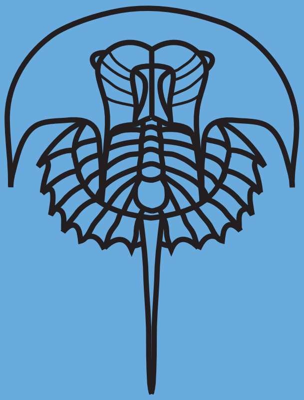

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Part B, Volume 2, Chapter 5: Microbially Induced Sedimentary Structures (MISS)

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PART B, VOLUME 2, CHAPTER 5: MICROBIALLY INDUCED SEDIMENTARY STRUCTURES (MISS)

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INTRODUCTION

To date, microbialites include five groups: stromatolites, thrombolites, leiolites, and dendrolites. All these microbialites occur in carbonate or silica lithologies. However, research during the past 25 years has defined an additional group of microbialites that occurs predominantly in clastic deposits. These structures are called microbially induced sedimentary structures, commonly simply abbreviated to MISS. As outlined in this chapter, the morphologies of MISS do not resemble those of precipitated microbialites due to the much different formation and different location of these structural groups. The genesis of the main types of MISS has been elucidated in studies in modern environments. The results were key for the search of such structures in the fossil record. Systematic exploration from youngest to oldest stratigraphic successions has given rise to a data set that allows identification of MISS in respective paleoenvironments. MISS are biosignatures helpful to understanding aspects of prokaryote evolution and the search for life on other planets.

This chapter first briefly focuses on the microbial communities that cause the structures, then discusses MISS formation, which is intimately related to the immediate setting. Next, the processes of their preservation is examined, and, finally, the chapter arrives at the classification of MISS.

BIOFILMS AND MICROBIAL MATS

Modern sedimentology recognizes that benthic microbiota are (and have always been) part of every sediment and that microbial activities may substantively contribute to sediment formation and lithification (Fig. 1).

In close-up view, sedimentary deposits are widely colonized by a great variety of benthic microorganisms. Most of these microbes organize into aggregates called biofilms, which are attached to a surface. Biofilms are probably the most common organization of life, developing everywhere in nature provided that water molecules and a surface are present (STOODLEY & others, 2002; NEU, 1994; GERBERSDORF & others, 2008; STAL, VAN GEMERDEN, & KRUMBEIN, 1985; RAMSING, FERRIS, & WARD, 2000; FRANKS & STOLZ, 2009; GERBERSDORF & WIEPRECHT, 2015; ESPINOZA-ORTIZ & GERLACH, 2021). Biofilms include both microbial cells and

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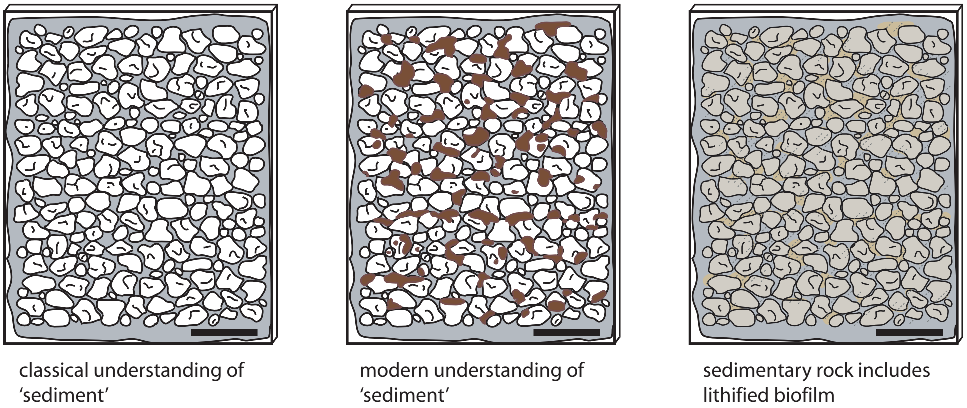

FIG. 1. Biofilms in classic and modern sedimentology. Modern sedimentology understands sediment not as a mere assemblage of mineral grains. Rather, biofilms colonize particles of sediment as long as water molecules are present. *In situ* lithification of the biofilm adds to cementation during diagenesis.

their extracellular polymeric substances (EPS); (e.g., DECHO, 1990, 1994). EPS are cohesive mucilages comprised of complex polysaccharide biomolecules that provide a suitable microenvironment for the microorganisms, buffering against rapid environmental changes, such as desiccation, sudden salinity changes, and other environmental stressors (DECHO, 1994; FLEMMING, NEU, & WOZNIAK, 2007; WESTALL & RINCE 1994; WESTALL & others, 2000). These mucilages serve to anchor cells on their substrate or enable the motion of cells within the structure of the biofilm. Biofilms are therefore assemblages of cells working interdependently with each other with the ultimate aim of effective resource exploration. In a biofilm community, cells are arranged in certain positions relative to one other, allowing collaborative nutrient harvesting and consumption (DECHO, 1994). Biofilm research, especially in the medical sciences, reveals a complex pattern of communication between cells. Such communication takes place between different groups of prokaryotes and even some eukaryotes. Quorum sensing between members of the biofilm ensures targeted action of the community (WATERS & BASSLER, 2005; DECHO, NORMAN, & VISSCHER, 2010; DECHO, & GUTIERREZ, 2017).

In marine settings, biofilms may merely envelope a sedimentary grain (Fig. 2.1); however, at suitable natural sites, they may develop into large, macroscopically visible layers. Such large-scale organic layers are termed microbial mats (Fig. 2.2–2.3).

In sedimentology, classical and well-studied examples of microbial mats include so-called algal mats in tidal settings, predominantly those constructed by cyanobacteria (BLACK, 1933; HARDIE & GARRETT, 1977; HORODYSKI, BLOESER, & VONDER HAAR, 1977; KRUMBEIN, 1983; GERDES, KRUMBEIN, & REINECK, 1985; COHEN & ROSENBERG, 1989; GERDES & KRUMBEIN, 1987; REINECK & others, 1990; GINSBURG, 1991; VAN GEMERDEN, 1993; STAL & CAUMETTE, 1994; TAHER & others, 1994; REID & others, 1995; STOLZ, 2000; PEARL, PINKNEY, & STEPPE, 2000; GERDES, KRUMBEIN, & NOFFKE, 2000; VASCONCELOS & others, 2006; TAHER, 2014). However, there are many types of microbial mats in a great array of environments including the deep-water marine (e.g. GALLARDO, 1977; HEIJS, SINNINGHE DAMSTE, & FORNEY, 2005; GALLARDO & ESPINOZA, 2007). Despite their impressive sizes—sometimes many square kilometers—microbial mats are still nothing more than biofilms.

A look at the vertical organization of a microbial mat reveals that it is comprised of

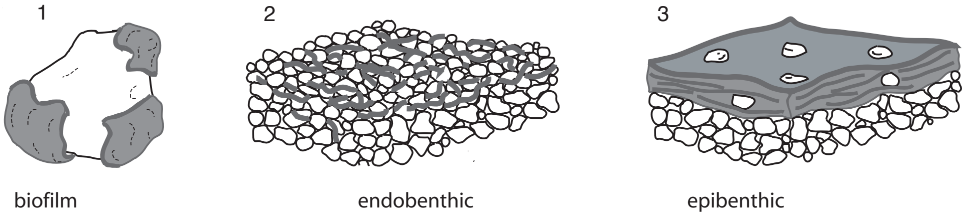

FIG. 2. The three endmembers of microbenthos type in an aquatic setting. A biofilm (*1*) is a microscopic coating around individual mineral grains. A microbial mat (*2–3*) is a macroscopic biofilm covering wide areas of sedimentary surfaces, sometimes square kilometers. Microbial mats can be separated into endobenthic mats, which occur within the uppermost layers of sediment (*2*), and epibenthic mats (*3*), which grow on top of the sediment surface. Sizes of grains, ~0.2 mm.

a stack of horizontal layers, each of which is dominated by a microbial community different to that of the layer above or below (Fig. 3). This arrangement into layered communities has been investigated with the example of the multicolored sand flat (microbial mats in tidal flats) in great detail (Stal, van Gemerden, & Krumbein,1985; Visscher & Stolz, 2005). The metabolic activities of the community of each layer interlock with the metabolic activities of the communities in the layers directly above and below. This interlocking arrangement results in a complex interactive system best described as a cooperative of microbial groups. It functions as what could be called a "disassembly line" that harvests energy from the environment and transforms it through many steps first into organic matter and then into mineral substances (Stal, van Gemerden, & Krumbein,1985; Des Marais & Canfield, 1994; Visscher & Stolz, 2005; Dupraz & others, 2009; Blumenberg, Thiel, & Reitner, 2015) (Fig. 3).

