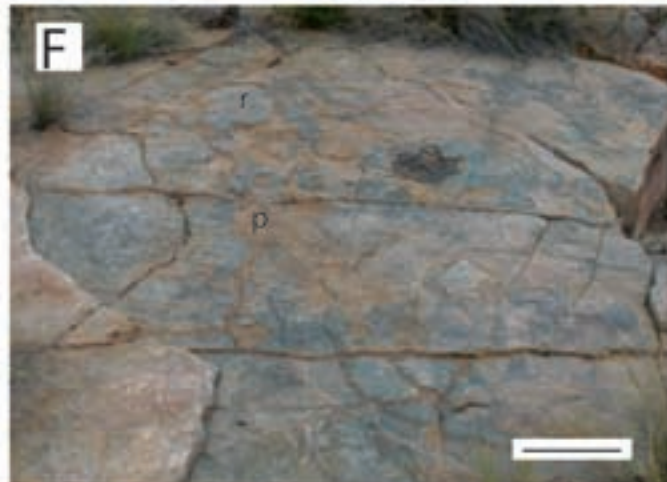
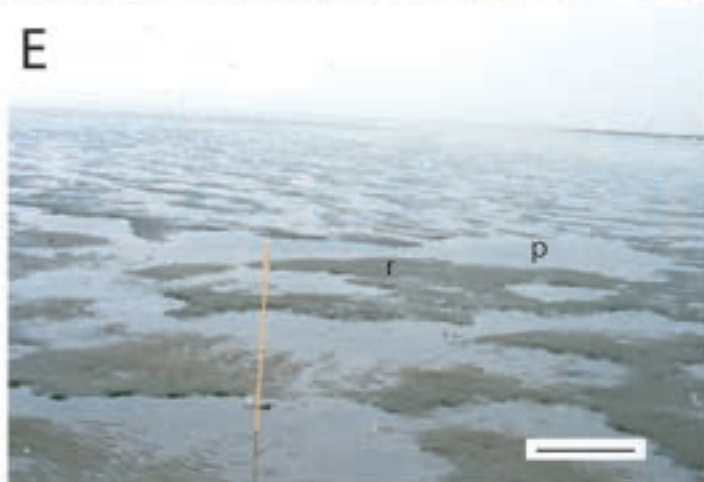
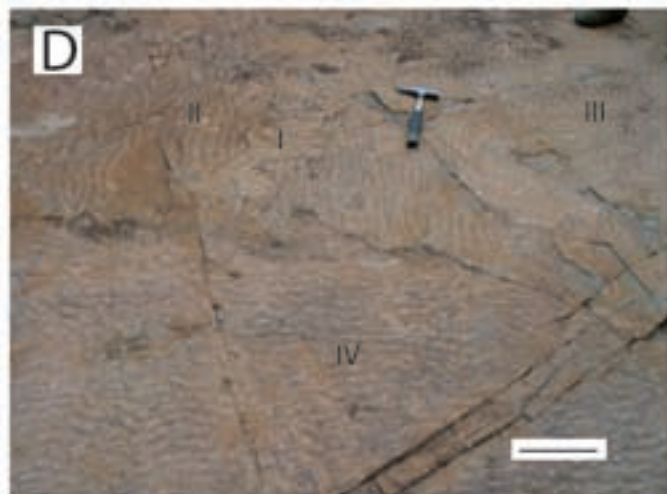
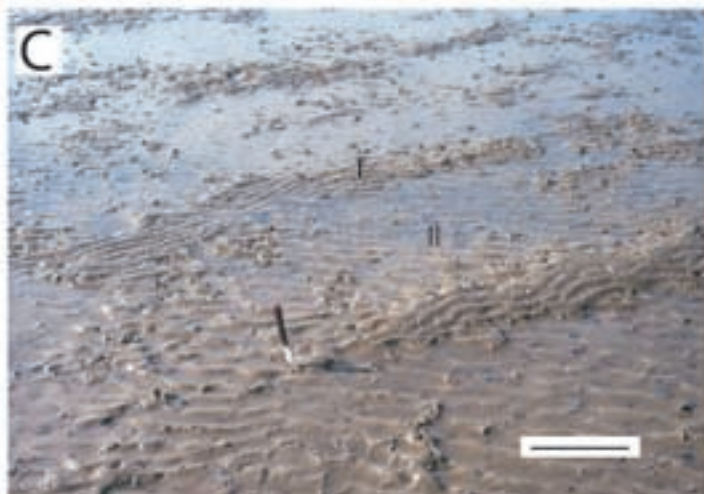
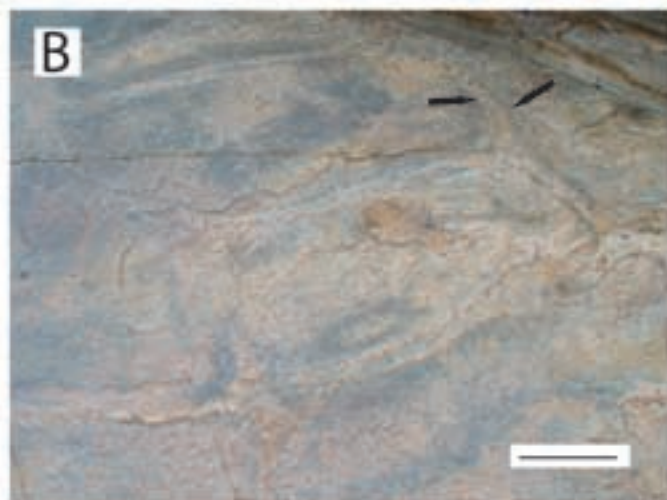
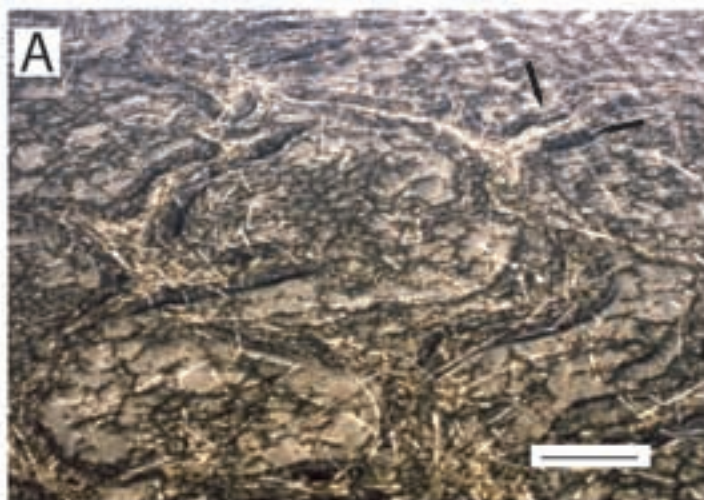
Only a few Archean (3.8–2.5 Ga) fossils and sedimentary structures allow a glimpse into Earth's oldest history. In carbonates and cherts, fossils of bacterial cells and the reef-forming stromatolites record the 3.5 Ga existence of prokaryotes (e.g., Buick, 1992; Hofmann et al., 1999; Grotzinger and Knoll, 1999; Allwood et al., 2007; Schopf et al., 2007). Tube-like fossils finely distributed in Archean seafloor basalts document the fact that living organisms even explored the upper portions of the oceanic crust (Furnes et al., 2004). Laboratory analyses reveal biomolecules in 2.7 Ga black shales in Australia (e.g., Brocks et al., 1999; Knoll, 1999), and various isotopes signal evidence of ancient life even in highly metamorphosed material such as the Isua Greenstone Belt, Greenland (e.g., Grassineau et al., 2006). However, siliciclastic deposits also bear paleontological information: trace fossils caused originally by benthic microbiota.