In modern tidal flats, the top layer of microbial mats comprises photoautotrophic

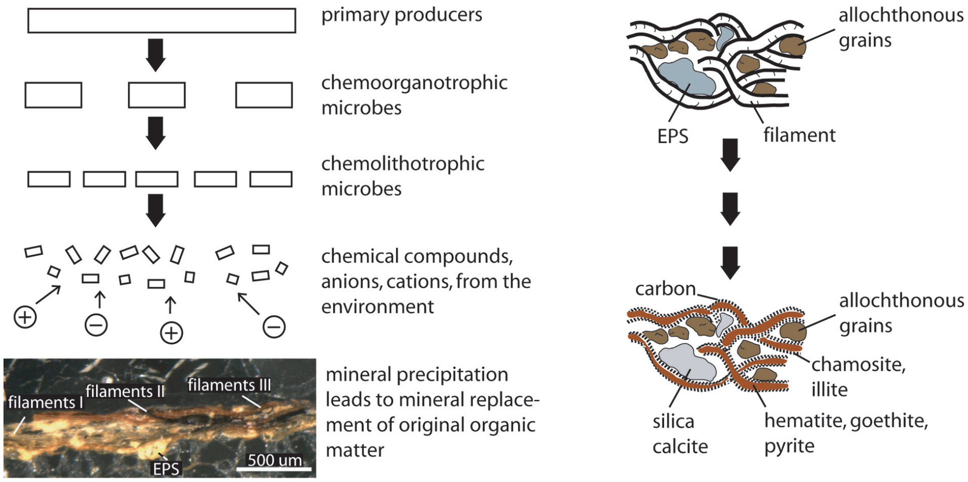

FIG. 3. The microbial energy disassembly line of a microbial mat (*left*) and the resulting formation of minerals (*right*). Left: The primary producers in the top of the mat harvest solar energy via photosynthesis and transform it into organic matter. This organic matter serves as the energy source for various heterotrophic microbial groups in deeper parts of the mat. *In situ* precipitation of minerals is a consequence of this metabolic disassembly line. Right: Dependent on the chemical composition of water in sediment, typical minerals crystallize, replacing the original organic matter. In many fossil microbially induced sedimentary st, the cell walls of filaments still include some of the original carbon, and chamosite and illite may form. Pyrite, goethite, and hematite may have replaced the ancient trichomes, whereas silica and calcite may have replaced fossil extracellular polymeric substances (EPS).

cyanobacteria that, as primary producers, harvest sunlight and store this energy as biomass. The layer immediately beneath the cyanobacteria includes chemoorganotrophic microbes that gain energy by disintegrating the complex biomolecules of the primary producers into inorganic compounds. Further beneath, in the third layer, these inorganic compounds are further disassembled by chemolithotrophic microbes. At the base of this stack of layers, small molecules such as methane and ions are released, for example by methanogenic bacteria or archaea (Kinsman-Costello & others, 2017). The finally released cations and anions at the base of the disassembly line immediately react with chemical compounds suspended in the surrounding water and sediment (Schultze-Lam & others, 1996). The results of these reactions can be nucleation points for mineral precipitates. Because the first mineral precipitates still include water molecules, they are commonly amorphous. In carbonate regimens, early crystalline dolomite or calcite may form, typically directly nucleating in the EPS (van Lith & others, 2002; Sánchez-Román & others, 2008; Dupraz & others, 2009). Later, during diagenesis, larger-scale crystallinity develops. Such processes lead to the replacement of organic matter by inorganic mineral substances and ultimately to the preservation of microbial mats (Ferris, Beveridge, & Fyfe, 1986; Ferris, Fyfe, & Beveridge, 1987, 1988; Schultze-Lam & others, 1996; Konhauser & Riding, 2012). Impressions of mat textures, as known from carbonate microbialites, have to our knowledge not been observed in siliciclastic material. In summary, the cooperative action of this microbial disassembly line transforms and transfers the original amount of solar energy, via several steps, first into organic matter and then into chemical compounds (Schultze-Lam & others, 1996). The microbes work as a cooperative until almost all of the original energy is used up.

The difference between MISS and carbonate/silica microbialites, such as stromatolites, is that in the latter rapid and ubiquitous *in situ* lithification of EPS takes place (Dupraz & others, 2009). The EPS constitute organic matrix, providing a template for nucleation of carbonate minerals (Dupraz & others, 2009). In MISS, such EPS lithification plays only a minor role in structure formation (Noffke & Awramik, 2013). Here, *in situ* replacement of filaments happens very quickly (Schieber & others, 2007; Noffke, 2010; Gomes & others, 2020).

FORMATION OF MISS AND MAIN MORPHOTYPES

In general, three main types sedimentary systems are distinguished: 1) clastic, 2) clastic-evaporitic, and 3) carbonatic (Warren, 1999). Clastic deposits are comprised of mineral grains, bioclasts, and lithoclasts. Such deposits are governed by physical sedimentary dynamics (erosion and deposition). Dynamic events are interrupted by a time period of quiescence called latency. Clastic-evaporitic settings are likewise characterized by such physical sedimentary dynamics but, in addition, also by evaporite mineral crystallization. Carbonate sediments are subject to both physical dynamics and evaporite mineral formation but are dominated by carbonate precipitation. The term sediment, however, cannot be understood as substrate merely comprised of particles that by diagenetic processes turn into a cement-stabilized sedimentary rock. The hydraulic activities are reflected by the wealth of sedimentary structures that are well familiar to sedimentologists (Pettijohn & Potter, 1964). In order to survive, macro- and microbenthos must be able to actively respond to sedimentary dynamics.

Clearly, given the small scales relevant to the microbial world, any instability of the substrate affects microbenthos significantly. In a high-energy setting, strong waves and currents may erode and rip off microbial mats from their substrate, forming meter-scale roll-ups (Cuadrado & others, 2015;

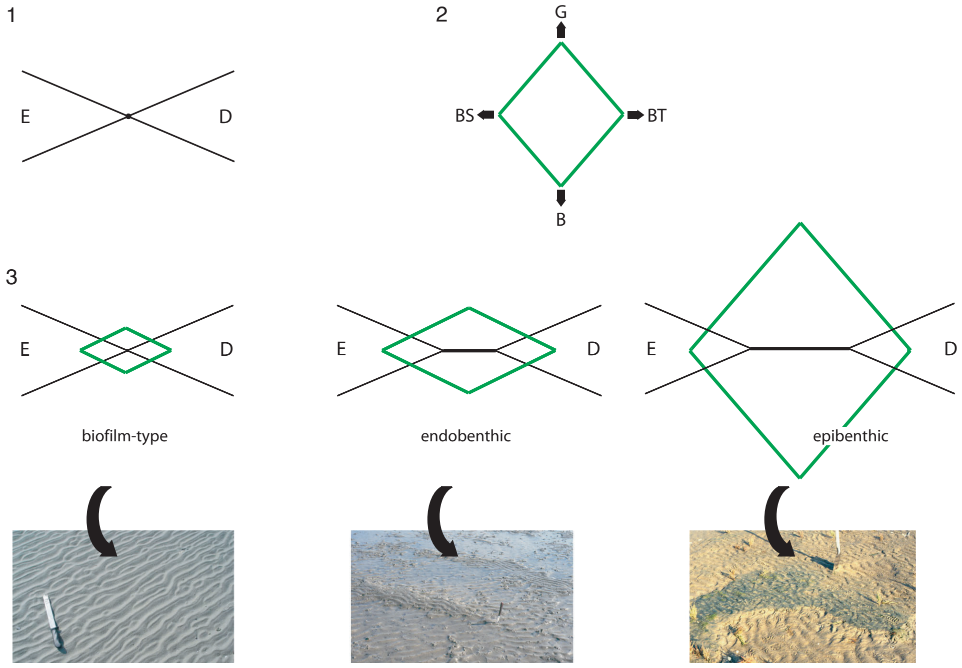

Fig. 4. Overview of the microbial modification of physical sedimentary dynamics. Microbial mats and biofilms influence physical sediment dynamics in such a fashion that the microbenthos constructs its own dynamically suitable habitat, the optimal dynamic window for mat development (see Noffke, Knoll, & Grotzinger, 2002). *1,* Physical sediment dynamics without microbial influence: E, erosion; D, deposition; *dot* at the crossing point, latency (time of no erosion or deposition). *2,* Physical sediment dynamics affected by microbial influence. The rhombus represents microbial activities: G, growth; BT, baffling and trapping; BS, biostabilization; B, binding. Microbial activities create the window of optimal dynamic conditions biostabilization (BS) acts against erosion, while baffling and trapping (BT) increases the rate of deposition, especially of grains of the silt- to fine-sand fraction. Growth (G) and binding (B) rise the sedimentary surface. *3,* The presence of small biofilms would not affect ripple morphologies (photo, *left*). However, where endobenthic microbial mats establish, biostabilization counteracting erosion (E) and baffling and trapping fostering deposition (D) sets in, and in consequence, the latency (black horizontal line separating E and D and representing time periods of dynamic quietness) increases. Endobenthic microbial mats modify physical sediment dynamics moderately and therefore their erosional remnants and pockets (photo, *middle*) appear as somewhat projecting surface morphologies. Epibenthic microbial mats affect erosion and deposition significantly and in consequence their erosional remnants and pockets are larger structures (photo, *right*).

Maisano, Cuadrado, & Gómez, 2019). In arid, terrestrial settings, roll-ups form through desiccation of a mat. In a low-energy environment, fine particles may continuously fall out of suspension and bury the microbenthos, potentially altering the physico-chemical properties of the sediment or blocking essential sunlight from reaching the bottom. In the face of such challenges, microbes ensure the survival of the biofilm community by active upward motion and escape from burial (Bebout & Garcia-Pichel, 1995; Paterson & Black, 2000; Shepard & others, 2005; Shepard & Sumner, 2010; Cuadrado, Carmona, & Bournod, 2011; Risgaard-Petersen & others, 2015). That means that microbes respond differently to erosion than to deposition, which results in lessened erosion rates and increased depositional rates. In fact, the microbial activities generate moderate dynamic sedimentary conditions more suitable for microbial colonization of deposits (Noffke, Knoll, & Grotzinger, 2002; Noffke, 2010). The microbenthos, thus, establishes what we've termed a "window of

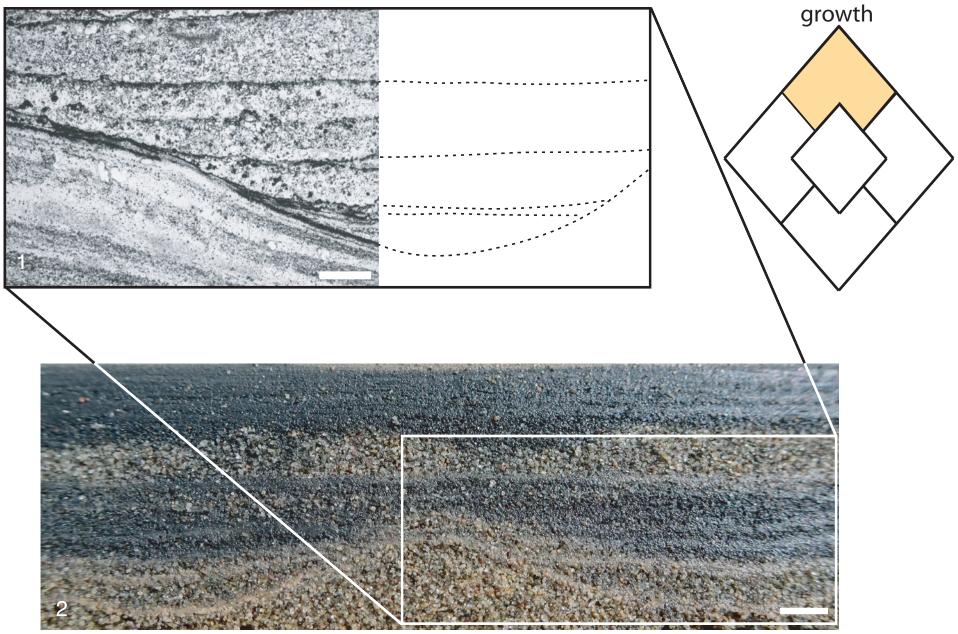

FIG. 5. Examples of microbially induced sedimentary structures formed by growth. A ripple valley is filled-in with layers of sediment (light) alternating with (dark) microbial mat laminae. *1,* Thin section of sample from 3.48 Ga Dresser Formation, Pilbara, Western Australia, scale bar, 0.1 cm. *2,* A scenario similar to (*1*) is visible in this vertical section through a modern sediment sample, Paso Seco coastal area, Argentina, scale bar, 0.5 cm.

optimal dynamic conditions" for biofilms and microbial mats to form and thrive (Fig. 4). The modification of sediment dynamics by the microbenthos is explained in detail in the following section.

Physical sedimentary dynamics include erosion, deposition, and latencies. Deformation plays a role once the sediment is deposited. Erosion differs from deposition in its physical sediment dynamics. Microbial activities differ from each other as well. Microbial growth is not the same as biostabilization, and both are distinct from baffling and trapping. Furthermore, binding also differs from the three other activities. Biostabilization is the response to erosion; baffling and trapping is the response to deposition; and growth (cell replication and EPS-production) or binding (organizing a mat fabrics by movement, not growth) is a response to latencies.

The microbiotic-physical interactions produce sedimentary structures (MISS) that, due to the different nature of their formational processes, differ morphologically from the physical sedimentary structures (*sensu* PETTIJOHN & POTTER, 1964) generated by purely physical dynamics. The following section takes a closer look at growth, binding, biostabilization, and baffling-trapping.

GROWTH

Sediment affected neither by erosion nor by deposition provides a most suitable substrate for a biofilm or microbial mat to grow. This moment (or time period) of quiescence is called latency. Growth is herein understood as the increase of biomass, both through cell replication and the production of EPS and the establishment of a fully functioning biofilm community best suited for its specific environmental locale. With continuous growth of a biofilm or microbial mat, its vertical thickness increases. A microbial mat covering a bumpy sedimentary surface will—if the growth remains undisturbed—eventually smoothen this uneven surface relief. Thus, surface becomes level, or planar (Fig. 5). In this context, laminated leveling structures may form (Noffke & others, 2001; Noffke, 2010; Liu & Zhang, 2017).

In microscopic close-up of a growing microbial mat, the biomass surrounding a mineral grain increases in thickness over time. The developing biomass forces grains upward and away from each other until the original grain-grain contact is lost (Fig. 6.2). Such individual grains in the mat matrix may be observed, especially in thin sections of epibenthic microbial mats. Typically, the grains rotate to a position with their long-axes parallel to the sedimentary surface, termed oriented grain (see Noffke & others, 1997) (Fig. 6.3).

BIOSTABILIZATION

Biostabilization includes three types of processes. It may be a response to 1) erosion by horizontally directed water currents, but also to 2) intra-sedimentary gas pressure, or to 3) mechanical stress leading to ductile deformation. Species diversity, EPS structure and adhesiveness, salinity, light conditions, and other factors play a role in the effectiveness of biostabilization (Yallop & others, 1994; Paterson, 1997; Amos & others, 2004; Consalevy & others, 2004; Friend & others, 2008; Taher & Abdel-Motelib, 2014; Gerbersdorf & Wieprecht, 2015; Dick, Grim, & Klatt, 2018).

Biostabilization type 1 is the response of benthic microbiota to erosive forces by a horizontally directed water current passing the mat surface (Fig. 6). The smooth, EPS-rich surface of epibenthic microbial mats induces a predominantly laminar flow across its surface (BS A in Fig. 6.1). Such laminar flow generally has a far less eroding effect than turbulent flow because of absence of the vertical component of motion (Stoodley & others, 2005; Noffke, 2010; Tice & others, 2011; Hagadorn & McDowell, 2012). Endobenthic microbial mats develop within the upper millimeters of a sedimentary surface such that, in microscopic close-up, individual mineral grains project upward from the surface (BS B in Fig. 6.2). The surface is rough. Thus, passing water currents have a turbulent character with a higher erosive effect. In local areas, where hydrodynamic reworking constantly exceeds mat stability, only limited biofilms can develop. They cover water-suspended grains, sometimes holding a few grains together. Constant water motion keeps such biofilm-grain-aggregates in suspension for a longer time than sterile mineral grains (BS C in Fig. 6.3). The reason for this prolonged suspension is that biofilm-grain aggregates have comparatively larger diameters and lower specific densities than individual sterile grains. It appears that one advantage of this microbially induced suspension mechanism

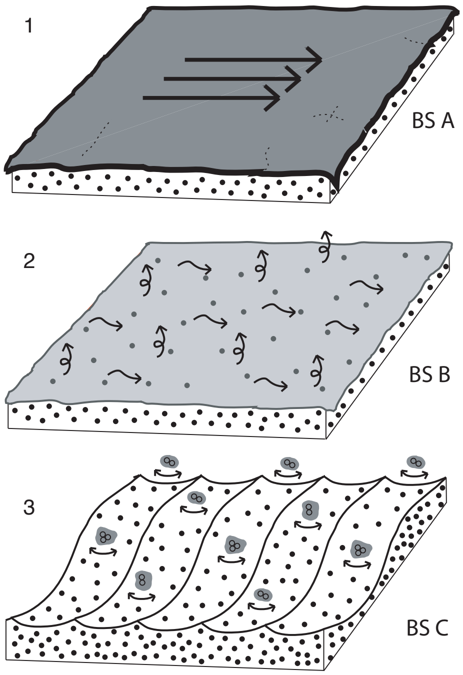

Fig. 6. Biostabilization type 1 by microbial mats and biofilms. Biostabilization BS A (*1*) is observed in epibenthic microbial mats sealing the sedimentary surface; biostabilization BS B (*2*) is observed in endobenthic microbial mats that form organic networks within the upper layers of the sedimentary deposits; biostabilization BS C (3) is observed in microbial-sediment aggregates.

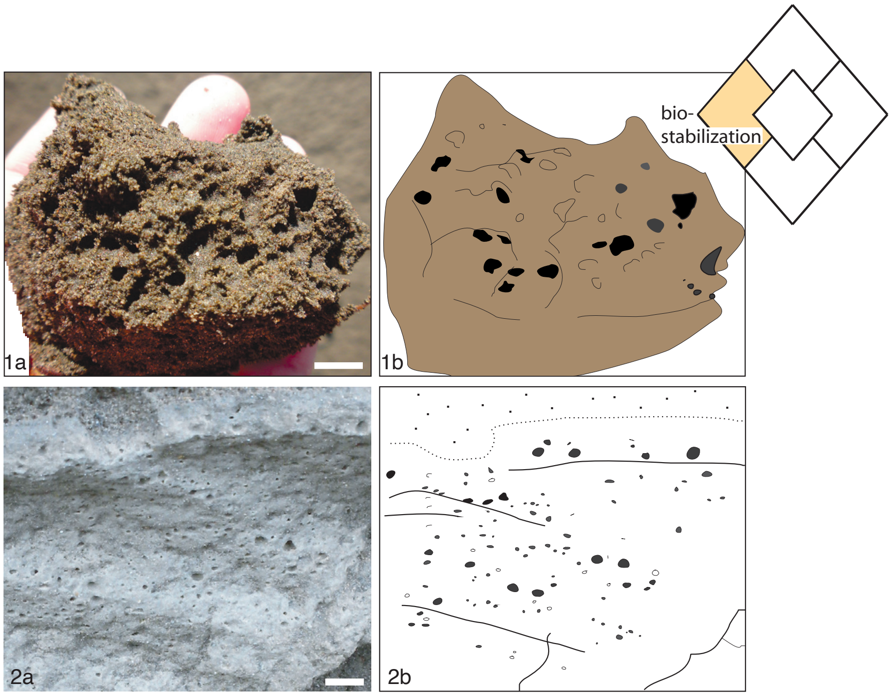

FIG. 7. Examples of microbially induced sedimentary structures caused by biostabilization. *1,* Sponge pore structure in modern sand flats, Paso Seco, Argentina (*a*), with accompanying drawing (*b*), scale bar, 1 cm. *2,* Sponge pore structure in the Rio Negro Formation (Miocene–Pliocene), Argentina, with accompanying drawing (*b*), scale bar, 1 cm.

is to prohibit the lethal burial of microbes by light-blocking sediment (Noffke, 2010). This type of biostabilization may also give rise to microsequences (Noffke & others, 1997). Microsequences are vertical successions of graded sediments layers covered by a microbial mat on the top of each bed. As soon as quiet conditions establish, the mat can develop. Each layer is preserved due to the biostabilization effect of the mat, which exceeds the erosion.

Biostabilization type 2 is the sealing of sediment by EPS that prohibit gas exchange between deposits and water or the atmosphere. Consequently, gases (O_2, CO_2, CH_4, H_2S, and others), which accumulate in the pore space of clastic deposits beneath microbial mats cannot escape. Consequently, gas pressure in the sediment may cause millimeter-scale pores visible in vertical section through mat-sealed sediment. Such sedimentary textures are termed sponge pore sand (Tebbutt, Conley, & Boyd, 1965; Noffke & others, 1996; Kinsman-Costello & others, 2017) (Fig. 7).

Gas domes are local centimeter-scale upheavals associated with biostabilization type 2, which locally form as a result of gas accumulations immediately beneath a microbial mat (Noffke & others, 1996; Wilmeth & others, 2014) (Fig. 8). Commonly, sponge pore fabrics and gas domes occur together.