In the 1980s–1990s, it was suggested that crinkled upper bedding planes (“elephant skin textures”) might record ancient microbial mats (e.g., Runnegar and Fedonkin, 1992; Gehling, 1999). Similar conclusions were reached by Seilacher et al. (1985) in lagoonal sediments of Solnhofen, Germany, and by Schieber (1998) in Mesoproterozoic shales of Montana, USA. Those early observations on microbial mat-related structures were summarized in Hagadorn et al. (1999), followed by a photo atlas (Schieber et al., 2007). At about the same time, the genesis of modern microbial mat-associated sedimentary structures was being elucidated (e.g., Cameron et al., 1985; Gerdes and Krumbein, 1987; Gerdes et al., 1991, 1994). The term “microbially induced sedimentary structures” (MISS) was coined in 1996, based on quantitative analyses of mat-related structures in sandy tidal flats (Noffke et al., 1996). The sixteen main types of MISS arise exclusively from the interaction of biofilms and microbial mats with the physical sediment dynamics (Noffke, 2009). This contrasts with the formation of stromatolites, in which chemical precipitation plays a major role. Because of their unique biotic-physical genesis, MISS differ significantly in morphology from stromatolites (Fig. 1).

Systematic studies, leading from modern to increasingly older deposits, have revealed that fossil MISS occur in tidal flat and shelf sandstones of Phanerozoic, Proterozoic, and Archean ages and appear not to have changed identifiably since at least 3.2 Ga (Noffke, 2000; Noffke et al., 2001, 2002, 2003, 2006, 2008). The morphologies and paleoenvironmental distribution of the structures record the former presence of photoautotrophic microbial mats.



Figure 1. Examples for microbially induced sedimentary structures (MISS) from modern sandy tidal flats (A, C, E, G) and from the fossil tidal sandstones of the 2.9 Ga Pongola Supergroup, South Africa (B, D, F, H). (A) Polygonal pattern of oscillation cracks, coast of Tunisia; scale: 12 cm. (B) Fossil oscillation cracks; scale: 8 cm. Arrows indicate margins of polygons. (C) Multidirectional ripple marks, Mellum Island, North Sea; scale: 40 cm. Two storm events are recorded (I, II). (D) Fossil example recording four storm events (I–IV); scale: 40 cm. (E) Erosional remnants (r) and pockets (p), Mellum Island, North Sea; scale: 50 cm. (F) Fossil example; scale: 100 cm. (G) Microbial mat chips, Fishermans Island, Virginia, USA; scale: 5 mm. (H) Fossil mat chips; scale: 5 mm.



INTERACTION OF BIOFILMS AND MICROBIAL MATS WITH PHYSICAL SEDIMENT DYNAMICS IN SILICICLASTIC DEPOSITS

Modern sandy tidal flats are widely overgrown by a great variety of benthic microorganisms, especially cyanobacteria. Initially, the microbes form thin, organic coatings around individual sand grains at the sedimentary surface. Such biofilms (Fig. 2A) are composed of cells and extracellular polymeric substances (EPS) (Decho, 1990; Dade et al., 1990). The EPS are adhesive mucilages that enable the benthic microorganisms to attach themselves to solid substrates (such as the surface of a quartz grain), to transport nutrients toward the cell, and to buffer the microbes against the changing salinities in their microhabitat. During times of little water movement, the biofilms continue to grow until an organic layer, composed of a dense and coherent network woven by millions of cyanobacterial trichomes, carpets large areas of the tidal flat surfaces (Fig. 2B) (Stolz, 2000). Other bacteria, fungi, and eukaryotes, such as diatoms, also occur in the mats.

Tidal flats are extreme environments where the twice-daily change from flooding to subaerial exposure provides harsh benthic conditions. However, the mobile trichomes of cyanobacteria are well adapted to quickly changing sedimentary dynamics (e.g., Halfen and Castenholz, 1971; Staley et al., 1989; Gerdes et al., 1991; Golubic and Knoll, 1993; Knoll and Bauld, 1989; Kruschel and Castenholz, 1998; Sumner, 2000).

Interactions of microbenthos with dynamic sedimentary regimes produce MISS. When sediment is deposited onto the mat surface, the filamentous cyanobacteria orientate themselves perpendicularly to the surface and reach into the supernatant sea water. Here they passively comb out suspended grains, a process known as “baffling and trapping” (Black, 1933). Over time, the microbes bind these particles during the formation of their mat fabrics. Binding takes place during quiet hydraulic conditions—a fact that prohibits the formation of microbial mats in strongly and constantly reworked depositional areas. This process can take from a few hours (*Oscillatoria limosa*, Hardie, 1978; Villbrandt, 1992) to a few weeks (*Microcoleus chthonoplastes*, Hardie, 1978; Gerdes et al., 1991). Microbial mats protect their sandy substrata against erosion by

microbial sediment fixation. Bathurst (1967) and Neumann et al. (1970) described the sediment-stabilizing properties of microbial mats in carbonate sediments of the Bahamas. Subsequently, their field observations were supported by experiments by Meadows et al. (1990), Dade et al. (1990), and Yallop et al., 1994, and the term “biostabilization” was introduced (Paterson, 1997). A microscopic vertical section through a resin-fixed microbial mat shows that the trichomes interweave the sand grains and that the EPS glue the mineral particles together. Both microbial effects significantly increase the resistance of the tidal surface against erosion—the mats can withstand current velocities of up to 1.60 m/s (e.g., Führböter and Manzenrieder, 1987).

TYPES OF MISS

Sixteen types of MISS are generally recognized, the result of growth, biostabilization, binding, baffling, and trapping (Fig. 3). Common examples include the following (see Fig. 1):

- **Polygonal oscillation cracks:** A polygonal pattern of cracks forms in the microbial mats in hot, semiarid climates characterized by seasonal rainfall in response to periodically changing degrees of moisture (Noffke et al., 2001) (Fig. 1A). The mat polygons defined by the cracks are generally 10–50 cm in diameter. In vertical section, the mat polygons are thickened; this is caused by lateral oscillation of the mat polygons due to seasonal wet-dry cyclicality. Because the moisture decreases from the lower portions of the organic layer toward the surface, the mat shrivels during desiccation, and the mat polygon margins point upward. With more water, the microbial mat overgrows the desiccation cracks and, viewed from above, two parallel running ridges can be seen, indicating the former presence of up-shrivelled polygon margins on the microbial mat surface (Figs. 1A and 1B, arrows). The seasonal repetition of desiccation and re moistening gives rise to polygonal oscillation cracks. In the 2.9 Ga Nhlazatse Section of the Pongola Supergroup, such cracks indicate that Archean paleoclimates there had seasonally high temperatures and variations in precipitation (Fig. 1B; Noffke et al., 2001, 2008).