Biostabilization type 3 involves the reaction of mat-stabilized sediment in ductile fashion. This biostabilization is typical in areas of vertically oriented water motion, e.g. where oscillating groundwater affects the sedimentary surface. A desiccating, microbial-mat-bound sand layer contracts, curls up, and loses contact with the sediment beneath (Gerdes, Klenke, & Noffke, 2000). Unconsolidated, loose sand in the absence of biology would react to desiccation simply by dispersing into individual grains. However,

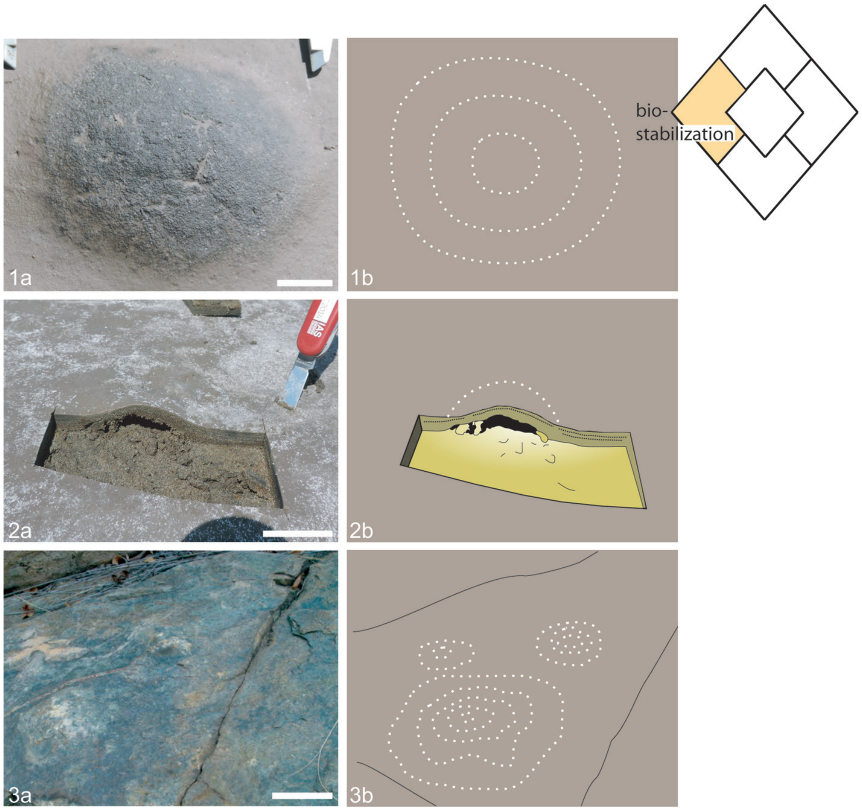

Fig. 8. Examples of microbially induced sedimentary structures caused by biostabilization (*a*), with accompanying drawings (*b*). *1,* gas dome in top view, Paso Seco, Argentina; scale bar, 2 cm. *2,* The cross-section view through a gas dome reveals a hollow cavern beneath the dome, scale bar, 5 cm. *3,* Gas domes *in situ* preserved in the 2.8 Ga Pongola Supergroup, South Africa; scale bar, 5 cm.

if a microbial mat holds grains in place, the sediment does not disperse. Rather, the mat-bound sediment layer has deformation properties similar to clay (ductile deformation). Deformation of mats may also result from mechanical dislocation of a microbial mat through transport and lateral shear (Pflüger & Gresse, 1996; Simonson & Carney, 1999; Tice & Lowe, 2004). MISS such as roll-ups or over-flips are good examples of this (Fig. 9)

In semi-arid climate zones, where significant seasonal changes affect sediments such that the degree of moisture switches periodically between dry and moist, MISS such as polygonal oscillation cracks form. The periodic shrinking and expanding of microbial mat polygons causes their edges to increasingly budge (Noffke, Gerdes, & Klenke, 2003). Additionally, the effects of gas pressure are thought to play a role in this process, since seasonally occurring gas domes are frequently associated with polygonal oscillation cracks.

BAFFLING AND TRAPPING

Microorganisms respond to deposition by baffling and trapping (Black, 1933), which are two different processes (Fig. 10). Baffling is the response of the microbenthos to sedimentation (Noffke, 1997; Gerdes, Krumbein, & Noffke, 2000; Schieber, 2004). In laboratory experiments, filaments of cyanobacteria are shown to orientate vertically and move upward in accordance with sedimentation rate (Gerdes, Krumbein, &

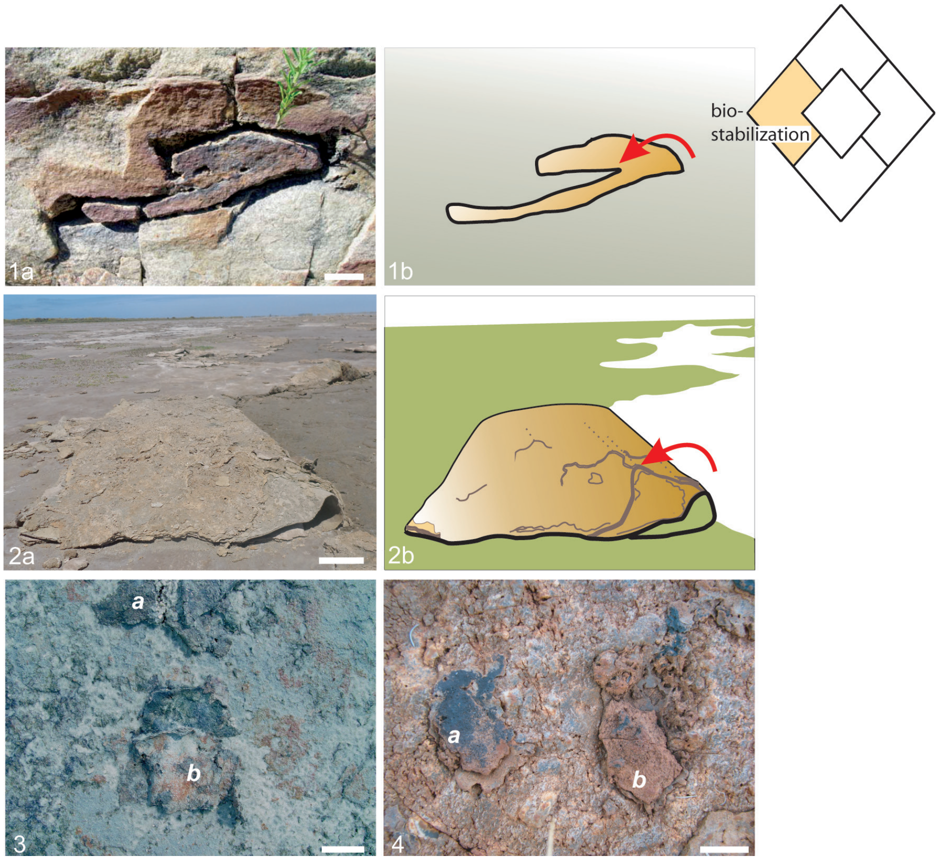

Fig. 9. Examples of microbially induced sedimentary structures caused by biostabilization. *1a,* Large-scale roll-up preserved in the 2.8 Ga Pongola Supergroup, South Africa, scale bar, 5 cm. *1b,* drawing, yellow arrow shows direction of roll-up. *2a,* Modern example of an overflip (roll-up, still connected to the parent mat), Paso Seco, Argentina, scale bar, 5 cm. *2b,* Color-coded drawing showing direction of roll up. *3,* Modern microbial mat chips on the tidal flats of Portsmouth Island, North Carolina, USA. Note that chip (*a*) is turned top-down, whereas chip (*b*) is turned top-up, scale bar, 2.5 cm; *4,* Top-down (*a*) and top-down (*b*) oriented mat chips preserved in the 3.48 Ga Dresser Formation, Pilbara, Western Australia, scale bar, 2.5 cm.

Reineck, 1991). Such vertical movement of cyanobacteria (and other photoautotrophic microorganisms) is called phototaxis; it allows the organisms to position themselves in optimal light conditions. Baffling caused the fall-out of grains of small sizes which, under the same hydraulic conditions but without microbial presence, would remain in suspension. Essentially, microbial baffling increases the rate of deposition of finer-grained material relative to that under ambient hydraulic conditions. This baffling-induced fall-out of suspended particles may clear the water column from fine particles that would otherwise cloud the water, hindering the penetration of light and thus impairing photosynthetic processes (Noffke, 2010).

Trapping commonly refers to the adhesive effect of sticky extracellular polymeric substances (EPS) from microbial mats on ambient particles (Gehling & Droser, 2009). Mineral particles (commonly of silt size) and other lithic fragments are baffled and trapped, and therefore adher to mat surfaces. Baffling and trapping may be a function of the length of filament protrusion above the mat or sediment surface, grain size and availability, grain weight,

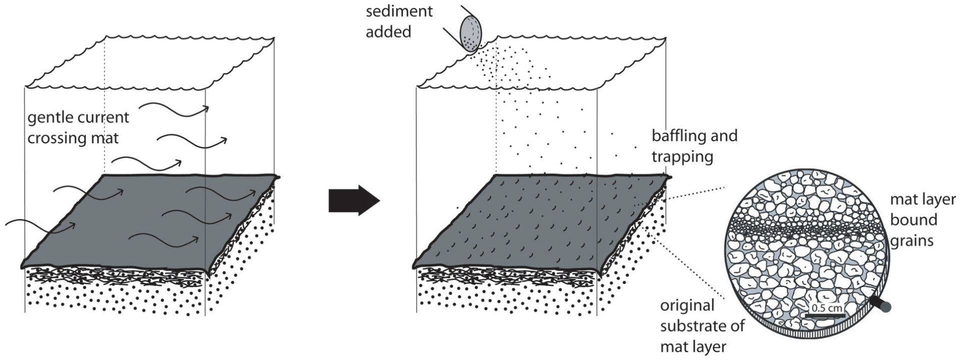

FIG. 10. Baffling and trapping. Left: gentle currents cross an epibenthic microbial mat. Right: When finer-grained sediment is introduced to the system, filaments orientate perpendicularly and promote deposition of the finer grains. The finer-grained sediment forms distinct layers in the deposits (see close-up view on the far right).

frequency and constancy of current transport, as well as the angle of incline of the mat (FRANTZ, PETRYSHYN, & CORSETTI, 2015 for stromatolites; SUAREZ-GONZALEZ & others, 2019). The stickiness or adhesiveness of EPS, which appears to differ between microbial groups, may also play a role in grain trapping (KAWAGUCHI & DECHO, 2000; TICE & others, 2011). Adhesiveness may also be controlled by electrolyte concentration or salinity in the ambient environment (SPEARS & others, 2008). Sometimes, heavy mineral grains and redox-sensitive metals can be found preferentially enriched in mat layers (GERDES, KRUMBEIN, & NOFFKE, 2000; TAHER & SOLIMAN, 2015; TICE, QUEZERGUE, & POPE, 2017; RICO, SHELDON, & KINSMAN-COSTELLO, 2020).