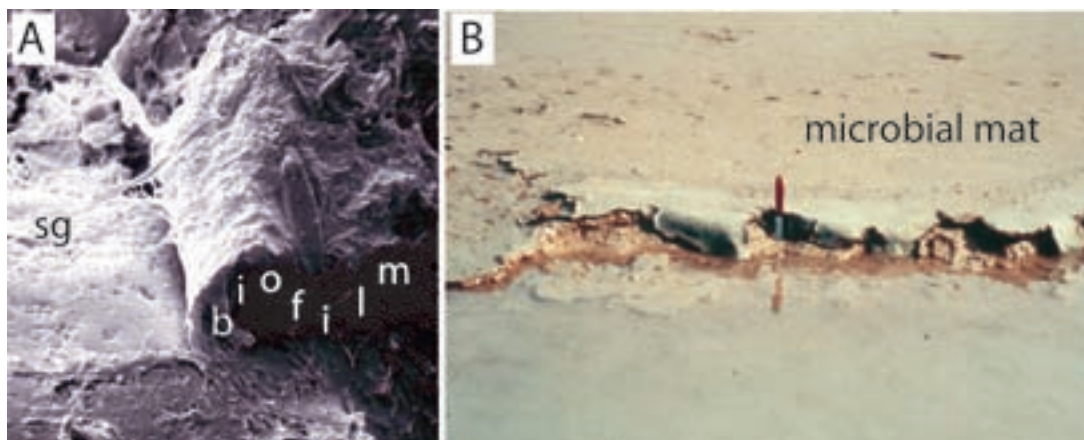


Figure 2. Biofilms and microbial mats. (A) A biofilm is a microscopic, thin organic coating composed of the bacterial mucilages (extracellular polymeric substances) and microbial cells; “sg” indicates the surface of a quartz grain. (B) Microbial mat—a macroscopic, dense and coherent layer that covers a large area of the sedimentary surface. Knife for scale (10 cm).

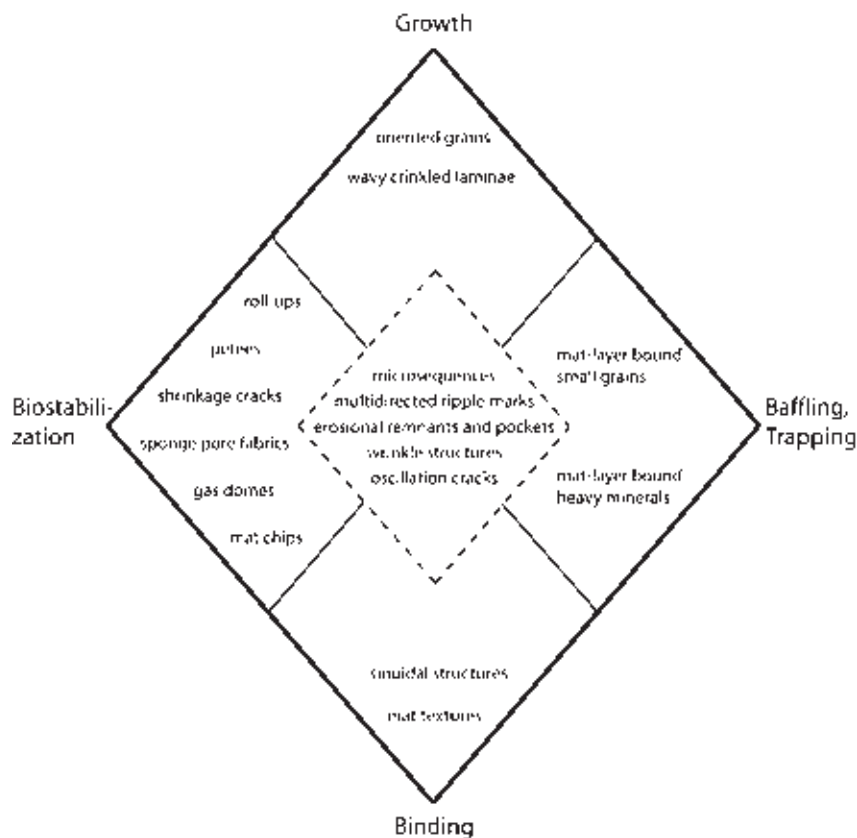


Figure 3. Genetic relationships and classification of microbially induced sedimentary structures (MISS). MISS are formed either by the growth of microbial mats (biomass production), binding (formation of the typical, carpet-like filamentous network), biostabilization (fixation of sedimentary grains), or baffling and trapping (accumulation of sedimentary grains by vertically oriented bacterial filaments). The MISS in the center form from all microbial activities, whereas those structures grouped around it are originated by mainly one microbial behavior (biostabilization, binding, baffling, trapping, or growth).