If a biofilm is to function effectively in harvesting energy, each microorganism must place itself into the most suitable position with respect to the other members of the community (STOLZ, 2000; FRANKS & STOLZ, 2009). The coordinated arrangement of filaments into a biofilm or mat fabrics is not possible if the substrate is constantly being reworked. Therefore, as soon as water motion settles down, microbes start to form a biofilm or mat network by actively moving through the sediment.

BINDING

The arrangement of a consortium of microbes into a biofilm or microbial mat is referred to as binding. Examples of active movement by cyanobacteria have been shown in lab experiments (BEBOUT & GARCÍA-PICHEL, 1995; SHEPARD & SUMNER, 2010; BIDDANDA & others, 2015) and observed in nature (WALTER, 1976, DECH, NORMAN, & VISSCHER, 2010). Ancient products of binding are described in FLANNERY and WALTER (2011). In contrast to biomass increase (which is largely dependent on nutrient supply, the dynamics of nutrient diffusion through the biofilm, and light availability), binding is controlled only by sedimentary parameters (SHEPARD & SUMMER, 2010). No biomass accumulation is involved. Binding causes structures, such as reticulate patterns comprised of centimeter- to millimeter-scale ridges and tufts, which may cover large areas of microbial mats (GERDES, KRUMBEIN, & NOFFKE, 2000; SHEPARD & SUMNER, 2010) (Fig. 11).

Field observations of modern mats show that such patterns may withstand high energy events (CUADRADO & PAN, 2018). Sinoidal structures are features caused by biofilms covering ripple mark troughs as seen in cross sections through buried sediment (CUADRADO, 2020) (Fig. 12). Fossil examples of such features are also known from the Dresser Formation, Pilbara, Western Australia (NOFFKE & others, 2013).

Field studies monitoring the formation of MISS in modern tidal flats have shown that some MISS form due to an overlap between

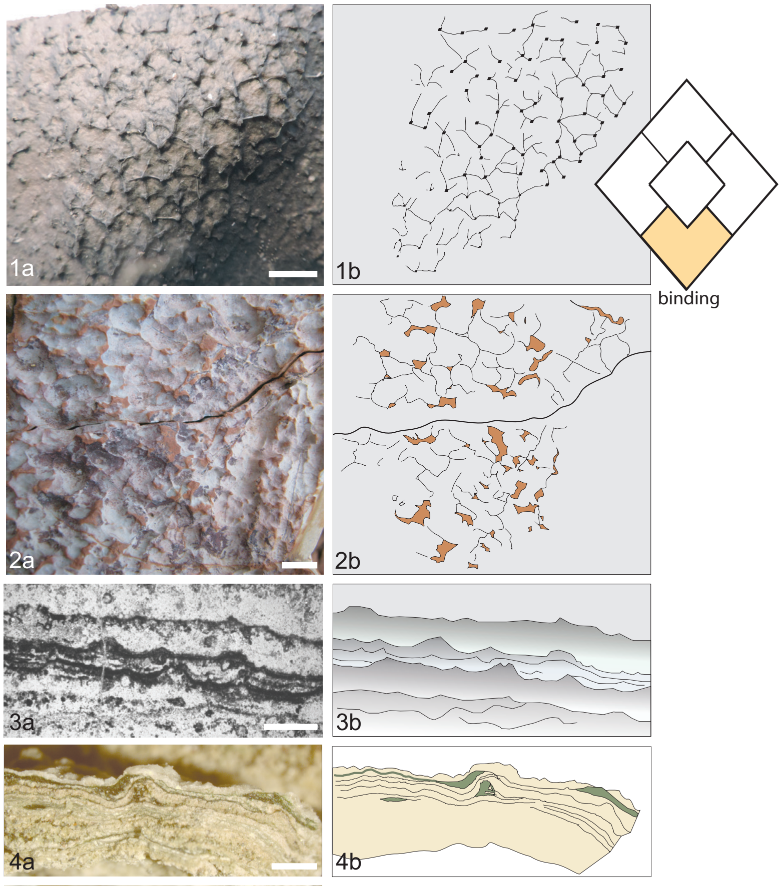

FIG. 11. Examples of microbially induced sedimentary structures caused by binding (*a*), with accompanying drawings (*b*). *1,* Reticulate pattern covering the surface of a modern microbial mat, Paso Seco, Argentina, scale bar, 1 cm. *2,* Reticulate pattern on the surface of a fossil microbial mat from the 3.48 Ga Dresser Formation, Pilbara, Western Australia, scale bar, 1 cm. *3,* Tufts preserved in the 3.48 Ga Dresser Formation, Pilbara, Western Australia, scale bar, 0.1 mm. *4,* Tufts overgrown by microbial mat laminae, Paso Seco, Argentina, scale bar, 1 mm.

all of the above-mentioned microbial activities. Good examples of MISS with complex formational histories are multidirectional ripple marks (Noffke, 1998; Hagadorn, Pflüger, & Bottjer, 1999) and erosional remnants and pockets (Reineck, 1979; Noffke, 1999; Noffke & Krumbein, 1999; Schieber, 2007a; Noffke, Hagadorn, & Bartlett, 2019) (Fig. 13).

Highly abundant in the depositional record are wrinkle structures (Hagadorn & Bottjer, 1997; Noffke, 2010; Chu & others, 2015; Homann, 2019) (Fig. 14), and several studies have investigated their formation. Wrinkle structures induced by microbes are crinkled surfaces commonly found on the upper bedding planes of fine-grained sandstone beds. They are composed of crests and grooves with irregular directions, with crests generally ranging between 0.1 to 2 mm in height, and a crest-to-crest distance of 0.1 mm to 2 cm. Patterns of crests and valleys vary from specimen to specimen (Fig. 14).

Elephant-skin textures—textured organic surfaces (TOS)—are very common (Fig. 14.4) and well preserved in Ediacaran sandstones (Gehling, 1999; Gehling & Droser, 2009; Bottjer & Hagadorn, 2007). Fossil impressions have been described as wrinkled

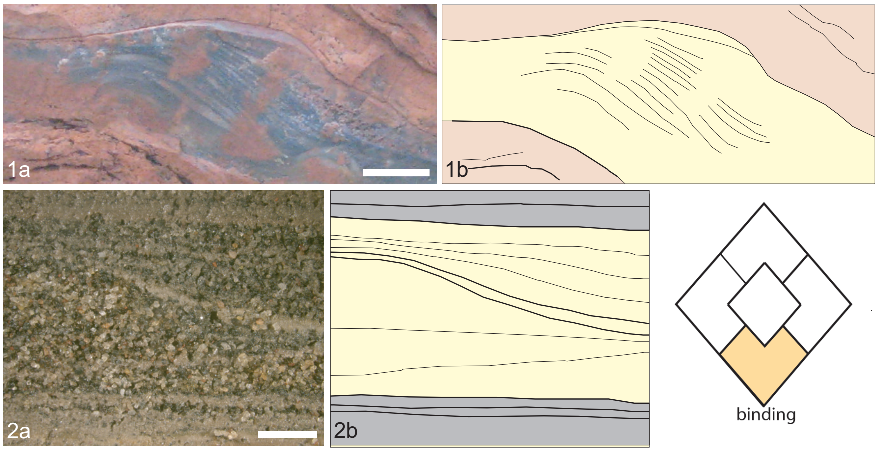

Fig. 12. Example of microbially induced sedimentary structures caused by binding (*a*), with accompanying drawings (*b*). *1,* Biofilms (*black*) overgrow ripple valleys, 3.48 Ga Dresser Formation, Pilbara, Western Australia. Such structures are called sinoidal structures, scale bar, 2 cm. *2,* Similar example for a sinoidal structure in a modern sediment, with mat layers appearing light in color, Paso Seco, Argentina, scale bars, 1 cm.

surfaces by Fedonkin (1992). Elephant skin textures are commonly associated with fossils of the Ediacara biota and may have influenced their preservation, according to the iconic death-mask-model (Gehling, 1999; Gehling & Droser, 2009). In both the modern environment and the lab, such reticulate structures and tufts on sedimentary surfaces result from migrating trichomes (Shepard & Sumner, 2010, Cuadrado & Pan, 2018). The gliding motility and tangling behavior of filaments leads to the formation of tufts resembling centimeter-scale needles on the mat surfaces (Gerdes, 2007; Strader & others, 2009; Sim & others, 2012).

Shearing off a microbial mat from its surface by passing bottom currents (Thomas & others, 2013) may cause irregularly crinkled surfaces. A microbial mat layer may be arranged into irregular tissue-like folds (Fig. 15.2) and the rapid preservation of such microbial mat fabrics produces crinkled mat surfaces, which sometimes have tears in the originally tissue-like material (fossil examples in Noffke, 2000, Noffke & others, 2008).

In lab experiments, wrinkle structures (Fig. 15.3) have been shown to form at the sediment-water interface by microbial-mineral aggregates moving back and forth with wave motion creating a *Kinneyia*-like pattern (Mariotti & others, 2014). Due to the original fossil *Kinneyi* Walcott, 1914 probably being abiotic, the name *Rugalichnus matthewii* was suggested for such *Kinneyiya*-like wrinkle structures, although the trace fossil character of MISS is debatable (Stimson & others, 2017).