- Multidirected ripple marks:** This is a chaotic pattern of patches of ripple marks of different directions (Figs. 1C and 1D). Multidirected ripple marks also occur in the supratidal zone and indicate seasonal changes in storm frequencies (Noffke, 1998). During conditions characterized by low hydraulic reworking of the sands, microbial mats start to grow, forming meter-wide patches. The original ripple marks beneath are preserved by biostabilization. On those surface portions still exposed, a storm leaves a new generation of ripple marks in a different direction. After a storm, microbial mat patches continue to enlarge laterally and overgrow those newly rippled surfaces. Another storm produces a third generation of ripple marks in the remaining sand that is not biostabilized. This repetitive alternation between mat growth, biostabilization, and reworking by storms creates the multidirected ripple marks (Noffke, 1998; independently termed by Pflüger [1999] “palimpsest ripple marks”). In the Pongola Supergroup, the multidirected ripple marks (shown in Fig. 1D) reveal a record of four storms and may indicate a storm-dominated coastline (Noffke et al., 2008).
- Erosional remnants and pockets:** This surface structure is composed of two morphological elements: elevated surface portions that have flat tops (erosional remnants) and depressions that sometimes are rippled at the bottoms (erosional pockets) (Figs. 1E and 1F; Noffke, 1999). The extent of erosional remnants and pockets varies from at least 30 cm to many decimeters in scale. Remnants and pockets are caused by the partial erosion of a mat-stabilized sand surface and occur from the lower supratidal

zone to the lower intertidal zone. An index derived from the geometries and dimensions of the erosional remnants and pockets quantifies the degrees of growth, biostabilization, and binding, as well as baffling and trapping in the formation of this structure (Noffke and Krumbein, 1999). Today, as well as in the Archean Pongola Supergroup, this index indicates the position of this surface structure on the former lower supratidal flats (Noffke and Krumbein, 1999; Noffke et al., 2008).

- Microbial mat chips:** Centimeter-scale pieces of a microbial mat can be ripped off by bottom currents and deposited at a different site (Figs. 1G and 1H). In the fossil record, such scattered mat pieces are one of the most abundant MISS (Pflüger and Gresse, 1996; Noffke et al., 2008). They are predominantly the result of the cohesiveness of microbial mats and therefore purely related to biostabilization.

MISS occur not only as macroscopic structures, but include microscopic textures as well. Microtextures, such as oriented grains (caused by growth) or mat layer-bound grain size populations (caused by baffling and trapping), are indicative of fossil MISS and serve as criteria for their biogenic origin (e.g., Noffke et al., 2003, 2009).

SIGNIFICANCE OF MISS FOR EARTH'S GEOLOGICAL RECORD

Research on MISS is still in its infancy, and reports on modern and fossil occurrences are likely to increase as the research matures. For now, it is clear that fossil MISS were constructed by mobile and photoautotrophic microbiota. Like today, MISS-forming microbial mats appear to have been distributed

exclusively in ancient photic zones, and they occur on only moderately reworked fine sand composed of more than 95% translucent quartz (Noffke et al., 2002). The structures also are clues for the reconstruction of the paleoenvironmental settings. The few examples for MISS listed herein quantify the former current and wave dynamics in ancient settings and suggest the presence of strongly seasonal paleoclimates.

MISS are found in equivalent settings throughout Earth's history, and the recently detected Nhlazatse Section of the Pongola Supergroup shows that neither morphologies nor distributions of MISS have changed for at least 2.9 billion years (Noffke et al., 2008). Given the similarity of today's biota to the 2.9 Ga Archean biotas, it would seem that the early evolution of cyanobacteria involved rapid diversification in perhaps only 200 million years, although their first appearance is uncertain—currently estimated to be 2.7 Ga (Brocks et al., 1999; Knoll, 1999). MISS, by virtue of their ubiquity and high preservation potential, may yet contribute to the answer. The first systematic collection of MISS is deposited in the National Museum of Natural History (Smithsonian Institution) in Washington, D.C., USA.

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