Finally, if a microbial mat is suddenly buried by a substantial amount of sediment, the squeezing out of mat-bound water can cause lateral grooves to form in the mat (Pflüger, 1999) (Fig. 15.4). Two main types of such wrinkle structures exist: transparent, in which any proceeding (physical) sedimentary structure, such as ripple marks, remain still visible underneath the wrinkles, and non-transparent, in which proceeding surface morphologies are covered completely by wrinkles and are therefore invisible. These two main types reflect endobenthic (transparent) and epibenthic (non-transparent) microbial mats (Noffke, 2000). *In situ* preservation of microbial mats occurs in several steps (Noffke, Knoll, & Grotzinger, 2002). It requires a pause in sedimentation, during which the mat develops and fine-grained material falls out, draping

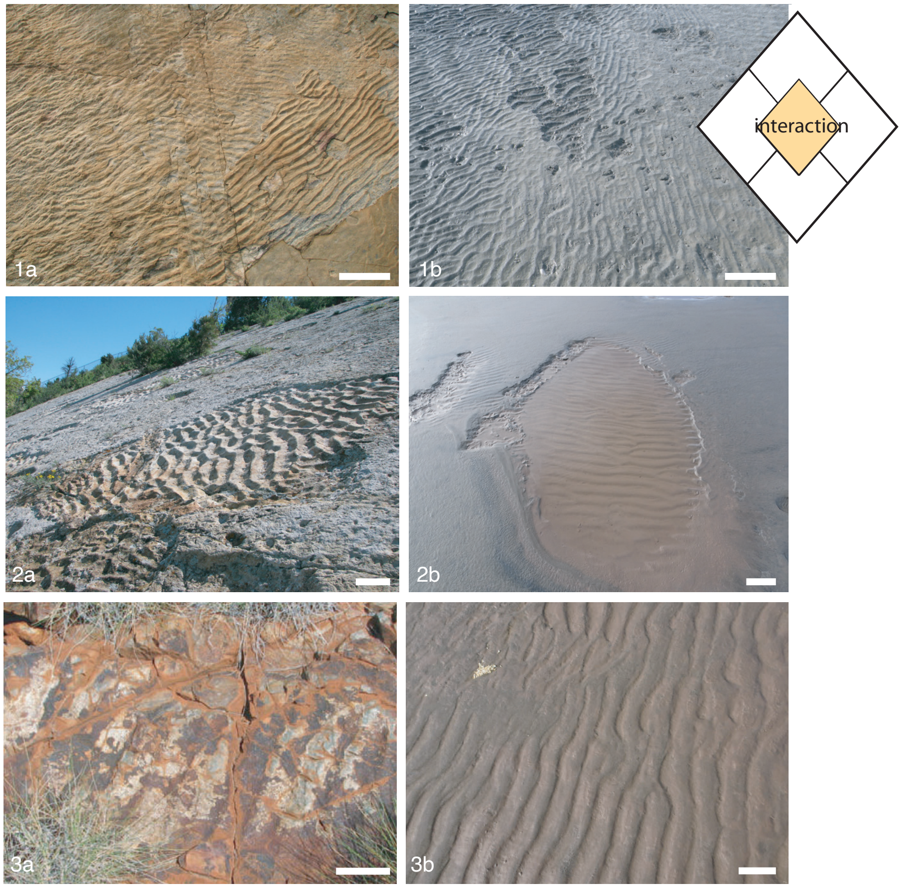

Fig. 13. Examples of microbially induced sedimentary structures produced by the interaction of all microbial activities. *1,* Multidirectional ripple marks in the 2.8 Ga Pongola Supergroup, South Africa (*a*) and in the modern sandflat of Bahia Blanca Estuary, Argentina (*b*), scale bars, 30 cm. *2,* Erosional pocket showing ripple marks in the Cretaceous Dakota Sandstone, USA (*a*), and in a tidal flat, Paso Seco, Argentina (*b*), scale bars, 10 cm. *3,* Rippled surface covered by minute fossil biofilm in the 3.48 Ga Dresser Formation (*a*) and in the modern Paso Seco, Argentina (*b*), scale bars, 10 cm.

the mat surface and becoming incorporated into the mat fabrics. Subsequently deposited sediment must not be able to erode the mat during placement for *in situ* preservation to occur (Noffke, Knoll, & Grotzinger, 2002).

It is important to understand that there are different ways to arrive at wrinkled patterns in clastic sediment and that such structures are not always biologically induced patterns (Hagadorn & Bottjer, 1997; Hagadorn, Pflüger, & Bottjer, 1999; Noffke, 2010; see details in Davies & others, 2016). Nonbiological mechanisms of formation include, for example, the imprinting of a surface by foam (foam marks), by rapid water motion in very shallow water depths (millimeter ripple marks), or through the deformation of semi-consolidated material by slumping or by ball and pillows formation on the lower bedding plane. Abiotic wrinkle structures may also be caused by tectonic crinkling or biased diagenetic processes (Hagadorn & Bottjer, 1999).

One last important aspect to consider, if sediment (at least on Earth) always includes biofilms, the question may arise as to whether purely physical sedimentary structures truly

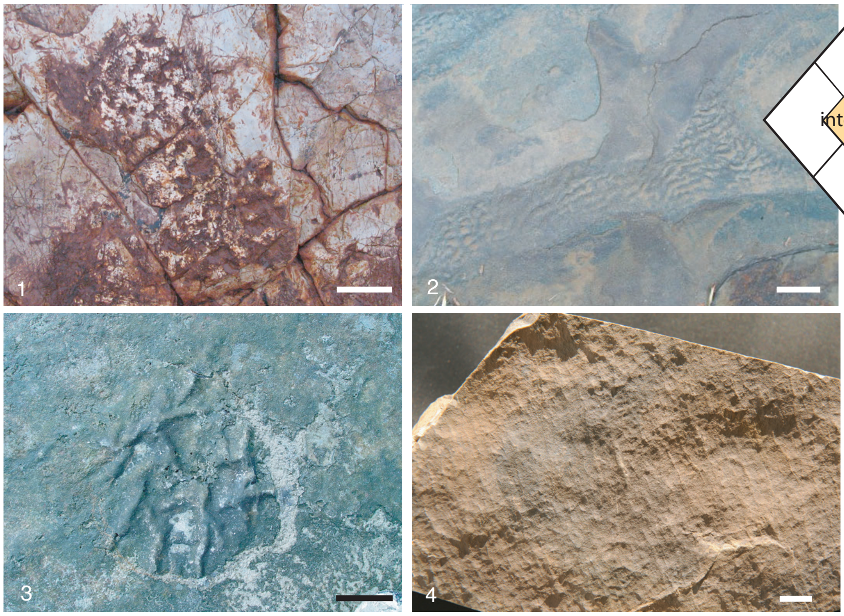

Fig. 14. Biogenic wrinkle structures. *1,* One of the oldest wrinkle structure known in the fossil record is preserved in the 3.48 Ga Dresser Formation, Pilbara, Western Australiam scale bar, 5 cm. *2, Kinneyia*-like wrinkle structure, 2.8 Ga Pongola Supergroup, South Africa, scale bar, 10 cm. *3,* A round piece of microbial mat became detached from its sandy substrate and crinkled. The cause may have been a current crossing the microbial mat in fall, when mats in this area start to compose; Portsmouth Island, North Carolina, USA, scale bar, 10 cm. *4,* Elephant skin texture, Tonian, circa 750 Ma, Qingshuijiangh Formation, South China, scale bar, 1 cm.

exist. Would the presence of biofilms in all deposits not mean that physical sedimentary structures in a natural environment are actually always microbiotic-physical structures? In answering this question, even where biofilms may smother surfaces, they commonly are of too little mechanistic impact to affect a structural representation. However, microbially induced sedimentary structures (MISS) exist, and so the question may be asked, where is the boundary between physical sedimentary structures and MISS? This question was approached by examining a tidal flat (Noffke & Krumbein, 1999). The study developed a modification index (MOD-I) that describes the degree of microbial influence on tidal surface morphologies (erosional remnants and pockets). A MOD-I of 0 would describe sedimentary surface morphologies that show no influence by microbenthos, a MOD-I of 1 describes maximal influence. The boundary between microbially induced or not would be any value >0, with fluctuations of structure-modification in response to seasons being typical. While this study worked well for a local tidal flat with a simple biofilm catena, any conclusion for general sedimentology or even the sedimentology of other planets is unwarranted.

PRESERVATION OF MISS

In thin sections through fossil microbially induced sedimentary structures (MISS), the different components of an ancient microbial mat texture may be visible. Mat textures are fossilized by different minerals depending on the ancient water chemistry providing anions and ions that nucleate into first precipitates.

1) Illite or chamosite, pyrite or goethite, and limonite may line the original trichomes of the microbes (Schieber, 1986, 1989, 1999; Pflüger & Gresse, 1996; Hagadorn & Bottjer, 1997, 1999; Logan & others, 1999; Noffke, 2000; Noffke, Hazen, & Nhleko, 2003; Westall & others, 2006; Noffke, Beukes, & others, 2006; Noffke,

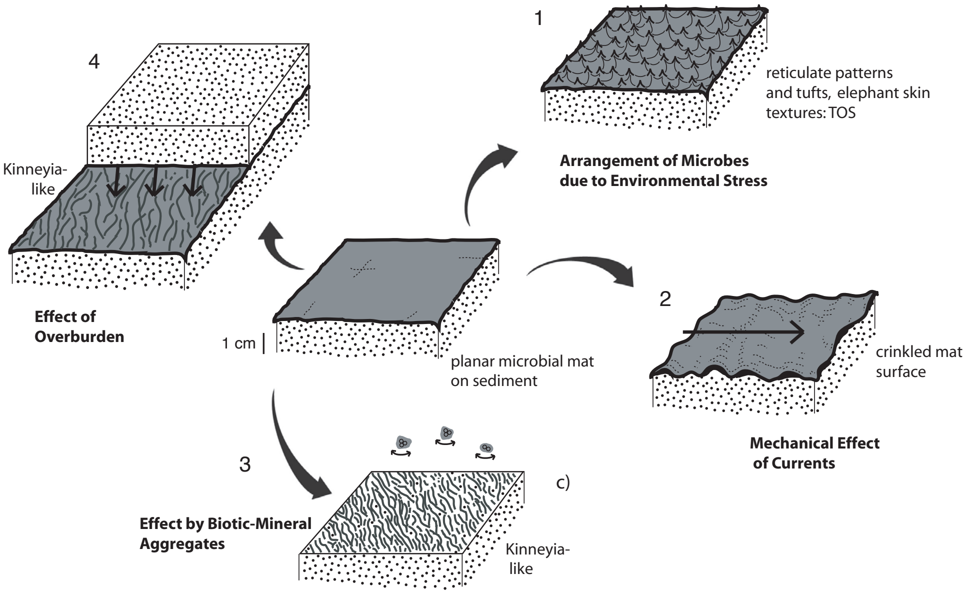

Fig. 15. Various causes and types of microbially induced wrinkle structures. A planar microbial mat is shown in the center of this figure. Variations are shown from *1* to *4*. *1,* filamentous microbes form tufts and reticulate patterns in response to environmental stresses causing textured organic surfaces (TOS); *2,* a coherent epibenthic mat is affected by a strong current dislocating the mat and folding it into irregular crinkles resembling folds in a tablecloth, tearing may also occur; *3,* mineral-biofilm-aggregates moved by waves give rise to *Kinneyia*-like structures. *4, Kinneyia*-like structures are caused by jetting water squeezed out of the underlying microbial mat layer when buried by new deposits.

Eriksson, & others, 2006; Noffke & others, 2013; Heubeck & others, 2016). The formation of clay coats in sandy estuarine and tidal environments can occur as a result of clay-EPS complexes developing along hydroxylated biofilm-clay interfaces or between biofilm proteins and the neutral siloxane surface in quartz sands (Duteil & others, 2020; Worden & others, 2020). Such precipitative clay mineral coatings can develop on microbial biomass surfaces within days as a result of metal ion binding (e.g. Fe, Al), which reduces the nucleation energy of aluminosilicates (Ferris, Fyfe, & Beveridge, 1987; Laflamme & others, 2011; Newman & others, 2016a, 2016b).

2) Cell walls may still include fragments of the original carbonaceous materials. The organic carbon remains provide opportunity for organic carbon isotope measurements and Raman and infra-red spectroscopic characterization. Anoxic conditions promote the *in situ* preservation of organic carbonaceous matter, as evidenced by the fossilization processes of Burgess Shale macrofossils (Briggs, 2003, Gaines, Briggs, & Zhao, 2008). However, cellular organic matter may also be protected against oxygenation by EPS, which reduces gas exchange between sediment and atmosphere or water significantly.

3) EPS is frequently recorded as silica (Westall & others, 2001, 2011; Noffke & others, 2013). In modern hot springs and also in peritidal sedimentary rocks formed in the silica-rich Archean oceans, rapidly precipitating silica produces an almost impermeable preservational time capsule, resilient even to low-grade metamorphism (Trewin, 1996; Kah & Knoll, 1996; Manning-Berg & others, 2019; Hickman-Lewis, Westall, & Cavalazzi, 2019; Hickman-Lewis & others, 2019; Hickman-Lewis & others, 2020). The embedding of silica in mat textures has been

demonstrated in modern hot spring microbial mats and in lab experiments (Taher & Abdel-Motelib, 2015; Johannessen, McLoughlin, & Vullum, 2018). Silicification may be microbially mediated within EPS even when silica concentrations within aqueous media are below supersaturation (Kah & Knoll, 1996; Manning-Berg & Kah, 2017; Moore & others, 2020). Calcite formation in EPS has also been studied in great detail in lab experiments and natural settings by Dupraz & others (2009) and Decho (2010).

In most if not all cases of exceptional preservation of microbial mat textures, lithification must have occurred very quickly. In thin sections, fossil MISS may reveal upright tufts (filament bundles) preserved *in situ* (Kah & Knoll, 1996; Noffke, 2000; Cao, Yuan, & Xiao, 2001; Homann & others, 2018; Hickman-Lewis & others, 2018; Hickman-Lewis, Westall, & Cavalazzi, 2019; Hickman-Lewis & others, 2019).

Textures preserved in MISS are essential for determining biogenicity. The example of wrinkle structures is quite frequently debated with respect to their biogenicity. In order to distinguish microbially induced wrinkle structures from abiotic wrinkle structures, thin sections should be examined to reveal the presence or absence of fossil microscopic textures. If a wrinkle structure-bearing specimen is too valuable to be destroyed by thin section analysis, X-ray micro Computed Tomography (X-ray CT) can be used to nondestructively resolve 3D morphologies using density contrasts between the different materials constituting the internal build-up of such structures (Fig. 16). The primary density contrast comes from the presence of laminated organic matter on top of and inside the rock bed. A number of views of a sample with tufts (Fig. 16) is quite revealing (Sheldon, 2012). Surface mapping (Fig. 16.2) indicates consistent tuft-peak height, which is verified by the 2D- and 3D-segmentation of internal organic-rich laminations (Fig. 16.3). Thus, it can be shown that the example consists of more than just a single microbial mat on the bedding plane surface but rather a series of microbial mats. Each microbial mat may exhibit tufts or evidence of deformation by loading pressure.

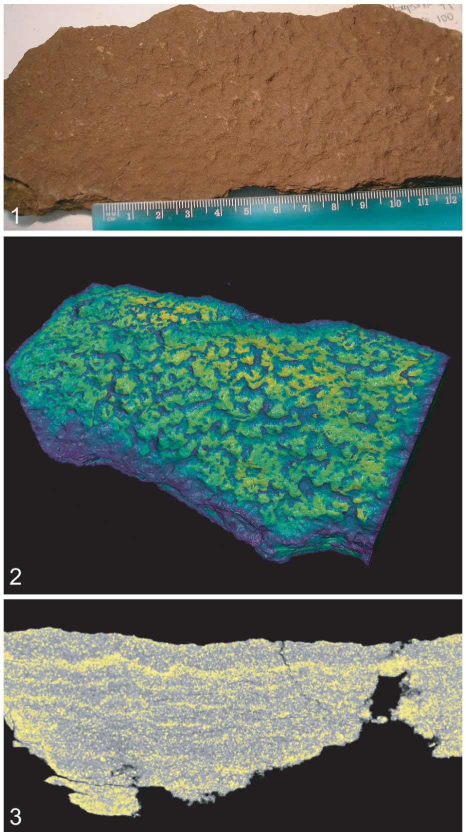

Fig. 16. X-ray CT scans of a microbially induced sedimentary structure sample. *1, Kinneyia*-like wrinkle structure on sandstone slab. *2,* X-ray CT scan of top surface exhibiting *Kinneyia* structure; the corresponding thickness map shows the morphology of the surface peaks. 3, 2D side-on views of the *Kinneyia* slab, where black microbial-like laminations are visible beneath the surface. Each lamination has been individually segmented to highlight the wavy morphology, which correlated with the peaked surface texture. All images collected with the Advanced Imaging of Materials (AIM) Facility at Swansea University, UK, and rendered using ORS Dragonfly software.

CLASSIFICATION OF MISS AND MIST

Conforming to the nomenclature of stromatolites, thrombolites, dendrolites, and leiolites, the overall group of microbially induced sedimentary structures (MISS) constitute the fifth group of microbialites (Riding, 2011; Noffke & Awramik, 2013; Grey & Awramik, 2020). The main characteristics of MISS that differ from other microbialites are: 1) structure-forming biofilms or microbial mats occur on top or within clastic deposits; 2) only minor to negligible mineral precipitation may occur and is predominantly caused by the biological degradation of organic matter of deceased primary producers and EPS; and 3) as a consequence, the structures are predominantly planar and have, in contrast to most of the other microbialites, low morphological relief.

MISS are divided into five classes, each of which includes individual structures (Fig. 17, see p. 20–21). These classes are named according to the dominant microbial activity that governs the formation of the structures within the respective class: class 1, structures caused by growth; class 2, structures caused by biostabilization; class 3, structures caused by baffling and trapping; class 4, structures caused by binding (formerly, Noffke & others, 2001, ascribed this class to imprinting); and class 5, structures caused by the interference of all abovementioned microbial activities (Fig. 17, in center dashed-line diamond). Each structure within each class is named according to its morphological appearance. This enables the surveying geologist to identify a structure even without any knowledge or prejudgment of its genesis. To date, 18 main MISS structures have been distinguished and no transitions seem to exist between them (Noffke & others, 1996, 2001; Noffke, 2010).

MISS include, in thin-section view, a wealth of microscopic microbially induced sedimentary textures (MIST) that witness the former presence of the MISS-producing biofilms or microbial mats (Fig. 17). Textures are divided into five classes according to their genesis: class 1, textures caused by microbial-physical interaction; class 2, textures caused by entombment of carbon; class 3, textures caused by mineralization of organic matter; class 4, textures caused by microbial-chemical interaction; and class 5, textures that rise from the combination of all the four processes. Following the classification of MISS, each MIST within each class is named according to its morphological appearance and pattern of chemical signals. Eleven MIST textures are suggested herein (Fig. 17), but future discussions and contributions will certainly add to this catalogue.

Schieber (2004) suggested different groups of mat structures, each categorized according to a leading process: 1) mat growth (comprising binding, baffling and trapping); 2) metabolism (encompassing mineral precipitation); 3) physical destruction (encompassing dehydration, erosion and transport); and 4) mat decay (gas development) and diagenesis (organic matter destruction and mineral precipitation). However, processes that the specific groups cannot be clearly distinguished from each other. For example, (2) metabolism encompassing mineralization overlaps with diagenesis and mineral formation, listed under (4).

Following the broad definition proposed by Burne and Moore (1987, p. 241–242) that 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,” Riding (2011) and Grey and Awramik (2020) classified MISS in the broad category of microbialites. Overall, MISS constitute the fifth category of microbialites—bedding modified by microbial mats and biofilms—in Pettijohn and Potter’s (1964) classification of primary sedimentary structures (Noffke & others, 2001).

MISS IN THE COURSE OF EARTH HISTORY

Microbially induced sedimentary structures (MISS) and microbially induced sedimentary textures (MIST) are known in clastic rocks of all Earth ages. Specimen occur in one of the oldest non-metamorphosed sedimentary rock successions, the 3.48 Ga old Dresser Formation in Western Australia (Buick & Dunlop, 1990; Noffke & others, 2013). Marine stratigraphic successions with Archean MISS once formed by photoautotrophic mats include the 2.9 Ga old Pongola Supergroup and the Witwatersrand Supergroup (Beukes & Lowe, 1989; Noffke, Beukes, & others, 2006; Noffke, Eriksson & others, 2006; 2008; Tice, 2009). Fossil microbial mats and biofilms are also widespread in carbonaceous cherts and sandstones of the Paleoarchean Barberton Greenstone Belt in South Africa (see Hickman-Lewis & others, 2018 and Homann, 2019 for a review). There, they occur in the 3.472 Ga Middle Marker horizon (Hickman-Lewis & others, 2018); the 3.45 Ga Hooggenoeg Formation cherts (Walsh, 1992; Hickman-Lewis & others, 2020); the 3.416 Ga Buck Reef Chert (Walsh & Lowe, 1999; Tice & Lowe, 2004, 2006; Tice, 2009; Tice & others, 2011; Greco & others, 2018); the 3.334 Ga Footbridge Chert (Hickman-Lewis & others, 2020); the 3.33 Ga Josefsdal Chert (Westall & others, 2001, 2006, 2011, 2015); the 3.26 Ga Mendon Formation (Byerly, Lower, & Walsh, 1986; Trower & Lowe, 2016); and sandstones of the 3.22 Ga Moodies Group (Noffke & others, 2006a; Heubeck, 2009, Homann & others, 2015, 2016, 2018). In these deposits, wavy-crinkly laminations have been interpreted as fossil microbial mats based on their laminated structure, sediment trapping and cohesive behavior, carbonaceous and carbon isotopic composition, and the occurrence of eroded and in places rolled-up mat fragments. Wrinkle structures occur but are quite rare. Most fossil mats occur either in carbonaceous banded cherts or interbedded with volcaniclastic sand- and siltstones and quartz-rich sandstones. The nearly *in situ* preservation of the delicate carbonaceous mat laminae in the Barberton Greenstone Belt show textures such as mat-laminae-bound small grains and oriented grains. Phototactic behavior may be recorded by an increase of mat thickness toward crests in undulating laminae (Tice & Lowe, 2004; Noffke, Gerdes, & Klenke 2003; Homann & others, 2015; Hickman-Lewis & others, 2016, 2018).

Trace and rare earth element data from mat-bearing horizons in cherts up to 3.47 Ga also show strong influences from continental weathering in the form of light rare earth element enrichment, chondritic to sub-chondritic Y/Ho ratios and negligible La and Y anomalies, and it is therefore evident that microbial life inhabited semi-restricted epicontinental basins by this time ~1.09 Ga Mesoproterozoic Copper Harbor Conglomerate (Elmore, 1983; Fedorchuk, 2014). Sheldon (2012) reported 1.1 Ga terrestrial MISS from low-energy fluvial floodplain paleoenvironments preserved in siliciclastic deposits from North America.

Late Neoproterozoic seafloors were widely overgrown by significant microbial mats (Schieber, 1986; Awramik, 1991; Hagadorn & Bottjer, 1997; Hagadorn, Plüger, & Bottjer, 1999; Bottjer, Hagador, & Dornbos, 2000). Neoproterozoic textured organic surfaces (TOS) record relationships between the Ediacara biota, the earliest macroscopic, multicellular organisms, and contemporaneous microbial mats (Gehling & Droser, 2009; Callow & Brasier, 2009; Laflamme & others, 2011; Darroch & others, 2012; Tarhan, Droser, & Gehling, 2015; Dunn, Liu, & Donogue, 2018). The extraordinary preservation of this soft-bodied biota suggests the extensive presence of microbial mats during this period of time (e.g., Hagadorn & Bottjer, 1999; Gehling, 1999; Seilacher, 1999; Liu & others, 2011; Tarhan, Droser, & Gehling, 2015; Menon & others, 2016; Liu & Dunn, 2020). Terrestrial MISS arising from microbes interacting with aeolian processes are known from the Neoproterozoic Venkatpur Sandstone (Basilici & others, 2020).

Phanerozoic occurrences are known from the Cambrian (Buatois & Mángano, 2003; Seilacher, Buatois, & Mangano, 2005; Mata & Bottjer, 2013; Buatois & others,

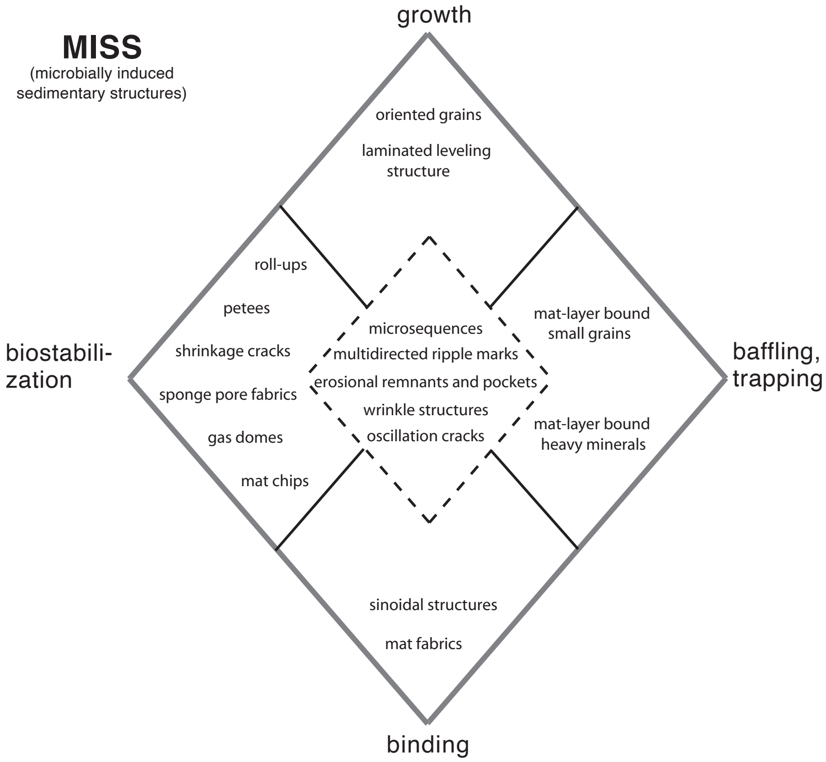

Fig. 17. Classification of MISS and their MIST (on facing page). The classification of both macroscopic and microscopic features each includes five genetic groups related to their means of formation. Descriptive names of individual structures and textures are listed to aid in identification in the field or laboratory.

2014; Liu & Zhang, 2017; Bayet-Goll & Daraei, 2020); the Ordovician (Gerdes, Klenke, & Noffke, 2000; Noffke, 2000; Buatois & others, 2009; Hints & others, 2014; the Silurian (Hillier & Morrissey, 2010; Calner & Eriksson, 2012); the Devonian (Draganits & Noffke, 2004; Gaillard & Racheboeuf, 2006); the Carboniferous (Mángano & others, 2002; Buatois & others, 2013; Callefo & others, 2019); the Permian (Webb & Spence, 2008); the Triassic (Pruss, Fraiser, & Bottjer, 2004; Pruss, Corsetti, & Bottjer, 2005; Pruss & others, 2006; Mata & Bottjer, 2009; Feng & others, 2019; Wignall & others, 2020); the Jurassic (Porada, Ghergut, & Bouougri, 2008; Peterffy, Calner, & Vajda 2016); the Cretaceous (Gerdes, Krumbein, & Noffke, 2000; Schieber 2007a; Fernández & Pazos, 2014; Noffke, Hagadorn, & Bartlett, 2019); the Neogene (Carmona & others, 2012); and the Quaternary (Kilias & others, 2020).

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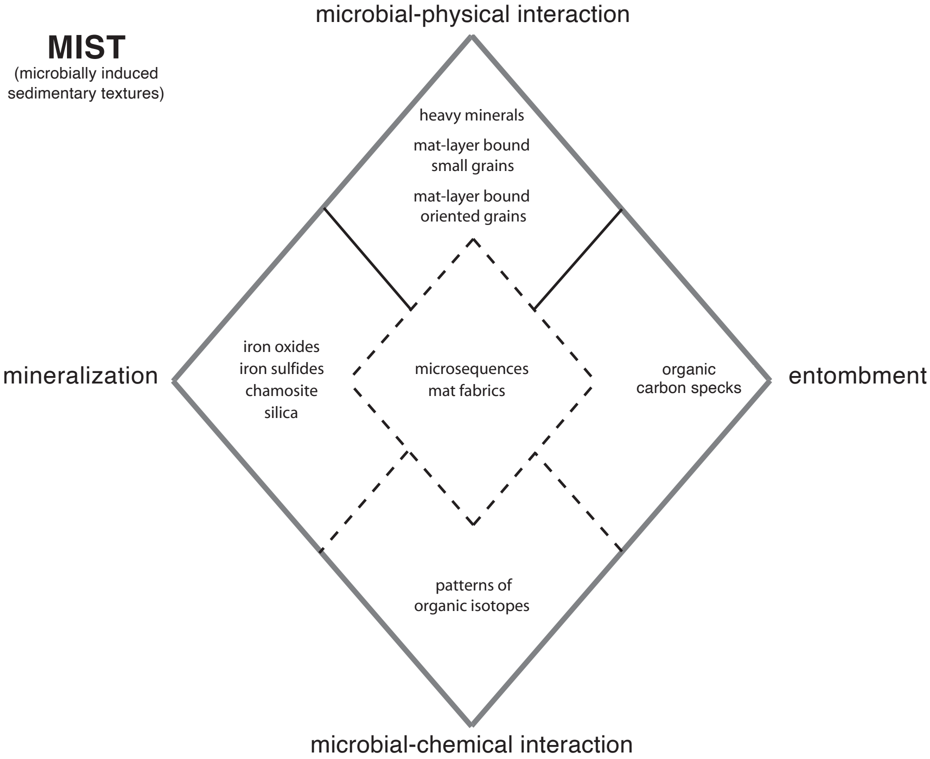

Fig. 17 (continued from previous page). Classification of MISS (facing page) and their MIST. Descriptive names of individual structures and textures are listed to aid in identification in the field or laboratory.

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